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Neural mirroring and social interaction: Motor system involvement during action observation relates to early peer cooperation

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Whether we hand over objects to someone, play a team sport, or make music together, social interaction often involves interpersonal action coordination, both during instances of cooperation and entrainment. Neural mirroring is thought to play a crucial role in processing other's actions and is therefore considered important for social interaction. Still, to date, it is unknown whether interindividual differences in neural mirroring play a role in interpersonal coordination during different instances of social interaction. A relation between neural mirroring and interpersonal coordination has particularly relevant implications for early childhood, since successful early interaction with peers is predictive of a more favorable social development. We examined the relation between neural mirroring and children's interpersonal coordination during peer interaction using EEG and longitudinal behavioral data. Results showed that 4-year-old children with higher levels of motor system involvement during action observation (as indicated by lower beta-power) were more successful in early peer cooperation. This is the first evidence for a relation between motor system involvement during action observation and interpersonal coordination during other instances of social interaction. The findings suggest that interindividual differences in neural mirroring are related to interpersonal coordination and thus successful social interaction.

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1. Introduction

Our daily life contains a multitude of social interactions in which we coordinate our actions with others. The involvement of the mirror system in action perception, monitoring, and prediction (e.g., Bekkering et al., 2009; Kilner et al., 2007; Southgate et al., 2009; Stapel et al., 2010) is thought to help us prepare and execute our own actions in coordination with others (Kourtis et al., 2013; Sebanc et al., 2006). Converging neuroimaging evidence has shown that our motor system becomes activated both when performing an action, and when observing an action (Marshall and Meltzoff, 2011; Rizzolatti and Craighero, 2004; Rizzolatti and Fogassi, 2014). This neural overlap between action production and perception has been called neural mirroring (e.g., Hari and Kujala, 2009). It has been suggested that neural mirroring provides the neurocognitive basis for processing others' actions and therefore plays a crucial role in successful interpersonal coordination during social interaction (Bekkering et al., 2009; Hari and Kujala, 2009).

Previous findings support this hypothesis of a close relation between neural mirroring and interpersonal coordination. For instance, adults who showed more motor system involvement when observing a partner's movements in a finger tapping task also coordinated their movements better with the partner (Naeem et al., 2012). While imitative actions occur during social interaction, especially complementary actions are relevant in which individuals perform different actions (Bekkering et al., 2009), for example when passing and catching a ball. Complementary actions were also related to motor involvement of the neural motor areas during action observation (Ménoret et al., 2014). Comparable findings are present for children, as young children who mirrored an adult action partner more than another adult in a turn-taking game made fewer errors in interpersonal coordination during that game (Meyer et al., 2011). Similarly, recently, Filippi et al. (2016) found that elevated levels of mirroring in 7-month-old infants predicted their imitation of others’ toy choices. These findings support a link between neural mirroring and interpersonal coordination within the same laboratory task. However, the degree to which interindividual differences in neural mirroring support the success in various instances of social interaction is unknown.
While the role of interindividual differences in neural mirroring for interpersonal coordination is unclear, studies of social cognition (e.g., empathy, perspective taking) highlight a role of mirroring for social skills that are not task-specific. In adults, neural mirroring is related to higher levels of perspective taking (Woodruff et al., 2011), empathy (Gazzola et al., 2006; Hooker et al., 2010; Kaplan and Iacoboni, 2006), and social competence as assessed with questionnaires (Pfeifer et al., 2008). In this study, we investigated whether interindividual differences in neural mirroring also might play a role in interpersonal coordination during social interactions outside the specific task.

In social interaction, two types of interpersonal coordination occur often: cooperation and entrainment. While in cooperation, coordination is planned and typically involves a goal-directed task, in entrainment, coordination emerges spontaneously without a joint goal (Knoblich et al., 2011). For instance, soccer players cooperate by keeping track of each other and adjusting their positions accordingly to obtain the ball and shoot it at the goal. During applause, on the other hand, people entrain by coordinating their clapping behavior spontaneously. In cooperation, it is important to monitor others’ actions with respect to the achievement of the common goal. In entrainment the focus rather is on the monitoring of the others’ movements. Importantly, both the observation of movements and goal-directed actions were found to activate the human mirror system (Rizzolati and Craighero, 2004; Rizzolotti and Fogassi, 2014). Therefore, we expected that higher levels of mirroring would be related to both higher levels of cooperation and entrainment situations outside the specific mirroring task.

Activation of the mirror system during action observation already has been demonstrated in infancy (Marshall and Meltzoff, 2011). Investigating the relation between neural mirroring and interpersonal coordination is especially important in early childhood, since proficiency in social interaction at this age, mainly with peers, predicts social competence later in life (e.g., Hay et al., 2009; Rubin et al., 2006). Children already demonstrate action coordination with peers in toddlerhood (e.g., Ashley and Tomasello, 1998; Brownell, 2011; Endedijk et al., 2015a; Hunnius et al., 2009). During the preschool years, children’s interpersonal coordination continues to develop, as they begin to respond more quickly to the behavior of others and become more stable in coordination, both in cooperation (Ashley and Tomasello, 1998; Endedijk et al., 2015a; Fletcher et al., 2012) and in entrainment tasks (Endedijk et al., 2015b). Throughout early childhood, children gain ample experience with interpersonal coordination. Children who face difficulties with social interactions early in life more often experience rejection by peers later on (Friedleimer, 2009; NICHD Early Child Care Research Network, 2008) with subsequent negative consequences for their social functioning in adolescence and adulthood (Bagwell et al., 1998). Clarifying the processes involved in early interpersonal coordination with peers is very important for understanding social development.

The current study examined the relation between interindividual differences in neural mirroring and young children’s social interaction skills. Children’s neural mirroring was assessed by measuring oscillatory brain activity (by means of EEG) during action observation. In particular, the mu- and beta-frequency bands over motor areas have been associated with motor system involvement during action observation (cf. Meyer et al., 2011; Pfurtscheller and Lopes da Silva, 1999; Pineda, 2008; Saby and Marshall, 2012; Vanderwert et al., 2013). To investigate the relation between neural mirroring and interpersonal coordination with peers, motor system involvement during action observation was assessed in 4-year-old children. As part of a longitudinal study their interpersonal coordination had been assessed earlier at 28, 36, and 44 months, in a cooperation task and in an entrainment task with different peers. Based on previous research suggesting the functional involvement of neural mirroring during interpersonal coordination (Meyer et al., 2011; Naem et al., 2012), we hypothesized that interindividual differences in children’s neural mirroring of others’ actions would be associated with both forms of interpersonal coordination (cooperation and entrainment).

2. Method

2.1. Participants

The sample consisted of 29 children (10 boys) who participated in an EEG experiment at 52 months of age ($M = 52.48$, $SD = 1.94$). Interpersonal coordination with peers had been assessed in play sessions at 28 months ($M = 27.96$, $SD = 0.33$), 36 months ($M = 35.98$, $SD = 0.34$), and 44 months ($M = 43.83$, $SD = 0.34$). The participants were part of a larger sample of 181 children whose social development was studied longitudinally from toddlerhood to early school age. Children were selected from the larger sample if they had participated in three play sessions (i.e. had not missed a session) and were willing to participate in EEG research. The play sessions took place in the lab with an unfamiliar same-gender peer (also of the longitudinal study sample), each play session with a different peer. All children were Dutch and from mixed socio-economic backgrounds. All were healthy and had no indications of atypical development. Parents were informed of the study and gave written consent. After each testing session, children received a book or a small amount of money “for their piggy bank” as a thank you for participation.

2.2. Procedure

The EEG session took approximately 60 min including familiarization with the experimenters, preparing the EEG cap, and the measurement itself (see Section 2.3). During testing, children were videotaped from two visual angles (with one camera directed at the child’s upper body and the other one at the child’s legs) in order to remove trials in which the child was moving or did not pay attention.

Previously, children had participated in three play sessions to assess their interpersonal coordination (see Sections 2.4 and 2.5). The play sessions started with 10–30 min of free play during which children got familiarized with each other and the experimenters. The introductory phase was followed by the cooperation task, which took about 5 min. The entrainment task followed with a maximum duration of 5 min. Parents were instructed to minimize their interactions with their child and if the child was clinging to them, respond in ways to stimulate involvement in the session without helping with the tasks. Each session lasted about 45 min and was videotaped from two visual angles using two video cameras.

2.3. Action observation task

To assess children’s individual levels of neural mirroring, EEG was measured while they watched videos of actions. The task had two conditions: action observation and abstract movement observation. In the action observation condition (Fig. 1, top row), children observed a video of an adult performing different actions on objects (e.g., stacking cups or moving a toy car into a garage). In the abstract movement condition (Fig. 1, bottom row), children observed abstract shapes moving across the screen, similar to a screensaver. This abstract movement condition was included to control for non-human movement perception. There were six action videos and six abstract movement videos, each lasting approximately 7 s. During both action observation and abstract movement observation condition, each video was repeated three times and preceded by a 1000 ms fixation cross that functioned
as baseline (see Fig. 1). The action observation condition was run twice with two different task instructions (to imitate the action or to name the color of the object after the observation of the videos; blocked and counterbalanced between children) as part of a different study. Thus, each action observation video was shown six times in total and each abstract movement video three times. After two action observation videos, one abstract movement observation video was shown. To assess children’s neural activity during action execution, EEG also was recorded while children imitated the actions after having observed them. EEG data during the verbal response were not used in the analysis.

Behavioral responses were coded for both the imitation instruction and color naming. Children were proficient in the color naming task, with one child naming 3 out of 6, two children naming 5 out of 6, and the remaining children naming all colors correctly. For the imitation task, the actions were divided in three parts, e.g. driving the car to, into, and out of the garage. Children received 1 point for each part of the action they imitated, resulting in a maximum score of 3 for each imitation trial. Children were at ceiling level with an average imitation performance of 2.59 (range 1–3).

EEG recordings were conducted using child-sized EEG caps with 32 electrode sites on the scalp. The Ag/AgCl active electrodes were placed in an actiCap, arranged according to the 10–20 system, and referenced to electrode FCz over the central midline. The signal was amplified using a 32-channel BrainAmp DC EEG amplifier, band-pass filtered (0.1–125 Hz), and digitized at 500 Hz. We strived to keep all impedances below 60 kΩ.

Analogous to previous studies (see Marshall and Meltzoff, 2011; for a review), we analyzed motor system activity by means of mu- and beta-oscillatory power over sensorimotor areas. Motor system involvement was analyzed during action observation, abstract movement observation, and action execution. Data analysis was performed using FieldTrip, an open source Matlab toolbox (Oostenveld et al., 2011). All data was divided into 1-s segments and re-referenced to the average of all electrodes. Segments during which children moved or did not look at the stimulus display were removed. We visually inspected the remaining segments to exclude EEG artifacts (such as noisy channels or eye blinks). One child was removed from the analyses due to the lack of baseline trials during the abstract movement observation condition. On average, per child 120 segments remained for the action observation (range 33–246), 38 segments for the abstract movement observation (range 4–81), 12 segments for the baseline preceding the action observation stimuli (range 3–24), and 5 segments for the baseline preceding the abstract movement stimuli (range 1–12). A DFT filter was used to remove line noise from the data, and for each segment we took out potential offset differences by subtracting the mean signal of the entire trial from the signal at each time point. We then calculated spectral power estimates using the Fast Fourier transform on the 1-s segments in combination with a Hanning taper as applied on the segments without overlap. Finally, we calculated an average power for each condition for each child, to use in the analysis.

Based on previous research (see Pfurtscheller and Lopes da Silva, 1999), we focused our analyses on electrodes over motor cortices (C3, C4). To control for interindividual differences in absolute power due to differences in scalp thickness and electrode impedance, the ratio of power during the condition relative to baseline (fixation cross) was computed for each condition. Since these ratios were not normally distributed, a log transformation was applied. These scores were used to indicate children’s motor system involvement in each condition (action observation, abstract movement observation) and during action execution. A smaller log ratio indicated more suppression in a condition compared to baseline. Based on the action execution ratio, the sample-specific mu- and beta-frequency range was identified (see Section 3.1). Normalized power values were pooled over the central electrodes (C3, C4) per condition in the identified mu- and beta-frequency bands for further analysis.

2.4. Cooperation task

The cooperation task was a peer version of Warneken et al. (2006) double-tube task. The setup consisted of two 1-m-long tubes mounted in parallel on a box with a 45° incline (see Fig. 2A). The children were given a Playmobil figure in a swimsuit and a small swimming pool. They were instructed that the figure wanted to go
through the sliding tube to the swimming pool. Because the tubes were too long for one child to simultaneously hold the swimming pool and insert the figure into the tube, the two children had to cooperate to perform the task successfully. A detailed description of the task can be found in Endedijk et al. (2015a).

Each child’s behavior was coded off-line from the video recordings. For each trial (defined as a slide of the figure through the tube), it was coded whether cooperation was successful or not. Cooperation trials were coded as successful if both the child who inserted the figure into the tube and the child who held the swimming pool chose the same tube. Cooperation trials were coded as unsuccessful if children chose different tubes or if one child performed the task alone, resulting in the figure falling on the floor. To control for the total number of trials, the data were transformed into a proportion of success on the task for each dyad. For the longitudinal study, the recordings of 20% of the dyads at each time point were coded by two observers. Cohen’s kappa was 0.94 on average (SD = 0.11).

2.5. Entrainment task

For the entrainment task two 10-inch drums of a Hayman children’s drum set and two plastic sticks were used (see Fig. 2B). The drums were placed on a stand that could be adjusted to the height of each child so that they could comfortably drum in standing position. The drums were connected via piezo contact microphones placed on the drumheads to collect MIDI data via an Alesis D4 drum module. Performances were recorded with Logic Express. Children were instructed separately to start drumming and did not receive any instructions about drumming together or coordinating their drumming with their dyad partner.

Cross-correlations commonly are used in interpersonal coordination studies to investigate entrainment (Repp, 2005). We calculated maximum cross-correlations that indicated how a child's hits best related to their partner's hits rhythmically across time. For this purpose, the time between the hits produced by each child were measured. Time series of these inter-tap-intervals of the two children were shifted alongside each other to find the highest correlation between the two time series. Thereby, the maximum cross-correlation measure describes the coordination of children’s rhythmic behaviors.

2.6. Analyses

To examine whether interpersonal coordination predicted motor system involvement during action observation (a proxy for neural mirroring), two hierarchical regressions were run, one predicting normalized mu-power and one predicting normalized beta-band power during action observation. To control for motor system involvement due to non-human movement, the normalized power during observation of abstract movement was entered in Step 1 of each regression. In Step 2 of each regression, the measures of interpersonal coordination were entered: the proportion of coordinated trials during cooperation, and the maximum cross-correlation during entrainment. The scores for these two variables were standardized for each play session and averaged across the three sessions, resulting in measures of interpersonal coordination aggregated over sessions and interaction partners. These three averaged z-scores were entered in Step 2 of the regression analysis.

3. Results

3.1. Neural mirroring

Based on the observed suppression of power during action execution (see Fig. 3, top), the frequency bands were identified on the basis of the grand average as follows: mu from 7 to 12 Hz and beta from 16 to 20 Hz. The topographic distribution of these frequency bands supports the a-priori selection of electrodes over motor cortices (see Fig. 3, bottom).

The analysis of these specified frequency bands yielded positive normalized power values for both mu and beta during action observation, $M = 0.23, SD = 0.28$, and $M = 0.20, SD = 0.31$, and abstract movement observation, $M = 0.25, SD = 0.44$, and $M = 0.22, SD = 0.44$, indicating relatively more power during experimental conditions than at baseline. Similar to action execution, the topographic distribution of normalized power in mu- and beta-frequency bands showed a relatively confined pattern of activation overlaying motor cortices (especially at electrode sites C3 and C4) during action observation (Fig. 4, top row). The topographic distribution during abstract movement observation appeared less confined but more widespread along the midline (Fig. 4, bottom row).

3.2. Relation between neural mirroring and interpersonal coordination

Table 1 summarizes the results of the hierarchical regressions. In step 1, motor system involvement during abstract movement observation was related to action observation values for the mu-frequency band, but not for the beta-frequency band. Adding the measures of cooperation and entrainment in Step 2 resulted in a
significantly better model for the beta-frequency band, $F_{\text{change}}(2, 21) = 5.14, p = 0.02, \Delta R^2 = 0.39$, but not for the mu-frequency band, $F_{\text{change}}(2, 21) = 0.31, p = 0.74, \Delta R^2 = 0.02$. For beta, while controlling for non-human movement, power reduction was strongly related to children’s performance on the cooperation task ($\beta = -0.52, p = 0.01$). Children who were more successful in cooperation with peers also showed more involvement of the motor system during action observation. There was no significant relation between entrainment and beta-band power.

### 4. Discussion

In this study, we examined the relation between interindividual differences in neural mirroring in young children and their social interaction with peers in a cooperation and an entrainment task. We found that young children who showed more motor system involvement when observing others’ actions (as indicated by a relative reduction in beta power), showed better cooperation skills with peers. The explained variance was high, suggesting that interindividual differences in mirroring are relevant for interpersonal coordination with peers in early childhood.

The relation between motor system involvement during action observation and children’s peer coordination is consistent with previous findings that mirroring is related to more reliable imitation (Bernier et al., 2007; Filippi et al., 2016; Warreyn et al., 2013), better interpersonal coordination of finger movements (Naeem et al., 2012), and fewer turn-taking errors (Meyer et al., 2011). However, these previous studies measured neural mirroring and behavioral
performance during the same instance of social interaction (i.e. one laboratory task) and thus did not address whether this relation is task-specific or reflects interindividual differences that generalize to social interactions outside the specific task.

To capture various forms of peer interaction, we investigated two types of interpersonal coordination: goal-directed cooperation, and entrainment without an overt common goal. We found that neural mirroring was related to children’s performance in the cooperation task but not in the entrainment task. This is consistent with previous research that highlighted the importance of goals for action mirroring (Koski et al., 2002). Bekkering et al. (2009) argued that monitoring and predicting another person’s goal rather than their movements is important for interpersonal coordination because it often requires co-actors to perform different movements to achieve a common goal. In the current cooperation task also, children had to assume complementary roles that required monitoring of each other’s actions.

The observed link between neural mirroring and cooperation was evident for beta power (16–20 Hz). For mu power (7–12 Hz), however, no indication for such a relation was found. Previous research has shown that both mu and beta power are modulated during action observation, although they have been associated with slightly different functions (Caetano et al., 2007; Meyer et al., 2011; Quandt and Marshall, 2014; Schuch et al., 2010). Mu-band activity is suggested to be involved in translating sensory input into motor processes (Naeem et al., 2012; Pineda, 2005; Vanderwert et al., 2013), which matches with its more posterior localization over sensorimotor regions of the brain (Ritter et al., 2009). In contrast, the location of beta oscillatory activity is typically more anterior and it is associated with activity in the motor and premotor cortex (Ritter et al., 2009). It has been suggested that both mu- and beta-band oscillations are involved in action predictions (Southgate et al., 2009; Stapel et al., 2010), while beta-band activity is associated specifically with prediction updating and error monitoring (Arnal et al., 2011; Koelewijn et al., 2008). Exactly these processes – monitoring others’ actions and integrating information in order to update action predictions – are important during cooperation (Kourtis et al., 2013; Sebanz et al., 2006). Updating action predictions and monitoring were essential for the current peer cooperation task. Predicting which tube the partner would

![Fig. 4. Topographic distribution of normalized power in mu- (left) and beta-frequency bands (right) during action observation (top row) and abstract movement observation (bottom row). Warm colors represent higher normalized power (enhancement) for the condition as compared to the baseline and cooler colors represent lower power (suppression) for the condition as compared to the baseline.](image-url)
choose, monitoring the partner’s behavior to check whether the prediction was correct, and updating one’s predictions were necessary to succeed on the task. This might also explain why a relation between cooperation performance and oscillatory modulation was observed in the beta-band, as continuous prediction and updating of predictions are inherent to action observation (Falck-Ytter et al., 2006; Gredebäck and Melinder, 2010; Kilner et al., 2007). Still, the exact functional differences between mu- and beta-band oscillations and their respective roles during action observation have to be determined in future research.

For both mu- and beta-power, we observed that power values were higher during action observation than baseline indicating enhancement rather than suppression. At first sight, this is surprising since previous research suggests that suppression of mu- and beta-power indicate increased involvement of the motor system (Marshall and Meltzoff, 2011; Rizzolatti and Fogassi, 2014). However, several recent studies also found that power in these frequency bands is not significantly suppressed during action observation (Cannon et al., 2016; Nyström, 2008; Perry and Bentin, 2010) or even enhanced (Marshall et al., 2013). Although in our study the neural response showed an unexpected directionality with regard to baseline, we are confident that the mu- and beta-band activity reflects a response of the motor system for two reasons. First, the effect was relatively confined to electrode sites overlaying over motor areas (C3, C4), which suggests a modulation of the motor system. Second, children were asked to sit motionless and watch three repetitions of each action video on the screen before they were allowed to respond. Thus, children likely tried to actively inhibit an overt motor response during the action observation, and this was associated with an increase in beta-power (Gilbertson et al., 2005). Notably, this motor inhibition did not affect the direction of the relation we found. That is, less beta power with respect to baseline (indicating relatively more motor activity) was related to more success during peer cooperation. Although children thus likely suppressed their motor activity in general to sit as motionless as possible, interindividual differences with respect to how sensitive their motor system was to action observation were still related to their cooperation behavior. To test whether inhibition indeed plays a role, it is important to structurally investigate this in future studies by including a condition without any instruction in which children observe exactly the same actions.

Our results suggest that interindividual differences in neural mirroring are related to successful cooperation. Yet, the causal direction underlying this relation remains an open question. Better interpersonal coordination likely is the result of higher general levels of neural mirroring. Previous research has shown that neural mirroring supports prediction (e.g., Southgate et al., 2009; Stapel et al., 2010) and monitoring of others’ actions (Becchio et al., 2012; Bekkering et al., 2009) as we can use our own action system to predict the actions of a partner (Kilner et al., 2007). Enhanced prediction and monitoring, in turn, might help us prepare for and execute own actions accordingly (Kourtis et al., 2013; Sebanc et al., 2006). Based on this reasoning, individuals with higher levels of neural mirroring might be better at coordinating their actions with others. However, neural mirroring and cooperation might also be the result of a third factor, such as social motivation. Children differ in their motivation to be involved in social interactions (Brownell and Hazen, 1999), which could impact both their level of mirroring and their cooperation success. Neuroimaging studies in adults have shown a role of social motivation for mirroring as they found enhanced mirroring when participants were socially primed (Hogeveen and Obhi, 2012; Oberman et al., 2007), and enhanced mirroring for in-group members than for out-group members (Gutsell and Inzlitch, 2010; Molenberghs et al., 2013; Rauchbauer et al., 2015). Studies with adults also support the role of social motivation in interpersonal coordination: Adults with a prosocial orientation coordinated their actions better than adults with a pro-self orientation (Lundsen et al., 2012). Whether children’s neural mirroring is really at the base of their interpersonal coordination or whether both are the result of their social motivation has to be addressed in future research. Hereby, it would especially be informative to develop stimulus videos acted by children for children, as these videos would be more socially relevant for them.

The question arises to what extent interindividual differences in neural mirroring play a role in children’s social development. Friedelmeier (2009) suggested that adapting behavior might be an indicator of social competence. And Cirelli et al. (2014) and Kirshner and Tomasello (2010) found more helping behavior in children after they experienced smooth interpersonal coordination. This increased prosociality could be an indicator of likeability, thereby suggesting that higher levels of mirroring result in better peer relations via successful interpersonal coordination. However, a relation between interpersonal coordination and peer preference was not present in a recent longitudinal study we conducted (Endeldijk et al., submitted). On the other hand, the increased helping behavior as response to interpersonal coordination also could suggest that mirroring supports estimation of the needs of peers. Baimel et al. (2015) argued that coordinating interpersonally helps reasoning about others’ mind, thereby fostering perspective taking and empathic concern. Although the exact social consequences of peer coordination are unclear, these lines of reasoning suggest that interindividual differences in neural mirroring may have several implications for children’s social development.

In summary, our findings suggest that interindividual differences in the degree to which children mirror others’ actions (as indexed by relative beta-power decrease) are closely related to how well they coordinate their own actions during cooperation with peers. To our knowledge, these findings provide the first evidence that interindividual differences in motor activation during action observation are related to interpersonal coordination outside the specific mirroring task and thus successful social interaction.

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