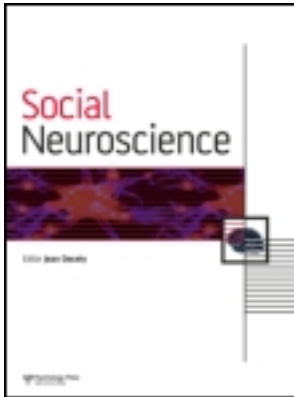


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Motor activation during observation of unusual versus ordinary actions in infancy

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Infants make predictions about actions they observe already during the first year of life. To investigate the role of the motor system in predicting the end state of observed actions, 12-month-old infants were shown movies of ordinary and extraordinary object-directed actions. The stimuli displayed a female actor who picked up an everyday object (a cup or a phone) and brought it to either her mouth or her ear. In this way, a similar movement could be ordinary (e.g., cup to mouth) or extraordinary (e.g., phone to mouth) depending on the object used. Infants' EEG and eye movements were recorded. We found a significantly stronger motor activation, indicated by a stronger desynchronization in the mu-frequency band over fronto-central areas, during observation of extraordinary compared to ordinary actions. This is explained within the computational framework of Kilner, Friston, and Frith (2007), who suggest that the motor system is used to generate predictions about actions we observe. If the observed action deviates from the initially expected path, additional predictions have to be generated, resulting in a stronger motor activation during perception of extraordinary actions. In sum, it appears that from early in life, the motor system is involved in making predictions about how an observed action will end.

Keywords: Infant; EEG; Action prediction; Motor system.

INTRODUCTION

From the first days of their life, infants watch their environment and the people acting in it. Recent research has demonstrated that infants form expectations and make predictions about others' actions. Looking time studies, for instance, show that infants tend to look longer at actions that end in an unexpected way (Phillips, Wellman, & Spelke, 2002; Reid, Csibra, Belsky, & Johnson, 2007; Woodward, 1998). Neuroimaging studies also suggest that infants respond differently to unexpected action endings (e.g., Reid et al., 2007, 2009). Moreover, infants as young as 6 months show predictive eye movements to the target area of actions they observe (Falck-Ytter, Gredebäck, & von Hofsten, 2006; Hunnius & Bekkering, 2010). However, which functional mechanisms

underlie infants' action predictions is still an open and intriguing question.

Infants take account of situational and contextual cues in their predictions of action goals. For instance, infants appear to have expectations about where an action should end based on the functional objects that are involved in the action. In a recent study of Hunnius and Bekkering (2010), infants between 6 and 16 months of age were presented with stimulus movies in which a person brought three everyday objects (a cup, a phone, and a hair brush) to either the normal target area associated with that object (a cup to the mouth, a phone to the ear, etc.) or to an extraordinary target area (e.g., a cup to the ear). Infants displayed more frequent predictive looks to the action target when the objects were brought to the ordinary target area. Thus, already early in life infants form expectations about

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the course of an action on the basis of their knowledge about the involved objects.

How do infants come to predict the goal of an action on the basis of the different cues they perceive? Previous research has shown that both in adults (e.g., Borroni, Montagna, Cerri, & Baldissera, 2005; Cochin, Barthelemy, Roux, & Martineau, 1999; Hari et al., 1998) as well as in infants (Southgate, Johnson, Osborne, & Csibra, 2009) the motor system becomes active not only during the execution but also during the perception of actions (a phenomenon called *motor resonance*). Moreover, a large body of literature suggests that the motor system may be crucial in the prediction of action goals during both action observation and execution (see, e.g., Csibra, 2007; Kilner et al., 2007; Prinz, 2006; Wolpert & Flanagan, 2001). For actions to be executed smoothly, we need to make predictions and cannot rely solely on feedback from the sensory system as this would simply be too slow. Therefore, the motor system is thought to function through forward and inverse models (Wolpert, Miall, & Kawato, 1998). These models, which predict the course of an action, need to integrate information about the environment, such as objects that are acted upon. The same models that enable action execution to run smoothly can be used to generate predictions about actions we observe. Previous electroencephalography (EEG) studies indicate that the motor system is involved in a predictive manner during action observation, as motor-related EEG components appear to be modulated ahead of time (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004; Southgate et al., 2009). Kilner et al. (2007) proposed a computational model of how the mirror neuron system (MNS) can generate predictions of which goal is driving an observed action. The model, which functions as a Bayesian network, strives to minimize the error between the predicted action path and the observed action path. The predictions about what an action should look like given an assumed goal are thought to be generated by the motor system. During action observation, the MNS continuously checks whether the goal ascribed to the action still matches what is being observed. In the case where an unusual or unexpected action is observed, there is an initial mismatch between the observed and the predicted action, and subsequently new predictions need to be generated. This is thought to result in stronger motor activation. In sum, the model implies stronger motor activation during observation of actions that are hard to understand, or that unfold differently than assumed beforehand.

Motor activation can be measured with several neuroimaging methods. One of the most frequently used neuroimaging methods for studying the infant

brain is EEG because of its noninvasiveness and because it imposes only minimal restrictions on the normal behavior of the infant. In the EEG, motor activation becomes apparent as a desynchronization in the mu-frequency band. Oscillations in the mu-frequency band are thought to originate from sensorimotor cortex and are found maximal over central and precentral sites (Pineda, 2005). Desynchronization in the mu-frequency band overlying central sites has been demonstrated during action observation both in adults (e.g., Gastaut & Bert, 1954; Muthukumaraswamy, Johnson, & McNair, 2004) and in infants (Southgate et al., 2009; van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008) and appears to be stronger for object-directed actions than for actions without objects (Muthukumaraswamy et al., 2004; Southgate, Johnson, Karoui, & Csibra, 2010). Moreover, mu-desynchronization has been shown to be stronger if the observed action is well established in the infant's motor repertoire (van Elk et al., 2008).

It was the aim of this study to investigate whether the motor system is differentially activated during infants' perception of ordinary and extraordinary actions. Twelve-month-old infants were repeatedly presented with stimulus movies displaying ordinary or extraordinary actions (e.g., an actor bringing a cup or a phone either to her mouth or to her ear). Infants' EEG was measured and concurrently, their eye movements were registered to investigate overt action predictions. By measuring motor activation in response to action observation, as reflected in desynchronization in the mu-frequency band of the EEG, we aimed to test the following hypothesis. If motor system activation reflects the discrepancy between the initial prediction of the action on the basis of previous knowledge and the actual observed action, we hypothesize that stronger motor activation would occur for observation of extraordinary compared to ordinary actions. That is, based on previously acquired object knowledge infants have expectations about the course and target of the observed actions (Hunnus & Bekkering, 2010). In a case where the observed action does not match the infant's expectations, new predictions have to be generated, thereby resulting in a stronger motor activation.

METHOD

Participants

In total, 36 12-month-old infants participated in the study. Measuring EEG and eye movements in 12-month-olds in parallel turned out to be difficult.

Twelve infants contributed sufficient artifact-free EEG trials to be included in the EEG analyses. The mean age of this group was 12 months and 5 days ($SD = 10$ days), and the group comprised 8 girls. For 11 infants, sufficient eye movement data were collected during the experiment (i.e., gaze information present for more than 50% of the testing time). This concerned 7 girls, and the mean age of this group was 12 months and 5 days ($SD = 11$ days). Seven infants contributed both eye movement data and EEG data.

Procedure

Infants were tested in an action observation setting. During stimulus presentation, their EEG and their eye movements were recorded with a Tobii eye-tracking system (Tobii 1750, Tobii Technology, Danderyd, Sweden). The child was seated in a regular car seat at approximately 60 cm distance from the computer screen. Before testing, the eye-tracker was calibrated using the Clearview software (Tobii Technology). A nine-point calibration procedure was used in which at every position of a screen-wide 3×3 grid expanding–contracting circles appeared on a black background. To draw the infants' attention to the calibration stimuli, the circles were presented together with a sound. If seven or more points were calibrated successfully, the experiment was started. Otherwise the calibration procedure was repeated for the missing calibration points in the grid.

Two movement tilt sensors (CW60A/30; Comus Group of Companies, Tongeren, Belgium) were attached to the infant's arm and leg to record limb movements during the experiment. Trials during which the infant moved were excluded from the EEG analysis, as body movements would confound the data. The experiment was conducted using a custom-made stimulus presentation and data registration program implemented in Presentation 12.1 (Neurobehavioral Systems, Albany, CA, USA). In addition, the test sessions were video-recorded and coded offline to exclude trials during which the infant did not attend the screen (offline coding was necessary when eye gaze was not captured by the eye-tracker), and when the child was moving (offline coding was necessary when infants had removed the movement sensors).

Stimulus material

Infants watched movies of approximately 6 s in which a female actor who was sitting at a table grasped an object with her right hand and brought it either to her mouth or to her ear. The objects were a cup and a

phone. These are both common everyday objects with distinct target areas (mouth, ear). In the Ordinary action condition, the phone was brought to the ear and the cup to the mouth (see Figure 1a for an example), whereas in the Extraordinary action condition the phone was brought to the mouth and the cup to the ear (see Figure 1b). The actor's looking behavior was kept constant between the conditions, and she never looked straight into the camera. All stimulus movies had a similar time course: First, the actor was looking at the object in front of her without any movement for about 1 s; then the actor grasped the object, lifted it and brought it either to her mouth or ear. When the object reached its target area, the actor held the object in this end state for approximately 1 s. The movement path of the grasping and lifting was similar in all conditions, and only after the object reached approximately the height of the actor's head did the paths diverge, depending on the end location. For each of the four conditions, six different movies were created with small variations to keep the infant interested (6 different phones and 6 different cups). Each movie was presented 5 times, and the stimuli were presented in blocks of 10 movies of the same condition. An advantage of presenting ordinary and extraordinary actions in different blocks is that it enhances semantic processing in contrast to random presentation, which is thought to evoke processing via a more automatic visuo-motor route (Tessari, Canessa, Ukmar, & Rumiati, 2007; Tessari & Rumiati, 2004). Within blocks, the order of the trials was randomized. All stimulus material was recorded with two female actors. The infants always watched one actor displaying the ordinary actions and the other one displaying the extraordinary actions. This contingency in the stimulus presentation was intended to give the infants' predictive system a maximal chance to work, as predictions of action end states are always based on a combination of the action itself and contextual information (van Rooij, Haselager, & Bekkering, 2008). Which actor displayed the correct actions was counterbalanced between participants.

The visual angle of the movies was 21.7° in the vertical direction and 21.5° in the horizontal direction. The angles of the movements were approximately 14° (vertical) and 12° (horizontal).

Eye-tracking

To register eye movements, an infrared eye-tracking system which was integrated in a 17-inch computer screen was used. The eye-tracker recorded the infants' gaze data continuously with a sampling rate of 50 Hz.



Figure 1. Example stimuli used in the experiment. (A) Snapshots taken from a stimulus used in the Ordinary \times Mouth condition. (B) Snapshots taken from a stimulus used in the Extraordinary \times Ear condition.

Analysis of the eye movement data

The amount of eye movement data per infant was considered to be sufficient for analysis if gaze data were available for at least half of the testing time. As the eye-tracking system is sensitive to head movements, for some babies eye data was gathered during only a part of the experiment. On average, 15 to 18 trials could be included per condition and participant.

A visual anticipation was defined as a fixation in the target area of the action before the object reached this area. The coordinates of the mouth and ear target areas (areas of interest, AoIs) were defined for each individual stimulus movie. The size and dimensions of these rectangular target areas were identical for each condition (see Figure 2). For each stimulus movie, the lifting phase was identified during which the object was lifted from the table towards the target area. The end of the lifting phase was defined as the last frame before the object entered the mouth area. For each trial, it was determined whether the infant was attending to the actor and the action during the lifting phase. Then, whether the proportion of the trials during which the infant showed an anticipatory fixation was different for Ordinary vs. Extraordinary

stimulus movies was determined. A custom-made software tool (GSA, Donders Institute, Nijmegen, The Netherlands) was used to process the eye movement

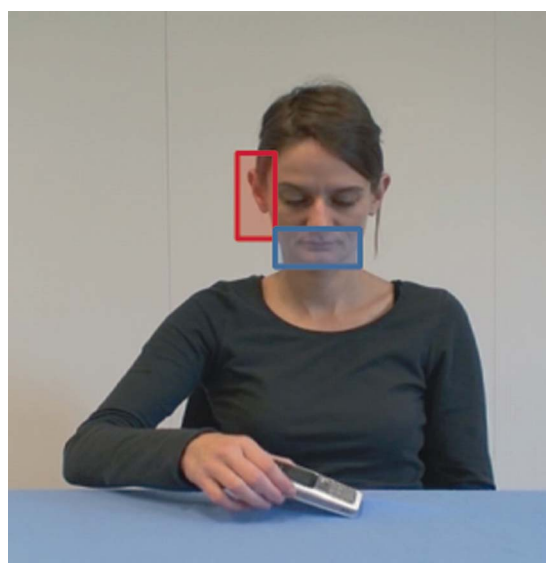


Figure 2. Areas of interest for the eye movement analysis. The blue rectangle depicts the mouth area used for the analysis of the anticipatory looks; the red rectangle depicts the ear area.

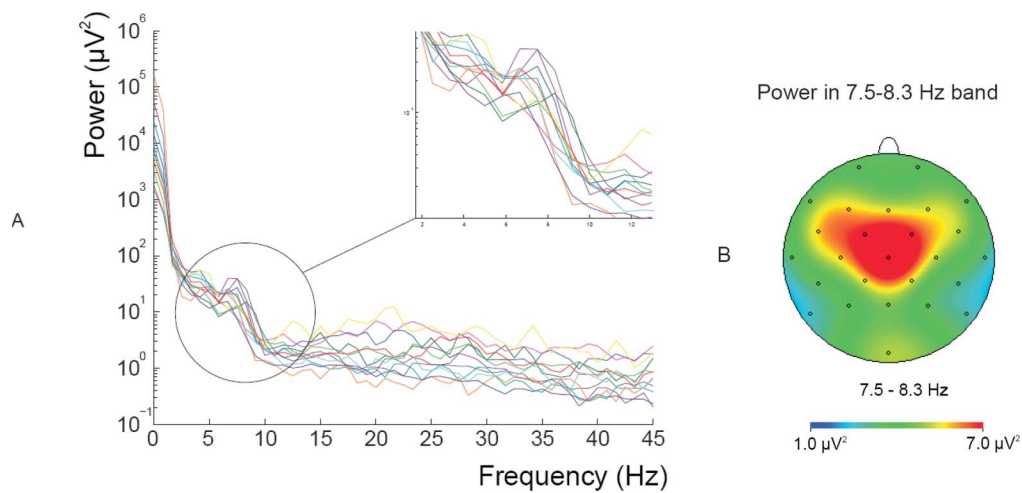


Figure 3. (A) Powerspectra of individual infants averaged over conditions and over the central electrodes. (B) Topoplot displaying the power in the frequency band from 7.5 to 8.3 Hz averaged over all conditions.

data and define whether and when fixations were in the AoIs. To test for differences in *frequency of anticipatory looks* between Ordinary and Extraordinary actions, a 2×2 repeated-measures analysis of variance (ANOVA) was conducted, with Target area as a second independent factor. Due to the limited overall number of visual anticipations, *latencies of anticipatory looks* could only be analyzed with the data collapsed over the two Target area conditions. The latency of the eye movements was defined as the difference between arrival of the eye gaze at the AoI and the object reaching the area of interest. A paired-samples *t*-test was used to test for differences in the latencies of anticipatory looks between the Ordinary and the Extraordinary action conditions.

Electrophysiological recording

EEG was recorded using a BrainCap with 30 Ag/AgCl electrodes (EasyCap, Herrsching, Germany) with a layout following the 10/20 system. All electrodes were referenced online to the left mastoid and re-referenced offline to the linked mastoids. A Brain-Amp AC amplifier using a bandpass filter of 0.1–80 Hz was used to record the EEG signal at a sampling rate of 500 Hz. The data were analyzed with Brain Vision Analyzer (Brain Products, Gilching, Germany).

Analysis of the EEG data

Artifact rejection was done manually on EEG segments that started with the lifting of the object and ended after 1200 ms. This interval was based on the

average duration of the lifting phase and corresponded to the time window of the eye-movement analyses.¹

Infants were included in the EEG analyses if their EEG data set contained at least 9 trials per condition that met the following criteria: (1) attention to the stimulus (based on eye-movement data, or, if missing, on the video recording of the test session), (2) no limb movements, (3) no EEG artifacts (such as eye blinks, electrode drifts, or broadband noise). Over each trial, fast Fourier transformations (FFTs) were conducted with the maximal spectral resolution (.833 Hz) over the 1200 ms interval. For each infant, the peak in the power of the mu-frequency band was identified by averaging the power over conditions and over the central electrodes (FC1, FC2, FC5, FC6, C3, Cz, C4, CP1, CP2, CP5, CP6) and plotting the log of the power against the frequency axis (see Figure 3a). Infants showed clear peaks in the lower frequency bands, whereas in the higher frequency bands large individual differences were observed. Closer inspection of the region where the mu-frequency band could be expected (see Figure 3a) revealed that eight of the twelve participants showed a peak at the central electrode sites around 7.5 or 8.3 Hz. This is in line with previous research, which shows that the power in the mu-frequency band peaks around 8 Hz at the age of 12 months or somewhat

¹ In the eye movements analyses, the exact time frame could be used from the start of the lifting movement to the last frame before the object entered the AoI. This resulted in small differences in window of analysis for each stimulus. For the EEG analyses, fixed time-windows were used instead, because frequency analysis requires fixed-length intervals.

Extraordinary - Ordinary action

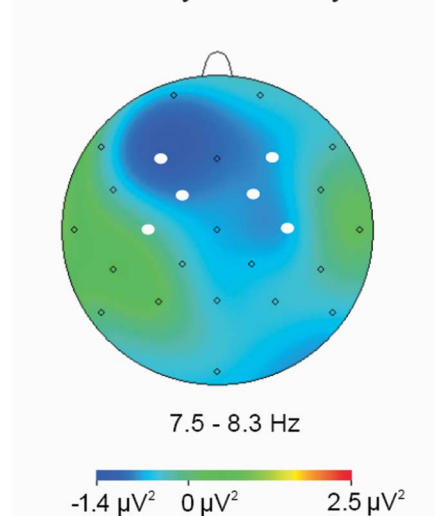


Figure 4. Topoplot displaying the difference in power between the Extraordinary and the Ordinary action conditions in the frequency band from 7.5 to 8.3 Hz. The white dots indicate the electrodes that were included in the analysis.

below this frequency (cf. Marshall, Bar-Haim, & Fox, 2002; Stroganova, Orekhova, & Posikera, 1999).

To further substantiate the origin of the observed peaks in the spectra, the topographical distribution of the average activity in the mu-frequency band was also plotted (see Figure 3b). This illustrates that the peak of the mu-frequency band showed a broad scalp-distribution, and was most prominent at fronto-central electrode sites.

Due to the relatively small number of artifact-free trials, data were collapsed over the Target area conditions for the analysis of the experimental manipulation. Grand averages of the FFTs were calculated for both the Ordinary and Extraordinary conditions. The difference between the grand averages of the two conditions was plotted (see Figure 4). Electrodes of interest, overlying fronto-central sites, were analyzed in a repeated-measures ANOVA with Action Type (Ordinary and Extraordinary) as within-subjects factor.

RESULTS

Visual anticipations to the target areas

First, it was investigated whether infants showed anticipatory looks to the target area of the actions they observed and whether the frequency of anticipatory looks differed between ordinary and extraordinary action movies. The mean percentage of visual antici-

pations to the mouth was 27.2 % ($SD = 9.1$) in the Ordinary Mouth condition and 27.2% ($SD = 21.2$) in the Extraordinary Mouth condition (see Figure 5a). Anticipations to the ear occurred less frequently (see Figure 5b). For the Ordinary Ear condition, anticipatory looks towards the ear were observed in 2.0% ($SD = 6.2$) of the attended trials; for the Extraordinary Ear condition, visual anticipations towards the ear were observed on average in 4.1% of the cases ($SD = 3.7$). A 2×2 repeated-measures ANOVA was conducted on trials in which the infant attended to the action, with Action Type (Ordinary vs. Extraordinary action) and Target area (Mouth vs. Ear) as independent factors and as dependent variable the frequency of anticipation. The analysis yielded a main effect of Target area, with more frequent anticipations to the mouth compared to the ear, $F(1, 10) = 59, p < .001$, Greenhouse-Geisser corrected). No other significant effects were found.

When comparing the latencies of anticipatory eye movements, infants showed no difference between the Ordinary ($M = -117$ ms; $SD = 300$) compared to the Extraordinary ($M = -140$ ms; $SD = 309$) action condition, $t(10) = 25, p = 0.8$.

Mu-suppression in the EEG signal during action observation

It was the aim of this study to examine whether the EEG signal in the mu-frequency range was more strongly suppressed during observation of ordinary actions compared to extraordinary actions. Therefore, the grand average FFT of the Ordinary action condition was subtracted from the grand average FFT of the Extraordinary action condition. For the frequencies of interest (7.5 to 8.3 Hz), infants showed a stronger desynchronization in the Extraordinary action condition compared to the Ordinary action condition and this effect was most pronounced over fronto-central sites (see Figure 4). The power in the mu-frequency band measured at these fronto-central electrodes was used as a dependent variable in a repeated-measures ANOVA with Action type (Ordinary vs. Extraordinary action), Hemisphere (Left vs. Right), and Front-to-Back (F3–F4, FC1–FC2, C3–C4) as within-subjects factors. A main effect of Action type was found, $F(1, 11) = 5.9, p = .04$, Greenhouse-Geisser corrected, with lower power in the Extraordinary action condition ($M = 5.4 \mu V^2$; $SD = 2.9$) compared to the Ordinary action condition ($M = 6.3 \mu V^2$; $SD = 3.7$). No other main effects were found. Moreover, there were no significant interactions, which suggests that the effect was evenly distributed over both hemispheres.



Figure 5. Frequency of visual anticipations. (A) The percentage of anticipatory looks to the mouth in the stimuli with the target area Mouth for Ordinary (left line) and Extraordinary actions (right line). (B) The percentage of anticipatory looks to the ear in the stimuli with the target area Ear for Ordinary (left line) and Extraordinary actions (right line).

DISCUSSION

This study investigated how infants perceive ordinary and extraordinary actions and examined the role of motor activation during the processing of these actions. Infants observed object-directed actions: A cup and a phone were brought either to the ordinary target location (cup to mouth; phone to ear) or to an unusual target location (cup to ear; phone to mouth). Infants showed stronger motor activation during the observation of extraordinary compared to ordinary actions, as reflected in a stronger desynchronization of the mu-frequency band of their EEG. These results suggest that the infants' motor system is involved in processing observed actions, but more importantly, their motor system seems to respond differently for ordinary and extraordinary actions.

When watching the stimulus movies, the infants in our study showed visual anticipations to the target area of the ongoing action. This is in line with the findings of Hunnius and Bekkering (2010), who found that infants from 6 months of age on display predictive looks to the target area of actions they observe. In their study, ordinary actions led to more frequent anticipatory looks than extraordinary actions. In the current study, however, no significant difference was found in the frequency of anticipatory looks. Infants showed predictive looks about as frequently for the ordinary as the extraordinary actions, which might be due to the fact that they learned about the unfamiliar object–target associations as a consequence of the large number of stimulus repetitions. Indications of learning effects had been present in the original study of Hunnius and Bekkering (2010), but less pronounced. In the current study, learning might have had a stronger effect, as EEG experiments

require far more trials than eye-movement studies. In this EEG experiment, infants were presented with up to 30 repetitions of each action compared to a maximum of 9 in the eye-tracking study of Hunnius and Bekkering (2010).

The current study was designed to study the neural correlates that distinguish ordinary actions from extraordinary actions. As mentioned before, desynchronization in the mu-frequency band reflects motor activation (Gastaut & Bert, 1954; Muthukumaraswamy et al., 2004). Though in the current study the mu-frequency desynchronization during action observation appeared rather frontal, similar scalp-distributions of motor related effects have been found before (see, e.g., van Elk, van Schie, Zwaan & Bekkering, 2010; Pfurtscheller, Brunner, Schlögl, & Lopes da Silva, 2006; displaying individual variation in topoplots in mu-frequency desynchronization). Furthermore, in our study, the power in the mu-frequency band averaged over all conditions was found maximal at fronto-central sites.

When comparing brain responses to extraordinary actions and ordinary actions, we found a stronger desynchronization in the mu-frequency band during perception of extraordinary actions. The finding that infants respond differently for actions with uncommon end states is in line with the literature. Infants appear to have expectations about the end state of other people's actions at early ages. For instance, when confronted with an action end state which deviates from the usual pattern, infants display longer looking times (see e.g., Phillips et al., 2002; Reid et al., 2007; Woodward, 1998). Furthermore, as previously mentioned, infants have been shown to visually anticipate to the target area of observed actions (Falck-Ytter et al., 2003; Hunnius & Bekkering,

2010). In addition to this behavioral evidence, a number of developmental neuroimaging studies show findings in line with our results that infants have expectations about how actions they observe should end. Reid and colleagues (2009), for instance, showed that 9-month-old infants differentiate between ordinary and extraordinary action end states. Infants displayed an N-400-like pattern when observing an extraordinary action end state, which indicates that their expectations as to how the action would end were violated. Moreover, infants appeared to notice if an action was stopped before its goal had been reached, as indicated by more gamma-activity over left frontal regions during observation of incomplete actions (Reid et al., 2007).

Previous research has thus demonstrated that infants make predictions about end states of actions they observe. However, which processes underlie these predictions has not been established to date. The present study is in line with the notion that the motor system might play a role in action prediction (see e.g., Kilner et al., 2007; Prinz, 2006; Wolpert & Flanagan, 2001; Schütz-Bosbach, & Prinz, 2007). According to the prospective coding framework (Kilner et al., 2007), actions that develop differently than expected beforehand should elicit stronger motor activation, because the predictions need to be updated to match the predicted visual scene with the actual visual input. Our results are compatible with this framework, as the infants showed stronger motor activation during observation of extraordinary actions compared to ordinary actions. Moreover, the difference in motor activation occurred during the lifting movement of the object, so while the action was still unfolding. The timing of this effect corresponds with the time-window in which one would expect the motor system to be at work to generate predictions about how the action will develop and how it will end. Importantly, the effects in the mu-frequency band cannot be attributed to differences in overt eye movements, because no quantitative differences were found between the visual anticipations in the two conditions.

Consistent with our findings, recent empirical research with adults has shown that the observation of actions that deviate from what participants would normally have expected is associated with stronger motor resonance. Koelewijn and colleagues, for instance, found a stronger desynchronization in the beta-frequency band originating from motor areas while participants were watching actions that were clearly mistakes compared to correct actions (Koelewijn, van Schie, Bekkering, Oostenveld, & Jensen, 2008). This modulation of the beta-band might reflect a stronger motor activation in response to deviant

action stimuli. Also, Manthey, Schubotz, and von Cramon (2003) describe a stronger motor activation when participants were watching movements that differed from what one would expect *a priori* (e.g., unlocking a bicycle lock with the key held transverse to the lock). Similarly, a recent fMRI study using pictures of extraordinary compared to ordinary action end states demonstrated a stronger activation of the inferior frontal gyrus (IFG), which is part of the frontal parietal motor network (de Lange, Spronk, Willems, Toni, & Bekkering, 2008). Comparable results come from neuroimaging studies that investigated neuronal responses to action language. In adults, processing of sentences and action pictures describing unfamiliar action scenarios is associated with stronger motor activation compared to sentences and action pictures of familiar action scenarios (Beilock, Lyons, Mattarella-Micke, Nusbaum, & Small, 2008 [fMRI, sensorimotor areas]; van Elk et al., 2010 [mu-frequency effect, fronto-central sites]). In sum, these studies provide converging evidence that in adults, motor resonance tends to be stronger for the perception of unusual actions.

Although motor processes are thought to play an important role in human action prediction, there are of course other ways to predict action end states (Rizzolatti & Sinigaglia, 2010; de Lange et al., 2008). In the infant domain, two more mechanisms have been suggested to support action understanding and action prediction (for an overview, see Csibra & Gergely, 2007). First, it has been put forward that young infants evaluate actions they observe on the basis of abstract cognitive principles of rationality (Gergely & Csibra, 2003). Following this account, infants infer action goals on the basis of the observed action path and the situational constraints. Second, infants might learn about others' actions and intentions through repeated observation of actions, as they couple actions to their effects (Elsner & Aschersleben, 2003). These three mechanisms—rationality, action–effect associations, and motor activation—are likely to complement and support each other. Also in the current study, infants might have formed action–effect associations that helped them to make predictions about the course of the actions they observed. The stimulus presentation we used supported the formation of such associations, as for instance the different action types (ordinary vs. extraordinary) were carried out by different actors and as a blocked design was used with 10 repetitions of the same action type in a row. This experimental design provided the infants with a maximal chance to make correct predictions of the action end state for both ordinary and extraordinary actions. Although the design allowed the infants to acquire action–effect

associations, this cannot account for the difference we found between ordinary and extraordinary actions. That is, learning opportunities for action–effect associations were comparable for ordinary and extraordinary action conditions (i.e., one actor performed ordinary actions; another actor always extraordinary actions), but still, a stronger activation of motor-related brain areas was found for extraordinary compared to ordinary actions. This motor activation might be a reflection of the predictions generated by the motor system. Extraordinary actions required additional predictions to be generated to infer the action end state, resulting in a stronger motor activation during perception of extraordinary actions. Our data thus suggest that the motor system is involved in action prediction and making sense of others' actions from early on, and might be even more fundamental for cognition than previously thought.

REFERENCES

- Beilock, S. L., Lyons, I. M., Mattarella-Micke, A., Nusbaum, H. C., & Small, S. L. (2008). Sports experience changes the neural processing of action language. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 13269–13273.
- Borroni, P., Montagna, M., Cerri, G., & Baldissera, F. (2005). Cyclic time course of motor excitability modulation during the observation of a cyclic hand movement. *Brain Research*, *1065*, 115–124.
- Cochin, S., Barthelemy, C., Roux, S., & Martineau, J. (1999). Observation and execution of movement: Similarities demonstrated by quantified electroencephalography. *European Journal of Neuroscience*, *11*, 1839–1842.
- Csibra, G. (2007). Action mirroring and action understanding: An alternative account. In P. Haggard et al. (eds). *Sensorimotor foundations of higher cognition: Attention and performance, XXII*. Oxford, UK: Oxford University Press.
- Csibra, G., & Gergely, G. (2007). 'Obsessed with goals': Functions and mechanisms of teleological interpretation of actions in humans. *Acta Psychologica*, *124*, 60–78.
- de Lange, F. P., Spronk, M., Willems, R. M., Toni, I., & Bekkering, H. (2008). Complementary systems for understanding action intentions. *Current Biology*, *18*, 454–457.
- Elsner, B., & Aschersleben, G. (2003). Do I get what you get? Learning about the effects of self-performed and observed actions in infancy. *Consciousness & Cognition*, *12*, 732–751.
- Falck-Ytter, T., Gredebäck, G., & von Hofsten, C. (2006). Infants predict other people's action goals. *Nature Neuroscience*, *9*, 878–879.
- Gastaut, H. J., & Bert, J. (1954). EEG changes during cinematographic presentation; moving picture activation of the EEG. *Electroencephalography and Clinical Neurophysiology*, *6*, 433–444.
- Gergely, G., & Csibra, G. (2003). Teleological reasoning in infancy: The naïve theory of rational action. *Trends in Cognitive Sciences*, *7*, 287–292.
- Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., & Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: A neuromagnetic study. *Proceedings of the National Academy of Sciences of the United States of America*, *95*, 15061–15065.
- Hunnus, S., & Bekkering, H. (2010). The early development of object knowledge: A study of infants' visual anticipations during action observation. *Developmental Psychology*, *46*, 446–454.
- Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: An account of the mirror neuron system. *Cognitive Processing*, *8*, 159–166.
- Kilner, J. M., Vargas, C., Duval, S., Blakemore, S.-J., & Sirigu, A. (2004). Motor activation prior to observation of a predicted movement. *Nature Neuroscience*, *7*, 1299–1301.
- Koelewijn, T., van Schie, H. T., Bekkering, H., Oostenveld, R., & Jensen, O. (2008). Motor-cortical beta oscillations are modulated by correctness of observed action. *NeuroImage*, *40*, 767–775.
- Manthey, S., Schubotz, R. I., & von Cramon, D. Y. (2003). Premotor cortex in observing erroneous action: An fMRI study. *Cognitive Brain Research*, *15*, 296–307.
- Marshall, P. J., Bar-Haim, Y., & Fox, N. A. (2002). Development of the EEG from 5 months to 4 years of age. *Clinical Neurophysiology*, *113*, 1199–1208.
- Muthukumaraswamy, S. D., Johnson, B. W., & McNair, N. A. (2004). Mu rhythm modulation during observation of an object-directed grasp. *Cognitive Brain Research*, *19*, 195–201.
- Pfurtscheller, G., Brunner, C., Schlögl, A., & Lopes da Silva, F. H. (2006). Mu rhythm (de)synchronization and EEG single-trial classification of different motor imagery tasks. *NeuroImage*, *31*, 153–159.
- Phillips, A. T., Wellman, H. M., & Spelke, E. S. (2002). Infants' ability to connect gaze and emotional expression to intentional action. *Cognition*, *85*, 53–78.
- Pineda, J. A. (2005). The functional significance of mu rhythms: Translating "seeing" and "hearing" into "doing". *Brain Research Reviews*, *50*, 57–68.
- Prinz, W. (2006). What re-enactment earns us. *Cortex*, *42*, 515–517.
- Reid, V. M., Csibra, G., Belsky, J., & Johnson, M. H. (2007). Neural correlates of the perception of goal-directed action in infants. *Acta Psychologica*, *124*, 129–138.
- Reid, V. M., Hoehl, S., Griutsch, M., Groendahl, A., Parise, E., & Striano, T. (2009). The neural correlates of infant and adult goal prediction: Evidence for semantic processing systems. *Developmental Psychology*, *45*, 620–629.
- Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nature Reviews Neuroscience*, *11*, 264–274.
- Schütz-Bosbach, S., & Prinz, W. (2007). Prospective coding in event representation. *Cognitive Processing*, *8*, 93–102.
- Southgate, V., Johnson, M. H., Karoui, I. E., & Csibra, G. (2010). Motor system activation reveals infants' on-line prediction of others' goals. *Psychological Science*, *21*, 355–359.
- Southgate, V., Johnson, M. H., Osborne, T., & Csibra, G. (2009). Predictive motor activation during action observation in human infants. *Biology Letters*, *5*, 769–772.

- Stroganova, T. A., Orekhova, E. V., & Posikera, I. N. (1999). EEG alpha rhythm in infants. *Clinical Neurophysiology, 110*, 997–1012.
- Tessari, A., Canessa, N., Ukmar, M., Rumiati, R. I. (2007). Neuropsychological evidence for a strategic control of multiple routes in imitation. *Brain, 130*, 1111–1126.
- Tessari, A., & Rumiati, R. I. (2004). The strategic control of multiple routes in imitation of actions. *Journal of Experimental Psychology: Human Perception and Performance, 30*, 1107–1116.
- van Elk, M., van Schie, H. T., Hunnius, S., Vesper, C., & Bekkering, H. (2008). You'll never crawl alone: Neurophysiological evidence for experience-dependent motor resonance in infancy. *NeuroImage, 43*, 808–814.
- van Elk, M., van Schie, H. T., Zwaan, R. A., & Bekkering, H. (2010). The functional role of motor activation in language processing: Motor cortical oscillations support lexical–semantic retrieval. *NeuroImage, 50*, 665–677.
- van Rooij, I., Haselager, W., & Bekkering, H. (2008). Goals are not implied by actions, but inferred from actions and contexts. *Behavioral and Brain Sciences, 31*, 38–39.
- Wolpert, D. M., & Flanagan, J. R. (2001). Motor prediction. *Current Biology, 11*, 729–732.
- Wolpert, D. M., Miall, R. C., & Kawato, M. (1998). Internal models in the cerebellum. *Trends in Cognitive Sciences, 2*, 338–347.
- Woodward, A. L. (1998). Infants selectively encode the goal object of an actor's reach. *Cognition, 69*, 1–34.