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Social context shapes neural processing of others' actions in 9-month-old infants



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ABSTRACT

From infancy, neural processes for perceiving others' actions and producing one's own actions overlap (neural mirroring). Adults and children show enhanced mirroring in social interactions. Yet, whether social context affects mirroring in infancy, a time when processing others' actions is crucial for action learning, remains unclear. We examined whether turn-taking, an early form of social interaction, enhanced 9-month-olds' neural mirroring. We recorded electroencephalography while 9-month-olds were grasping (execution) and observing live grasps (observation). In this design, half of the infants observed and acted in alternation (turn-taking condition), whereas the other half observed several times in a row before acting (blocked condition). Replicating previous findings, infants showed significant 6- to 9-Hz mu suppression (indicating motor activation) during execution and observation ($n = 24$). In addition, a condition (turn-taking or blocked) by time (action start or end) interaction indicated that infants engaged in turn-taking ($n = 9$), but not in the blocked context ($n = 15$), showed more mirroring when observing the action start compared with the action end. Exploratory analyses further suggest that (a) there is higher visual-motor functional connectivity in turn-taking toward the action's end, (b) mirroring relates to later visual-motor connectivity, and (c) visual attention as indexed by occipital alpha is enhanced in turn-taking compared with the blocked context.

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Together, this suggests that the neural processing of others' actions is modulated by the social context in infancy and that turn-taking may be particularly effective in engaging infants' action perception system.

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Introduction

From their first year of life, infants observe, interact with, and learn from others' actions. Action and the perception of others' actions are closely linked in early childhood (e.g., Woodward & Gerson, 2014). The neural overlap of action production and perception (also called neural mirroring) provides the neurocognitive basis for processing others' actions and likely is the foundation for successful social interactions (Bekkering et al., 2009; Hari & Kujala, 2009). Evidence from adult studies suggests that neural mirroring might not be a passive perceptual process; instead, neural mirroring was found to be flexible to different social situations (Kilner, Marchant, & Frith, 2006; Kourtis, Sebanz, & Knoblich, 2010; Ménoiret et al., 2014). For instance, when adults are engaged in social interactions, their neural motor activation in anticipation of and during action observation is enhanced (Kourtis et al., 2010; Ménoiret et al., 2014). This enhanced neural mirroring in socially relevant situations is further linked to joint action performance (e.g., Kourtis, Sebanz, & Knoblich, 2013), emphasizing the role of mirroring for successful social interactions. Early in life, processing of others' actions plays a crucial role in learning new actions and for social development (e.g., Marshall & Meltzoff, 2014; Paulus, Hunnius, & Bekkering, 2013). As yet, however, whether social context can enhance neural mirroring of infants in their first year of life is an open question. In infancy, when neural mirroring is first emerging, is it already sensitive to the social context or does contextual modulation emerge later in childhood as social interactions and collaboration become more complex? In the current study, we examined whether the context of turn-taking, an early-occurring form of social interaction, enhances mirroring of others' actions in 9-month-old infants.

Social context modulates mirroring in adults, children, and monkeys

Top-down effects on neural mirroring have been found in children and adults (Campbell & Cunnington, 2017; Kilner et al., 2006; Kourtis et al., 2010; Ménoiret et al., 2014; Meyer, Hunnius, van Elk, van Ede, & Bekkering, 2011). For instance, 3-year-old children show enhanced motor activation when observing a social partner perform an action in a turn-taking game compared with observing the same action when not engaged in a social interaction (Meyer et al., 2011). In contrast to infants, 3-year-olds can be verbally instructed, which allows creating different social interaction contexts. Comparable enhancement of neural mirroring during a social interaction was reported in adults (Kourtis et al., 2010; Ménoiret et al., 2014). In an electroencephalography (EEG) study, Kourtis et al. (2010) investigated the effect of being engaged in a social interaction on anticipatory motor activity in adults. Their results show that in expectation of a social partner's actions, participants' motor system was more activated than when expecting actions of a person with whom they were not interacting. In a second EEG study, Kourtis et al. (2013) further provided evidence of a link between anticipatory motor activation for a social partner's actions and interpersonal coordination performance. More specifically, higher anticipatory motor activation was associated with an improvement in interpersonal coordination. In addition to evidence from human adults and children, complementary evidence comes from research with macaque monkeys suggesting an influence of social contextual information on mirror neuron activity (Coudé et al., 2016). Coudé et al. (2016) used gaze as a socially informative cue to study whether the ventral premotor cortex mirror neurons in the macaque monkey are sensitive to social context. Their findings show that the activity of these neurons during action observation is modulated by social context induced by gaze. Together, convergent evidence

from these studies with human adults and children as well as monkeys suggests that social context significantly modulates neural mirroring.

Does social context modulate neural mirroring in infants?

Following the initial discovery of neurons with mirroring properties in macaque monkeys (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; see also Rizzolatti & Fogassi, 2014), the last decade of research in the field of developmental cognitive neuroscience has examined the characteristics of neural mirroring and its relation to social-cognitive and motor development in early childhood (Hunnius & Bekkering, 2014; Marshall & Meltzoff, 2014; Woodward & Gerson, 2014). EEG findings with infants around 9 months of age suggest that infants' neural motor system is activated by both performing and observing others' actions (Nyström, Ljunghammar, Rosander, & Von Hofsten, 2011). Infants particularly activate their neural motor system in anticipation of how others' actions unfold, for instance, while someone reaches toward an object in order to grasp it (Monroy, Meyer, Schröder, Gerson, & Hunnius, 2019; Montirosso et al., 2019; Southgate, Johnson, Karoui, & Csibra, 2010; Southgate, Johnson, Osborne, & Csibra, 2009). Several studies have assessed the properties of actions that elicit changes in the level of neural mirroring in infants. For instance, the extent to which infants activate their motor system during action observation is influenced by whether an action is goal directed (Nyström et al., 2011), lies in the motor repertoire of an infant (Gerson, Bekkering & Hunnius, 2015; Paulus, Hunnius, van Elk, & Bekkering, 2012; van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008; Yoo, Cannon, Thorpe, & Fox, 2016), is visually familiar (Stapel, Hunnius, van Elk, & Bekkering, 2010), or is performed on heavy or light objects (Marshall, Saby, & Meltzoff, 2013). However, whether and how top-down processes, such as social context, affect their action processing remains unclear.

If social context modulates processing and perception of others' actions in infancy, this could potentially have implications for social learning and imitation. Indeed, enhanced motor activation during observation of reach-to-grasp actions predicted the likelihood of subsequent goal imitation in 7-month-old infants (Filippi et al., 2016). Here, we exploited early-emerging forms of social interaction, specifically turn-taking, to examine whether the social context of action observation can enhance neural mirroring. Communication and social interaction with others is rooted in turn-taking behaviors early in life (e.g., Casillas, 2014; Meyer & Hunnius, 2020; Tomasello et al., 2005). Taking turns in performing actions is inherent to many joint actions and essence of early dyadic engagement (Meyer & Hunnius, 2020; Tomasello, Carpenter, Call, Behne, & Moll, 2005). Infants engage in turn-taking during vocal interactions with their caregivers as early as 2 months of age (Gratier et al., 2015). By about 9 months, objects are often included in turn-taking exchanges such as passing a toy back and forth. This extends dyadic social interaction to a triadic one (Carpenter, Nagell, Tomasello, Butterworth, & Moore, 1998). Across the first few years of life, infants become increasingly more active in coordinating turn-taking with adults. For instance, they contribute to the temporal contingency between turns and to the smooth coordination with their interaction partner (Casillas, 2014; Meyer & Hunnius, 2020; Meyer, Bekkering, Paulus, & Hunnius, 2010; Rutter & Durkin, 1987). Beyond infancy, when children are 3 years old, turn-taking elicits neural motor activation when children observe the other's turn (Liao, Acar, Makeig, & Deak, 2015), and this activation is stronger during turn-taking than when not being engaged in turn-taking with the other person (Meyer et al., 2011). Thus, taking turns in acting might be a natural way in which action observation could be made more relevant also to infants, enhancing their action processing.

Initial indications for a potential role of turn-taking on context-dependent neural mirroring in infancy come from an EEG study with 14-month-olds (Saby, Marshall, & Meltzoff, 2012). In that study, infants performed one of two actions (i.e., pressing a button or grasping a toy) in turns with an experimenter who always performed the same action (i.e., pressing a button). Saby et al. (2012) found enhanced neural mirroring when the experimenter's action was preceded by the same action performed by the infant. In other words, neural mirroring was enhanced when 14-month-olds' actions were being imitated. Potentially, this increase in neural activation reflects the effects of the reciprocal (turn-taking) nature of the imitative action. Yet, because their study focused on investigating the

effect of being imitated, Saby et al. (2012) did not systematically vary the social interaction context. Thus, this interpretation remains untested.

Another study with 14-month-old infants contrasted an observation condition in which infants were engaged in a dyadic interaction with an adult with an observation condition in which infants passively observed someone perform an action that was outside of their motor repertoire (Reid, Striano, & Iacoboni, 2011). Results indicated higher neural motor activation for 14-month-olds during the dyadic interaction than while passively viewing an action outside of their motor repertoire. This finding further hints at the role of social interaction for neural mirroring in infancy. Yet, from this study it remains unclear whether the neural effect is due to the observed action being inside or outside of children's motor repertoire or due to the engagement in the social interaction.

The current study

We conducted an EEG study with 9-month-old infants in which we collected neural data while infants reached for and grasped toys (execution) and observed an experimenter reach for and grasp toys (observation). To examine whether infants show flexible mirroring dependent on the social context, we manipulated the structure of the interaction between participants (blocked vs. turn-taking). In the blocked condition, 10 consecutive trials of observation were followed by 10 execution trials. In the turn-taking condition, observation and execution trials were performed in turns. We hypothesized that turn-taking would elicit stronger neural mirroring than observing actions repeatedly before acting. To assess neural mirroring, we analyzed the 6- to 9-Hz alpha frequency power over sensorimotor regions of the brain, also called mu suppression. Mu suppression has been established as an index of neural motor activation in infants of the same age during both action execution and observation (Fox et al., 2016; Marshall & Meltzoff, 2011; Southgate et al., 2010).

Method

Participants

A total of 66 9-month-old infants (37 female) participated in this EEG study. Half of the infants (17 female) were randomly assigned to the blocked condition, and the other half were assigned to the turn-taking condition (20 female). Participants represented a diverse racial background (41% European, 29% Hispanic, 22% African American, and 8% Asian) and were from relatively highly educated backgrounds (maternal education). Participants were recruited in an urban Midwest region in the United States and had no known developmental delays. Fifteen infants were excluded from analyses due to prematurity (<37 weeks gestation; $n = 1$), refusing to wear the EEG net ($n = 1$), unusable EEG data preceding preprocessing ($n = 1$), performing less than two grasping or observation trials during the testing session ($n = 3$), or offline video-coding ($n = 9$) (see "Analysis" section for details). An additional 27 participants did not have at least two artifact-free EEG trials per condition after all EEG processing steps. Therefore, the final dataset consisted of 24 infants (15 in the blocked condition and 9 in the turn-taking condition) with a mean age of 8.7 months (12 female). Note that this was an alone-standing study, not preceded by any other testing on the same day to avoid any carryover effects on our manipulation. This study was approved by the campus institutional review board.

Procedure

Before the approximately 30-min testing session, parents were informed about the testing procedure. As part of a separate longitudinal study, parents also completed the Early Motor Questionnaire (EMQ; Libertus & Landa, 2013). See online [supplementary material](#) for a correlational analysis of motor development scores and neural data. After written consent from each infant's legal guardian was obtained, the infant and caregiver were accompanied to an adjacent EEG testing room by two experimenters (E1 and E2). Videos of the session were recorded from different camera views. The infant sat on the lap of the caregiver and was fitted with a 128-sensor HydroCel Geodesic Sensor

Net (Electrical Geodesics, Eugene, OR, USA). Impedances were kept below 100 k Ω where possible. The EEG was digitized at 1000 Hz (Net Station software, Version 4.5.7; Electrical Geodesics), and electrode Cz was used as an online reference. The experiment consisted of action observation and action execution trials presented in a live setting (see also Shimada & Hiraki, 2006) in which the infant sat in front of a wooden puppet stage facing E1 (see Fig. 1). The puppet stage allowed the infant to see E1 during each Observation and Execution trial and occluded E1 between trials. Using a hidden mechanism, E1 could operate the puppet stage doors and the cardboard tray on which toys were presented without the infant seeing the experimenter's hands moving. Before each trial, while hidden from infants' view, E1 placed a toy on a cardboard tray covered in blue felt and rang a bell designed to orient the infant to the stage. The period during which E1 was hidden from view lasted approximately 3 s.

Action observation trials

Each action observation trial began with E1 opening the sliding doors of the stage with a hidden mechanism allowing her to open the doors without her hands being visible. E1 looked at the child and smiled (baseline). Then, 1 s after E1 was fully visible to the infant, E1 ensured that the infant was attending by saying, "Hey baby," "Look," or "Hi there." If the infant did not look toward the experimenter, E1 repeated the prompt. Once the infant looked or after three repetitions of the prompt, E1 used her right hand to reach toward, grasp, and pick up the toy on the tray. After placing the toy back on the blue felt, E1 looked back toward the infant, smiled, and closed the doors.

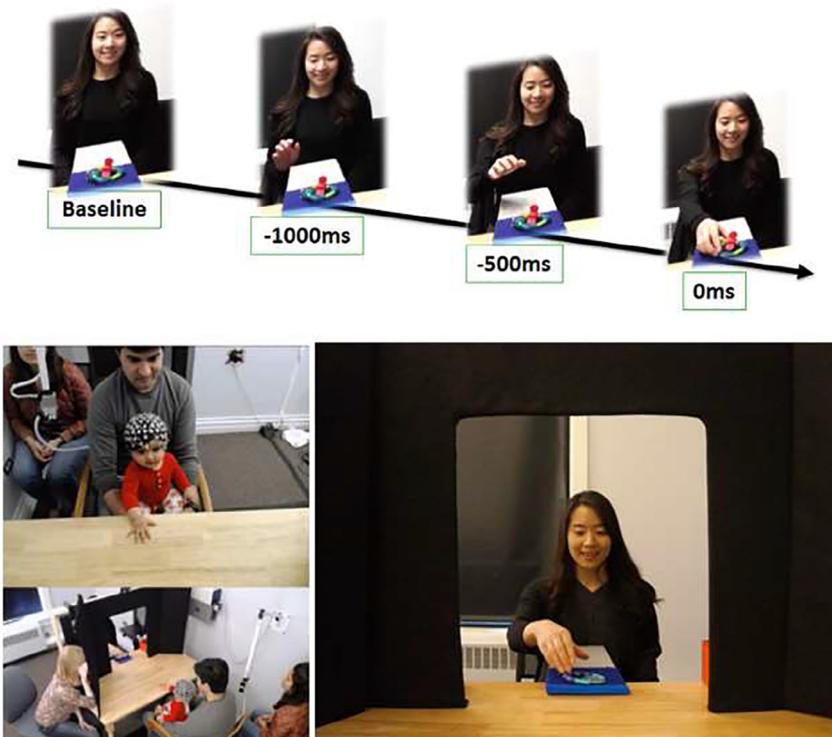


Fig. 1. Experimental set-up and design. Top: Schematic timeline of an observation trial. Bottom left: Example of an infant participant in the setup. Bottom right: View of the infant and the experimenter performing a goal-directed reach-to-grasp action.

Action execution trials

As in the action observation trials, E1 began each trial by opening the doors. She then looked and smiled at the infant (baseline), waited 1 s, and addressed the infant with the same prompts used in action observation. Once the infant looked at E1 or after three repetitions of the prompt, without her hands being visible, E1 moved the cardboard tray with the toy forward, within reach of the participant. Once the infant reached for and grasped the toy, E1 retracted the cardboard and closed the doors. The infant had 3 s to play with the toy, after which E2 appeared behind an occluder to retrieve the toy from the child. If the infant did not reach for the toy within 5 s, E1 moved the board slightly away from and toward the infant again to attract the infant's attention. If the infant still did not reach for the toy within the next 10 s, E1 retracted the board and closed the doors.

Turn-taking and blocked conditions

For the main research question of interest, the order of action observation and action execution trials was manipulated between participants to create two conditions (turn-taking and blocked), with half of the infants assigned to each condition. In the turn-taking condition, participants were presented with the trial types in alternation, with 20 trials per type: 1 observation, 1 execution, 1 observation, 1 execution, and so on. In the blocked condition, participants were presented with two sets of 10 trials per trial type for a total of 20 trials per type: 10 observation, 10 execution, 10 observation, 10 execution. In each condition, infants could receive up to 40 trials. Ten unique toys were used in a random order such that all toys appeared twice for each trial type (i.e., toys were used equally in action observation and action execution trials).

After 40 trials or once the infant lost interest, the experimental session ended. 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 U.S. \$20 as compensation. As described in detail in the "Analysis" section, events in the experimental session were video-coded offline and time-locked to the EEG recording for further analysis.

Analysis

Video-coding analysis

Video-coding the data offline served two purposes: (a) time-locking events of interest for the EEG analysis and (b) capturing infants' movements and looking behavior for the exclusion of trials from further analysis. Datavyu, an open software (Datavyu Team, 2014), was used for coding videos offline. To time-lock events, we defined the baseline and experimental time window for each trial in the EEG analysis. The baseline was coded from the frame in the video when the sliding doors were fully open (the first frame when the doors were not moving and were at their widest opening point). At this moment, E1 was visible but not moving for about 1000 ms. Because this was a live study, there could be slight variations in the timing of events. Thus, we extracted the median duration from the moment the doors were fully open to the first frame in which E1 visibly started moving her hand for each participant in the final sample. On average, the median duration for this period was 1028 ms ($SD = 125$). The experimental time window was coded based on the first frame in which E1 (Observation trials) or the infant (Execution trials) touched the toy and the contact led to grasping or picking up the toy. For the reaching period, the median duration from the moment E1 first started moving to the moment she reached and touch the toy was on average 1122 ms ($SD = 78$). Infant movements and looking behavior were coded to exclude trials from analysis in which the infant made unwanted movements or looked away from the puppet stage. To interpret the results of neural motor activation as index of processing others' actions rather than infants' own execution of actions, it is essential to include in the EEG analysis only trials on which infants were not moving themselves (during action observation and baseline trial segments). Otherwise, the neural responses of the infants could be attributed to infants' own actions rather than the actions they observed. Therefore, we applied conservative exclusion criteria to minimize the contribution of infants' overt movements to the neural signal. Infant grasping actions were coded, which included grasping an object (e.g., table, arm of the chair, mother's hand) or grasping

movements without an object (e.g., making a grasping movement in the air). In addition to goal-directed actions, any gross motor movements (e.g., moving a limb, waving arms in the air) were also coded and excluded. To assess infants' looking behavior, we coded and excluded periods during which infants were not looking toward the direction of the puppet stage. We also coded when parents were interfering (e.g., bouncing infants) and when infants were excessively crying. All action observation and baseline EEG segments (see details below) that overlapped with parental interference, crying, not looking, or moving were excluded from further analysis. For details on the average number of excluded segments per category, see Fig. 2. In keeping with our a priori theoretical considerations of excluding gross motor movements, we also found that when keeping gross motor movement in the data ($n = 47$), the number of trials identified with gross motor movements during observation was correlated with infants' mu suppression during action observation ($r = -.318, p = .029$). This suggests that infants' own movement was driving a large part of the mu response during observation if not excluded and justifies the need for rejecting those trials from our main analysis.

EEG data analysis

The EEG data were exported to a MATLAB-compatible format (The MathWorks, Natick, MA, USA) using Net Station software. EEG processing was conducted using EEGLAB (Version 14.0.0). First, video-coded events were imported into the EEG datasets and data were downsampled to 500 Hz. The subsequent processing steps were identical to those applied by Debnath, Salo, Buzzell, Yoo, and Fox (2019). The 24 electrodes at the boundary of the 128-channel net were removed, mostly overlaying the neck and ear regions (E17, E38, E43, E44, E48, E49, E113, E114, E119, E120, E121, E125, E126, E127, E128, E56, E63, E68, E73, E81, E88, E94, E99, and E107), with 104 channels remaining. The continuous data were filtered (0.3–49 Hz) using windowed-sinc FIR (finite impulse response) filters with a Hamming window (FIRfilt plugin of EEGLAB). Then, artifactual EEG channels were identified and removed using the EEGLAB plug-in FASTER (fully automated statistical thresholding for EEG artifact rejection) (Nolan, Whelan, & Reilly, 2010). FASTER identified channels with a z score of ± 3 for variance, mean correlation, or Hurst exponent as artifactual, and these channels were excluded. Artifact correction using independent component analysis (ICA) was performed on a copied dataset. Prior to ICA, the copied dataset was highpass filtered (1 Hz), segmented (1-s epochs), and cleaned from excessive artifacts by applying a combined voltage threshold of $\pm 1000 \mu\text{V}$ and spectral threshold (range = -30 to $+100$ dB) within the 24- to 40-Hz frequency band to extract muscle artifacts. If this procedure identified artifacts for more than 20% of a segment of a given channel, that channel was removed from the copied and original dataset. Independent components containing artifacts as identified by a semiautomatic process using ADJUST (artifact detector based on the joint use of spatial and temporal features; Mognon, Jovicich, Bruzzone, & Buiatti, 2011) and visual inspection were removed from the original dataset. Next, time windows of interest (baseline and Observation trial segments) that were contaminated by infants performing goal-directed actions or gross motor movements, infants crying or not looking, or parents interfering were excluded from further analysis based on video-coding. A detailed overview of trials excluded per criterion is provided in the Fig. 2. The remaining data were segmented into baseline segments (i.e., 1 s after the doors were fully open and E1 was visible but not moving) and experimental segments (i.e., 1 s before the moment E1 or the infant touched the toy to grasp it). To remove any remaining eye artifacts from these segments, a voltage threshold rejection ($\pm 150 \mu\text{V}$) was applied on six frontal channels (E1, E8, E14, E21, E25, and E34). Artifactual segments in these six channels were rejected. For all other channels, artifactual channels in each segment were interpolated. If more than 10% of channels within a segment needed to be interpolated, that segment was rejected. In this step, on average 1.5 baseline trials and 2.4 experimental trials were rejected. After artifact rejection, missing channels were interpolated using spherical interpolation. Data were re-referenced to the average of all electrodes. The preprocessed data were then converted into current source density (CSD) using the CSD Toolbox (Kayser & Tenke, 2006), and event-related spectral perturbation (ERSP) was calculated on CSD transformed data to estimate the baseline-corrected spectral power (in dB) from 3 to 30 Hz for all channels and trials. Segments were separated by condition. A total of 24 participants (15 in the blocked condition and 9 in the turn-taking condition) with at least 2 artifact-free trials per condition remained in the final analysis. This resulted in 5 trials

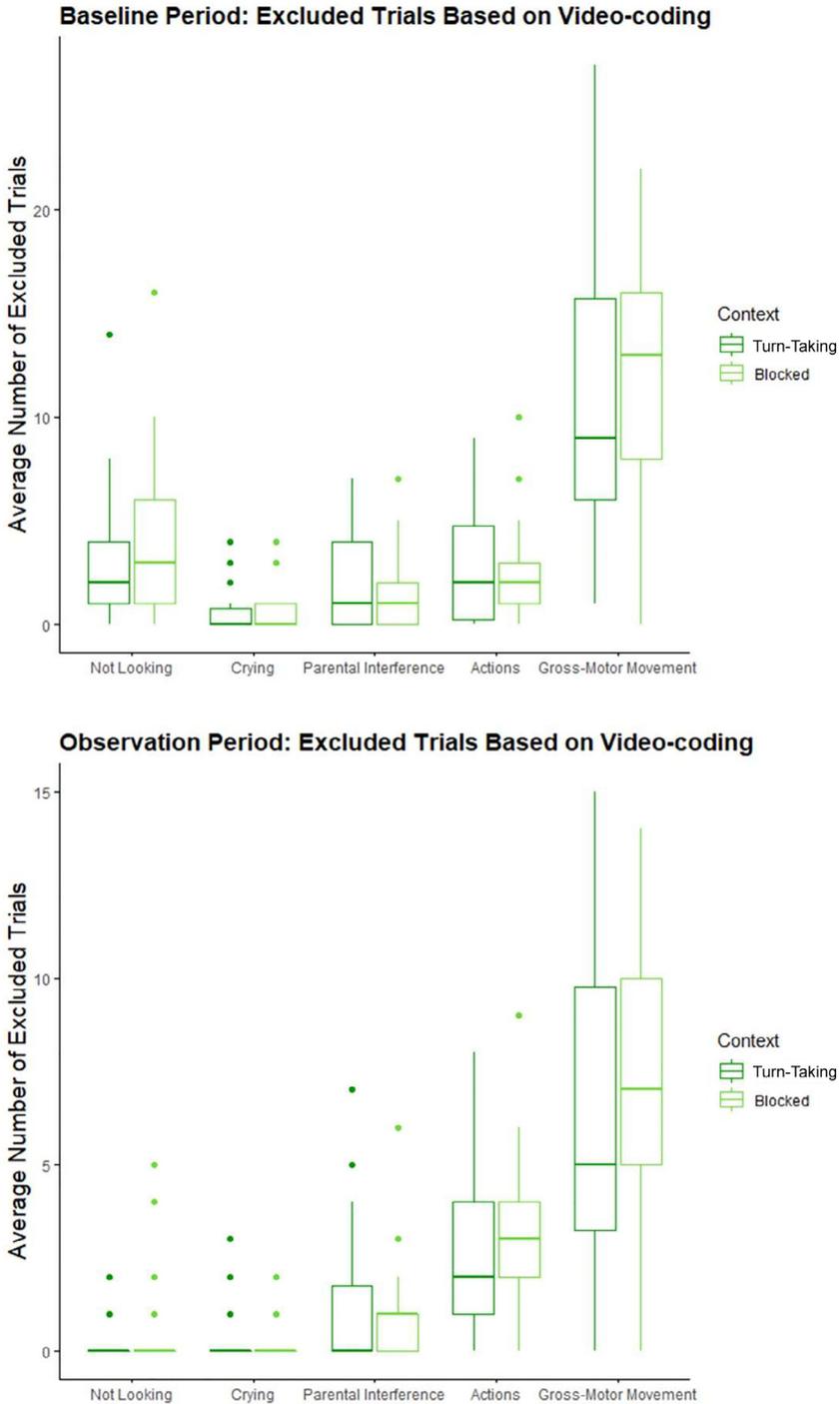


Fig. 2. Boxplot representation of the average number of excluded trials of baseline (top) and action observation (bottom) electroencephalography (EEG) segments based on five different criteria of the video-coding analysis.

on average (range = 2–10) for the action execution condition and 5.5 trials on average (range = 2–12) for the action observation condition.

As in [Debnath et al. \(2019\)](#) study, and consistent with previous research (see [Fox et al., 2016](#); [Marshall & Meltzoff, 2011](#)), analyses focused on the 6- to 9-Hz alpha frequency band in channels overlying sensorimotor regions (C3 and C4) to assess infants' neural motor activity during action observation and action execution. Power in this frequency band over motor regions is also referred to as mu power. Thus, power values in 6–9 Hz were averaged across trials and central channel clusters (C3 = E29, E30, E35, E36, E37, E41, and E42; C4 = E87, E93, E103, E104, E105, E110, and E111). This was done separately for two time windows leading up to the moment E1 or the infant touched the toy to grasp it: –1000 to –500 ms and –500 to 0 ms. These time windows capture the initial movement toward (–1000 to –500 ms) and final reaching resulting in grasping of the toy (–500 to 0 ms). Once baseline-corrected mu power of central channel clusters was extracted per condition, it was compared in two main comparisons addressing *general mirroring* and *context-dependent mirroring* during observation of action. To further assess whether any condition differences were driven by infants' visual processing, we examined baseline-corrected alpha power at occipital channel clusters (O1 = E66, E69, E70, E71, and E74; O2 = E76, E82, E83, E84, and E89), also called occipital alpha. Suppression of occipital alpha has been associated with visual processing and visual attention to the environment ([Herring, Thut, Jensen, & Bergmann, 2015](#)). To dissociate neural activation of the motor and visual systems, [Cuevas, Cannon, Yoo, and Fox \(2014\)](#) suggested as best practice to assess alpha power over visual in addition to motor cortices. For this purpose, we ran two control analyses. First, we correlated occipital alpha and mu power while controlling for condition across action observation. Second, we submitted occipital alpha power to the same statistical analysis as mu power on context-dependent mirroring to assess whether any social context also affects infants' visual processing. For additional exploratory analyses on visual processing, see [supplementary material](#) (in particular [Supplementary Fig. 1](#)).

Main statistical analysis

General mirroring. To examine whether the current data replicated previous findings showing that mu power during action execution and action observation is significantly lower than during baseline ([Fox et al., 2016](#); [Marshall & Meltzoff, 2011](#)), we conducted one-sample *t* tests against zero for the action observation and action execution conditions throughout the reach-to-grasp action (averaged across the time windows). This was Bonferroni corrected for multiple comparisons.

Context-dependent mirroring. To address our main research question about infants' neural mirroring, we submitted the extracted action observation data to a mixed analysis of variance (ANOVA) with the between-participants factor condition (turn-taking or blocked) and the within-participants factor time (–1000 to –500 ms or –500 to 0 ms).

Additional exploratory analysis

Connectivity analysis. Infants' neural processing of others' actions does not occur in isolation of solely motor-related brain areas, but motor activation is likely embedded in a larger neural network. To examine whether social context modulated connectivity between motor regions and other brain areas (frontal, parietal, and occipital) in the alpha frequency range, we conducted an exploratory connectivity analysis based on work by [Debnath et al. \(2019\)](#). More specifically, we calculated interchannel phase coherence (ICPC) as a measure of connectivity between two regions. This measure captures how consistent phase angles differ between channel clusters. We computed ICPC values between central and frontal channel clusters (C3–F3 and C4–F4), central and parietal channel clusters (C3–P3 and C4–P4), and central and occipital channel clusters (C3–O1 and C4–O2) for each time window within the 6- to 9-Hz range. Because [Debnath et al. \(2019\)](#) did not find any differences in connectivity between hemispheres, we collapsed over hemispheres, resulting in three channel cluster pairs (central–frontal, central–parietal, and central–occipital). To test for differences in coherence between regions, we submitted the ICPC values to a mixed ANOVA with the between-participants factor condition (turn-taking or blocked) and the within-participants factors channel pair (central–frontal, central–parietal, or central–occipital) and time (–1000 to –500 ms or –500 to 0 ms).

Visual processing. In addition to infants' neural mirroring, one might ask whether the social context manipulation also had an impact on infants' visual processing. Although rejecting gross motor movement trials from the main analysis is important for the interpretation of the mu suppression results, rejection might not be as crucial for visual processing indexed by occipital alpha. In line with this, we found no statistical evidence for a relation between the number of infants' gross motor movement trials and alpha at occipital channel clusters ($r = -.144, p = .334$). This offers the possibility to explore the question of whether infants' visual processing of the observed action was modulated by the social context with a larger sample of data. For this purpose, we ran an additional exploratory mixed ANOVA on occipital alpha power with the between-participants factor condition (turn-taking or blocked) and the within-participants factor time (-1000 to -500 ms or -500 to 0 ms), with the larger sample of data including trials with gross motor movement ($n = 47$).

Results

Video-coding results

In addition to using the video-coding in the preprocessing of the EEG data, we also conducted independent-samples t tests to compare the number of trials on which infants did not look or moved (grasping and gross motor movement) between conditions (turn-taking and blocked). This comparison did not yield any significant differences between conditions for the entire video-coded sample (all $ps > .10$) or for the final EEG sample (all $ps > .10$). Still, excluding gross motor movements from the data is essential to interpret motor activation as the processing of others' actions and not infants' own actions (see "Analysis" section).

Main EEG results

General mirroring

Fig. 3 illustrates infants' baseline-corrected mu power during action execution and action observation. During execution of a reach-to-grasp action infants' baseline-corrected mu power was on average -1.79 dB ($SE = 0.33$), and during observation of a reach-to-grasp action it was on average -1.05 dB ($SE = 0.33$). Results of the one-sample t tests against zero showed significant suppression of mu power with respect to baseline in both the action execution condition, $t(23) = -5.303, p < .001$, and the action observation condition, $t(23) = -3.161, p = .004$. This is in line with previous work on neural mirroring in infants as indexed by suppression in mu power (Fox et al., 2016; Marshall & Meltzoff, 2011). Moreover, we did not find evidence for a correlation between mu and occipital alpha power for action observation ($r = -.268, p = .21$, controlling for condition).

Context-dependent mirroring

The mixed ANOVA on central mu power during action observation indicated a main effect of time, $F(1, 22) = 10.42, p = .004, \eta_p^2 = .32$, and a significant Condition \times Time interaction effect, $F(1, 22) = 7.60, p = .011, \eta_p^2 = .26$. No other main effect was significant. The interaction is illustrated in Fig. 4. Follow-up post hoc t tests revealed significant differences in the time course of infants' mirroring dependent on the observation context. More specifically, there was significantly stronger mu suppression during the initial reaching movement compared with the time of finalizing the reach-to-grasp action for infants in the turn-taking condition, $t(8) = -4.37, p = .002$. In contrast, no evidence was found for a difference in mu suppression between the beginning and end of the reach-to-grasp action for infants in the blocked condition, $t(14) = -0.35, p = .731$. Thus, whereas in the turn-taking condition mu suppression was stronger during the initial reaching phase ($M = -1.86$ dB, $SE = 0.57$) than toward the end of the reach-to-grasp action ($M = -0.71$ dB, $SE = 0.51$), mu suppression remained similar throughout observing the reach-to-grasp action unfold in the blocked condition (-1000 to -500 ms: $M = -0.95$ dB, $SE = 0.43$; -500 to 0 ms: $M = -0.86$ dB, $SE = 0.47$).

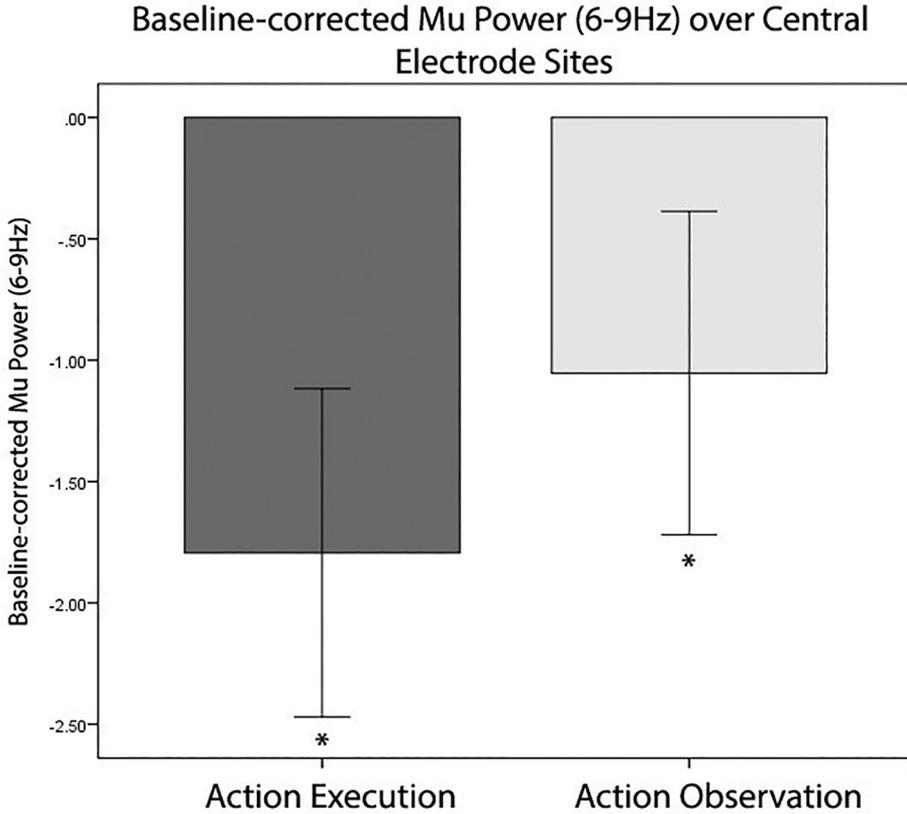


Fig. 3. Bar graph illustration of mu suppression (6- to 9-Hz power over central electrode sites) relative to baseline in the action execution and action observation conditions averaged over 1 s reaching-to-grasp the object through the infant (action execution) and the experimenter (action observation). Error bars represent -1 standard error of the mean. *Represents statistical significance ($p < .05$).

Fig. 5 further illustrates the topography of the condition differences in the action observation condition. The condition difference appears to be strongest over sensorimotor regions, suggesting specificity for sensorimotor processing. Moreover, the condition effect descriptively appears stronger in the right hemisphere. However, follow-up exploratory analysis including hemisphere (C3 or C4) in the mixed ANOVA did not reveal any additional main or interaction effects with hemisphere (all $ps > .05$, all $\eta_p^2s < .15$). In addition, as recommended by Cuevas et al. (2014), we also tested for condition differences in alpha power at occipital channel clusters. This mixed ANOVA did not reveal significant main or interaction effects (all $ps > .10$, all $\eta_p^2s < .10$) in the sample. Thus, there is no evidence for any condition differences in infants’ visual processing of others’ actions from this analysis (but see “Additional exploratory results” section for further details).

Additional exploratory results

Connectivity analysis

The mixed ANOVA on ICPC during action observation yielded a significant Condition \times Channel Pair \times Time interaction, $F(2, 44) = 3.56, p = .036, \eta_p^2 = .14$. No other main or interaction effects reached significance (all $ps > .10$, all $\eta_p^2s < .10$). The interaction is illustrated in Fig. 6. Following up on the three-way interaction with repeated-measures ANOVAs for each infant group revealed a Time \times Channel

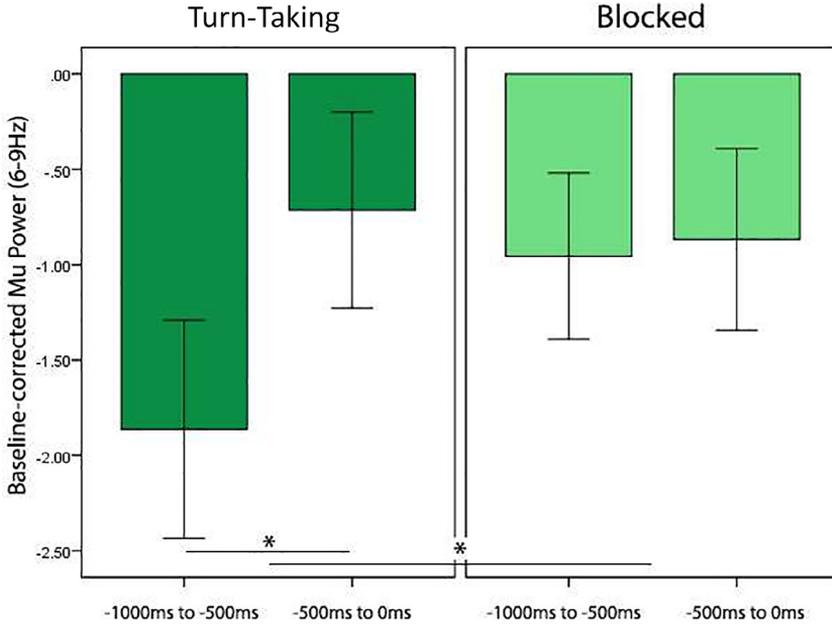


Fig. 4. Bar graph illustration of mu suppression (6- to 9-Hz power over central electrode sites) relative to baseline in the action observation condition separate for the turn-taking and blocked groups as a function of time (–1000 to –500 ms or –500 to 0 ms, with 0 ms being the moment of touching the toy). Error bars represent ± 1 standard error of the mean. *Represents statistical significance ($p < .05$).

Pair interaction for the turn-taking group, $F(2, 16) = 3.66, p = .049, \eta_p^2 = .31$. No other main or interaction effects for the turn-taking or blocked group were found (all $ps > .10$, all $\eta_p^2s < .11$). Post hoc t tests showed significant differences in the time course of infants’ functional connectivity values between central and occipital regions, $t(8) = -2.64, p = .030$, with higher coherence values toward the end of the reach-to-grasp action ($M = 0.54, SE = 0.05$) compared with the beginning of this action ($M = 0.44, SE = 0.03$). However, no evidence was found for differences in ICPC across time windows for central–frontal and central–parietal channel pairs (all $ps > .10$). Further following up on the three-way interaction, a mixed ANOVA testing for effects of condition and channel pair collapsing over time windows did not reveal any significant differences (all $ps > .10$, all $\eta_p^2s < .10$). Together, this suggests that the three-way interaction is driven by an increase in central–occipital alpha connectivity over the time course of the observed action only in the turn-taking group. This may indicate that turn-taking increases functional connectivity between motor and visual areas as the action unfolds, with higher connectivity at the moment the goal of the observed action is reached. Increased motor–visual functional connectivity, and thus integration of perceptual and motor systems, with dissociable sources in motor and visual cortices was previously reported for neural mirroring in 9-month-old infants (Debnath et al., 2019). This should be interpreted with caution, however, given the exploratory nature and limited data for this analysis.

Relation between mirroring and visual–motor connectivity

The findings that mu suppression is stronger in the turn-taking group (indicating more neural mirroring) at the beginning of the reach and that connectivity between motor and visual areas is higher toward the end of the reach-to-grasp action raise this follow-up question: Does motor activation at the beginning of the reach relate to the degree of neural communication between motor and visual areas at the end of the action? And if so, is this relation specific to motor activation (mu power) or present also for visual processing (occipital alpha power)? To address this follow-up question, we

Topographic distribution of baseline-corrected 6-9Hz Power

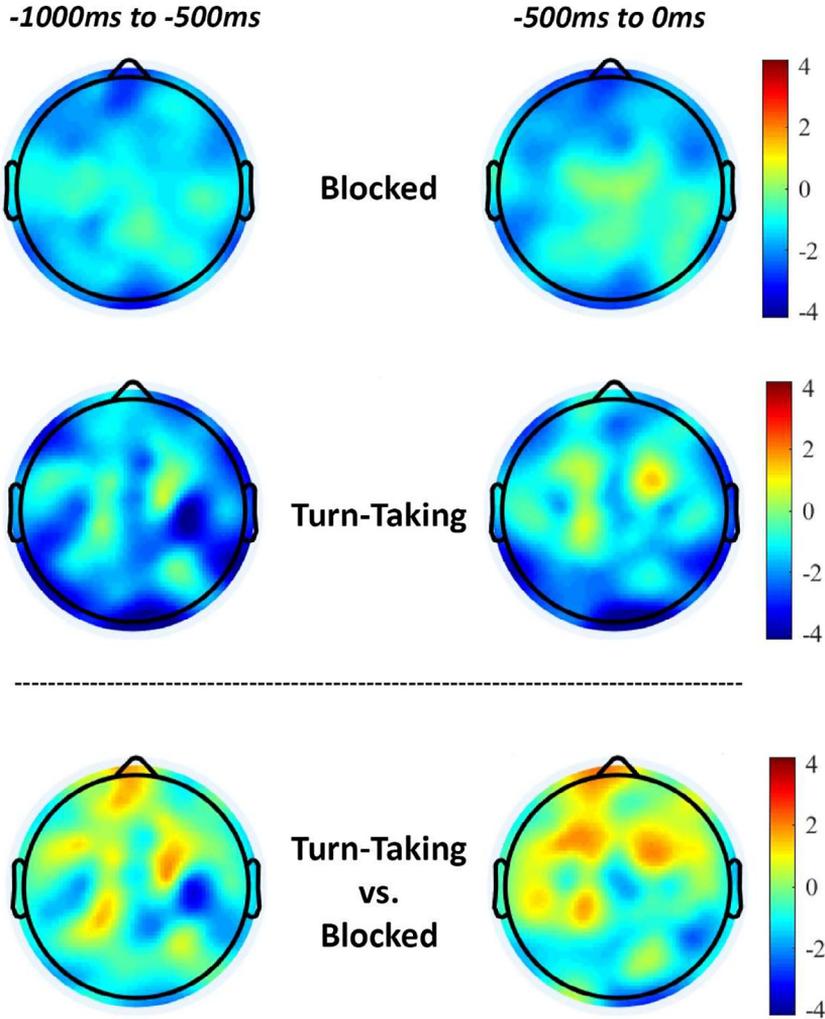


Fig. 5. Topographic distribution of alpha power (baseline-corrected 6- to 9-Hz power) per condition (top two panels) and differences between the turn-taking and blocked groups (bottom panel) for the initial reaching phase (left) and the final reach-to-grasp phase (right). For the contrast, cooler colors represent less relative power for the turn-taking group compared with the blocked group. Less relative power in this frequency band over sensorimotor regions is associated with more motor activity. (For interpretation of the reference to color in this figure legend, the reader is referred to the Web version of this article.)

ran an additional correlational analysis to test whether mu power or occipital alpha power at the beginning of the observed action related to functional connectivity between infants' central and occipital channel clusters at the end of the action. Although we had condition-specific expectations about mu power, we hypothesized a link between mu power and subsequent visual-motor functional connectivity to be a general phenomenon not specific to the conditions. Taking into account that data

Interchannel Phase Coherence during Action Observation (6-9Hz)

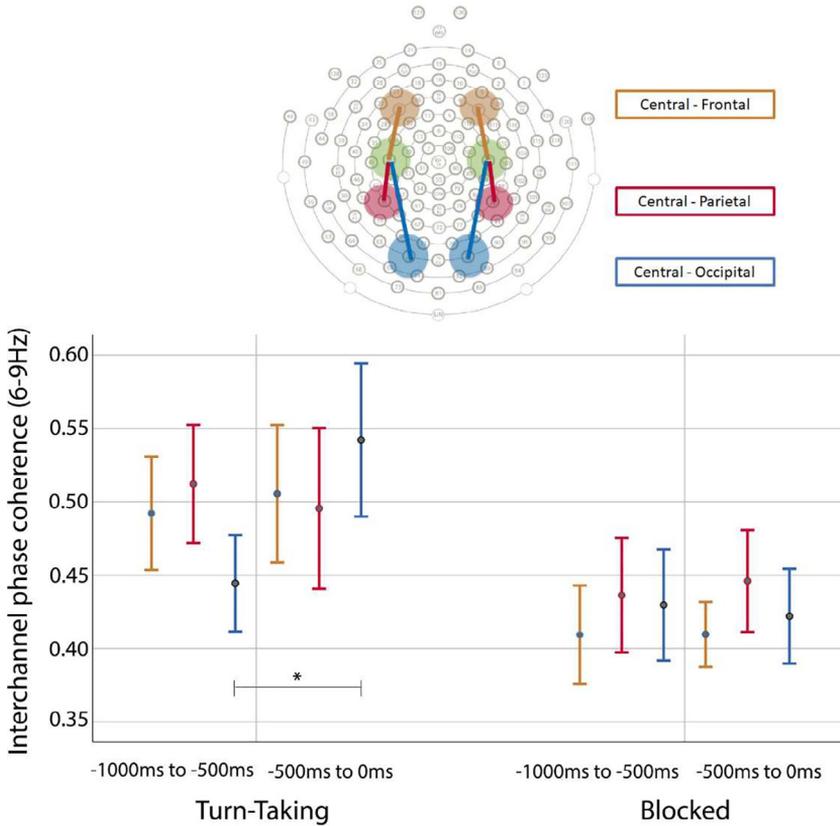


Fig. 6. Interchannel phase coherence (ICPC) during action observation in the 6- to 9-Hz range as a function of condition (turn-taking or blocked), channel pair (central–frontal, central–parietal, or central–occipital) and time (–1000 to –500 ms or –500 to 0 ms). Error bars represent ±1 standard error of the mean. *Represents statistical significance ($p < .05$).

came from different conditions, we corrected for condition by running partial correlations with condition as a covariate. We applied Bonferroni correction to account for multiple comparisons (corrected alpha level = .025). Results of the correlational analyses, as illustrated in Fig. 7, show that more mu suppression at the start of the action significantly correlated with higher functional connectivity at the end of the action ($r = -.483, p = .020$, controlling for condition). The correlation of occipital alpha power and the connectivity measure did not reach significance ($r = -.285, p = .18$, controlling for condition). This suggests a link between the engagement of infants’ motor system at the beginning of the action and a subsequent increase in neural communication between motor and visual regions.

Visual processing

The results indicated a main effect of condition, $F(1, 45) = 5.08, p = .029, \eta_p^2 = .102$. No other main or interaction effects were significant (all $ps > .10$). As illustrated in Supplementary Fig. 1, suppression of occipital alpha was stronger throughout action observation for the turn-taking group of infants ($M = -3.54, SE = 0.46$) compared with the blocked group of infants ($M = -2.34, SE = 0.29$). This suggests enhanced visual processing when infants observe an action in the context of turn-taking in contrast to the repeated presentation of an action without their own intermediate action turn.

Correlation between Mu Power and ICPC for Central-Occipital Channel-Pair

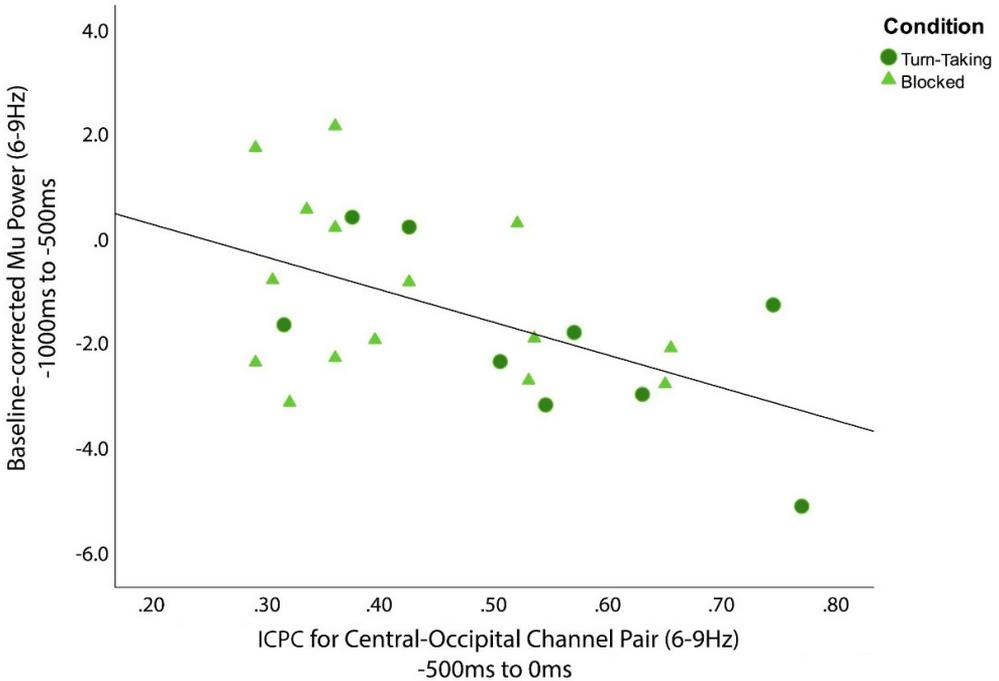


Fig. 7. Scatterplot illustrating the relation between mu suppression (6- to 9-Hz power over central electrode sites with respect to baseline) at the beginning of the observed action (-1000 to -500 ms) and interchannel phase coherence (ICPC) at 6 to 9 Hz for the central-occipital channel cluster at the end of the observed action (-500 to 0 ms).

Discussion

In the current study, we tested 9-month-old infants in a live EEG paradigm to assess whether social context influences infants' neural processing of others' reach-to-grasp actions. In our study, we made use of turn-taking, an early-emerging form of social interaction, to examine whether the engagement in this social context enhances infants' neural mirroring. The current results replicated previous findings of neural mirroring in infancy; the 9-month-olds demonstrated overall mu suppression relative to baseline during action execution and observation. Importantly, the findings extended beyond general mirroring. That is, the time course of infants' neural mirroring was modulated by context. When observing others' actions, infants who were engaged in a turn-taking context activated their motor system more strongly during the initial reaching phase than during the final reach-to-grasp phase. Whereas infants in the blocked context showed a similar extent of mu suppression throughout the observed action. Our results suggest that this effect is specific to sensorimotor processing, as indicated by the localization of the topographic distribution and lack of evidence for a relation between mu suppression during action observation and occipital alpha power. Together, our findings, in line with those of Debnath et al. (2019), speak for dissociable motor and visual processes in infants indicated by power changes at different channel sites (central vs. occipital) in the alpha frequency range. For a more detailed discussion on visual attention effects, see the "Social observation context affects visual attention in 9-month-olds" section below.

Importantly, although activation of motor and visual cortices is dissociable, it is also likely interconnected as reflected in motor–visual functional connectivity (e.g., [Debnath et al., 2019](#)). Exploratory analyses also suggest that, compared with infants who repeatedly observed others' actions, those infants who were actively engaged in turn-taking with others had higher functional connectivity between motor and visual brain regions in the alpha frequency range when the goal of the action was reached. In addition, stronger neural mirroring at the start of the reaching action correlated with more neural communication as indexed by phase coherence between central and occipital channel clusters at the final phase of the action. Thus, turn-taking, an early form of social interaction, led to enhanced neural mirroring when infants watched how an action started, and the strength of this neural mirroring further related to the subsequent neural communication between motor and visual cortices as the action goal was reached.

Social observation context affects neural mirroring time course in 9-month-olds

We had hypothesized that infants would engage their neural motor systems more strongly during action observation in the context of turn-taking, as was previously found in social interactions in older children and adults ([Kourtis et al., 2010](#); [Meyer et al., 2011](#)). However, we did not predict that social context would affect the time course of infants' action processing. We propose three possible, yet not mutually exclusive, interpretations of the main findings. First, the time-course effect on neural mirroring might reflect anticipatory motor activity predicting the upcoming trajectory and goal of the observed action. Previous research including eye-tracking and EEG studies with infants have shown that infants predict the goal of an action from the beginning of that action (e.g., [Falck-Ytter, Gredebäck, & von Hofsten, 2006](#); [Southgate et al., 2009, 2010](#)). For instance, [Southgate et al. \(2010\)](#) presented 9-month-old infants with partially occluded reach-to-grasp actions. Their findings of mu suppression during the reaching phase of the observed actions suggest that infants generated online predictions of the upcoming action goal. Similarly, [Montirosso et al. \(2019\)](#) found mu suppression for 14-month-olds during the reaching phase of an action observation paradigm. Moreover, eye-tracking research with infants shows that social context affects how infants predict others' actions ([Fawcett & Gredebäck, 2013](#)). Infants anticipated the actions of an individual differently depending on whether the person was engaged in a social interaction or not. Analogously, the current results might reflect social context effects on infants' anticipatory motor activity. That is, enhanced motor activation during the initial phase of the reach could reflect that infants who engaged in turn-taking, in contrast to infants who observed others' actions repeatedly, might have been better able to predict others' actions from the beginning of the action.

Interestingly, results of our exploratory analyses further suggest that infants' motor activity at the beginning of the action (potentially reflecting their anticipation of the action goal) correlated with functional connectivity between motor and visual cortices as the action unfolds. One might speculate that infants generate predictions at the start of the action about how the action unfolds and compare it with the visual input at the end of the action when the goal is reached to verify whether the initial prediction was accurate. In other words, the enhanced neural communication between motor and visual areas might reflect a feedback loop comparing the initial action prediction with the observed action and its outcome. Predictive processing accounts of action perception coupling similarly propose feedback loops between visual and motor regions (e.g., [Kahl & Kopp, 2018](#); [Friston, Mattout, & Kilner, 2011](#)). Although it remains speculation, this interpretation for the current findings fits with both motor activation and visual–motor connectivity results.

A second (less likely) explanation for the current findings could be that infants engaged in turn-taking might be preparing their own reaching action in the initial phase of observing others' reaching. Once the observed reach is unfolding, infants might realize that it is not their own turn to act but rather the other's turn to act. Thus, the initial enhancement in motor activation might reflect infants' preparation to act. In contrast, infants who observe the other person acting repeatedly might become familiar with this structure, no longer preparing to grasp the toy themselves, unlike in the turn-taking context. If this were true, then one would expect motor activation to increase during observation of

the initial reaching phase for infants in the turn-taking context but to decrease for infants in the blocked context across trials. Although this is a testable hypothesis, the low number of EEG trials in the current dataset does not allow this hypothesis to be tested reliably here. It should, however, be noted that only observation trials during which infants were not moving were included in the current analyses. Therefore, if infants plan their movements to the extent to which they actually initiate reaching, those trials would not be represented in the current EEG analyses. In addition, if infants in the turn-taking condition prepared their own movements, one might expect them to overtly move more in this condition than in the blocked condition. Interestingly, when comparing infants' overt movements during action observation, no evidence for a significant difference between conditions is detected (see Results and Fig. 2). Although a null effect should be interpreted with caution, this provides no positive evidence for the interpretation that the conditional differences stem from infants' own action preparation. Thus, overall, although this remains a possible explanation, it seems less plausible.

Third, rather than being driven by time-course changes in the turn-taking context, the current interaction might be more related to changes in the blocked context. In other words, similar to habituation and repetition suppression paradigms, repeated exposure to the same stimulus in succession might have led infants to activate their neural motor system less over time in the blocked context (e.g., Turk-Browne, Scholl, & Chun, 2008). The intermediate own turn that infants had in the turn-taking context might have broken up and thereby slowed down potential habituation or repetition suppression effects in the turn-taking condition. This interpretation also generates testable hypotheses such as examining whether neural mirroring decreases across trials in the blocked context faster than in the turn-taking context. Although this cannot be pursued with the current dataset, future habituation or EEG studies could directly address this possibility. Notably, however, in contrast to predictions from habituation studies, we found no significant differences between contexts in the number of trials on which infants looked away. Thus, infants' behavior in the task did not provide evidence for this explanation.

Although we cannot decisively differentiate among these three possible interpretations, the first explanation does fit all data, whereas the second and third explanations do not seem to be supported by all EEG and behavioral findings. Irrespective of which explanation might hold true, we can conclude that the time course of neural mirroring in 9-month-old infants differs depending on the social observation context.

Social observation context affects visual attention in 9-month-olds

Findings of exploratory analyses on occipital alpha suggest enhanced visual attention to others' actions for infants who were engaged in turn-taking rather than infants who repeatedly observed actions without their own intermediate action turns. In contrast to modulations in the time course of infants' neural mirroring, enhanced visual processing lasted consistently throughout the observed action independent of its unfolding time course. One might speculate that turn-taking may have made the action observation scene more salient as a whole to 9-month-olds by increasing the relevance of the others' actions through the contingency with their own actions. In line with this, evidence based on occipital alpha in adults suggests context-sensitive visual processing and in particular enhanced visual activity when others' actions are relevant for one's own behavior (Perry, Stein, & Bentin, 2011). That is, Perry et al. (2011) found more suppression in occipital alpha when adults had a task related to the actions they observed (i.e., in their case determining the number of wins for a competitive action game) compared with watching the same actions without any relevance to their own subsequent behavior. Interestingly, Perry et al. (2011) reported the same trend for suppression of occipital alpha, although not statistically significant, for observing others' actions when being engaged in competitive games with the other people. In both cases, the observed action is relevant to the observers' subsequent behavior, which might boost visual processing of the scene.

Together, our findings suggest that both motor processing (as indicated by mu suppression) and visual processing (as indicated by suppression of occipital alpha) were enhanced during action observation when 9-month-old infants were engaged in turn-taking. Although visual effects seem to continue throughout action observation (invariant to the action time course), motor effects were

dependent on the time course of the observed action. Still, given the exploratory nature of the additional analyses on connectivity and visual processing, the additional results should be interpreted with caution, and replication is needed to critically test their reliability.

Potential limitations

In our analysis, we excluded any action observation trial containing infants' overt goal-directed reach-to-grasp actions and any other gross motor movements such as infants moving their arms in the air and banging on the table. We applied this conservative exclusion criterion to ensure that the neural motor activation during action observation was not erroneously attributed to others' action processing when it was actually a combined signal of infants' movement execution and observation of others' actions. In our study, therefore, two combined factors led to a relatively high dropout, leaving 24 participants in the final analysis (15 in the blocked condition and 9 in the turn-taking condition). That is, we used developmental EEG recordings in a live paradigm and had the specific constraints imposed by investigating neural mirroring. Crucially, we believe that careful coding, examination, and exclusion of movements allowed for a more transparent interpretation of neural motor activation during action observation. In fact, we saw that the number of gross motor movement trials was related to infants' neural motor response to action observation before the infants were excluded. Although the final sample size is small, it is comparable to those of previous research on neural mirroring (e.g., [Marshall et al., 2013](#)). Thus, we believe that despite the high dropout rate, the current results are meaningful and provide valuable information on the characteristics of neural mirroring in infancy.

Conclusion

These findings replicate previous research showing neural mirroring in the first year of life. In this live paradigm, 9-month-old infants activated their neural motor system during the execution and observation of reach-to-grasp actions. Beyond general mirroring in infancy, we found that the time course of neural mirroring differs between infants engaged in turn-taking and infants who first repeatedly see actions before they get to act. Implications of these findings are both theoretical and practical. The theoretical implications of the current findings underline the role of the observation context for how infants process other people's actions. Thus, our findings suggest that already early in infancy neural mirroring is flexible and sensitive to top-down influences such as social context. Even at an age prior to final maturation of brain areas associated with cognitive and top-down control (e.g., [Bunge, Dudukovic, Thomason, Vaidya, & Gabrieli, 2002](#); [Somerville & Casey, 2010](#)), infants' neural processing speaks against merely passive action perception and for flexible, context-sensitive processing of others' actions. The results also suggest that neural mirroring is embedded in and intertwined with social interaction from the start. This might have further implications for action learning in social interaction. When teaching infants new actions, rather than demonstrating new actions multiple times in succession, it might be beneficial to demonstrate new actions in turns with infants getting to act themselves. Previous research with infants has demonstrated that enhanced mirroring during action observation predicted later imitation ([Filippi et al., 2016](#); but see also [Köster, Langeloh, Kliesch, Kanngiesser, & Hoehl, 2020](#)). Therefore, one might speculate that engaging infants in turn-taking might stimulate their neural processing of others' actions and their subsequent imitation. Future studies could systematically test whether infants' neural mirroring during turn-taking is related to infants' subsequent action learning and performance. Together, and in the light of social learning and imitation in the first year of life, our findings suggest that turn-taking might be particularly effective in engaging infants' action perception systems.

Furthermore, the practical implications of the current results pertain to the basic experimental design choices for studies on infants' action processing and neural mirroring. More specifically, our findings highlight that seemingly minor design choices, such as the order of action execution and observation trials, may significantly affect the outcomes of a study. With this knowledge, upcoming developmental EEG studies investigating neural mirroring in early childhood could make informed decisions about optimal task orders for their research purposes.

CRedit authorship contribution statement

Marlene Meyer was responsible for conceptualization, methodology, data collection, analysis, and writing the manuscript. Haerin Chung was responsible for conceptualization, methodology, data collection, analysis, and reviewing the manuscript. Ranjan Debnath was responsible for providing feedback on the study design, data analysis and reviewing the manuscript. Nathan Fox was responsible for providing feedback on the study design and data, and reviewing the manuscript. Amanda Woodward was responsible for conceptualization, methodology, and reviewing the manuscript.

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Data sharing and data accessibility

The data that support the findings of this study are available from the corresponding author (M. Meyer) upon reasonable request.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jecp.2021.105260>.

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