

Neural correlates of action perception at the onset of functional grasping

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Event-related potentials were recorded while infants observe congruent or incongruent grasping actions at the age when organized grasping first emerges (4–6 months of age). We demonstrate that the event-related potential component P400 encodes the congruency of power grasps at the age of 6 months (Experiment 1) and in 5-month-old infants that have developed the ability to use power grasps (Experiment 2). This effect does not extend to precision grasps, which infants cannot perform (Experiment 3). Our findings suggest that infants’ encoding of the relationship between an object and a grasping hand (the action–perception link) is highly specialized to actions and manual configurations of actions that infants are able to perform.

Keywords: grasping; experience; infant; P400; event-related potential

The ability to grasp for objects and encode other people’s goal-directed actions are important skills that allow infants to interact with their environment. Both skills start to develop directly after birth and become functional around 6 months of age. Already at birth, infants’ actions have a rudimentary organization; they keep their arms in sight and extend them towards salient objects (van der Meer *et al.*, 1995). Those early grasping actions, although important for the developmental course, are not sufficiently organized to allow object manipulation (von Hofsten, 1982). It takes another 4–6 months before infants are able to produce functional grasping with detailed prospective planning, smooth trajectories, and appropriate pre-adjustment of fingers (von Hofsten, 1980). Action understanding, which is another important skill that allows for interaction with the surrounding world, develops in a similar manner. An elementary form of action understanding is observed in newborns, as they prefer to look at goal-directed, rather than non-goal-directed, reaching actions (Craigheo *et al.*, 2011). At 6 months of age, in addition to preferring to look at goal-directed actions, infants also specifically encode and predict the goal of other people’s reaching actions (Woodward, 1998; 2009; Kochukhova and Gredebäck, 2010; Kanakogi and Itakura, 2011). Furthermore, 6-month-olds are able to formulate expectations about the location and size of other people’s action goals based on the direction and aperture size of the perceived grasping hand (Daum *et al.*, 2008, 2009; Daum and Gredebäck, 2011).

Several studies documented that action understanding develops in synergy with the infant’s own ability to perform similar actions (Sommerville and Woodward, 2005; Daum *et al.*, 2011; Kanakogi and Itakura, 2011; Cannon *et al.*, 2012). The connection between grasping ability and anticipation of grasping actions has been demonstrated in 4- to 12-month-old infants and adults (Kanakogi and Itakura, 2011; Melzer *et al.*, 2012). The link between own perception and performance of the same action is not restricted to grasping but has been reported with respect to the perception of means-end actions (Sommerville and Woodward, 2005), displacement actions (Melzer *et al.*, 2012), pointing (Behne *et al.*, 2011) and other actions such as

feeding (Gredebäck and Melinder, 2010) and solving puzzles (Gredebäck and Kochukhova, 2010). Together, these findings support the notion that infants’ own proficiency in producing an action is important for their ability to perceive other people’s actions as goal-directed (here referred to as the action–perception link).

The almost simultaneous emergence of grasping production and perception is particularly meaningful in light of recent neuroscientific research. The link between action production and perception has been related to the mirror neuron system (MNS), a neural network located on the pre-motor cortex of both humans (Mukamel *et al.*, 2010) and macaque monkeys (Rizzolatti *et al.*, 1996). It becomes active during the execution of an action, as well as during the observation of the same action performed by another (Rizzolatti and Craighero, 2004). The MNS hypothesis of action perception suggests that an observed action is mapped onto the observer’s own motor representation of that action, facilitating action perception and the prediction of action goals (Gallese, 2009).

From a developmental perspective, MNS activity has been indexed using the mu frequency band, a frequency signature of motor cortex activity in adults (Pineda, 2005) and infants. In the latter case, attenuation of the electroencephalogram (EEG) signal in the mu-rhythm band has been shown in both 6-month-olds (Nyström, 2008) and 8-month-olds (Nyström *et al.*, 2010) during the observation of goal-directed reaching actions. Other studies have demonstrated a direct connection between mu activity during the perception and production of reaching actions (Southgate *et al.*, 2010) and between crawling proficiency and neural activity during the observation of another’s crawling (van Elk *et al.*, 2008).

In sum, the neurophysiological and behavioural investigations described above indicate that infants’ ability to produce an action and the ability to perceive the goal of the same action are closely linked in development. However, the neural processes that guide this link remain incompletely understood. In this study, we performed three experiments to investigate 4- to 6-month-old infants’ event-related potentials (ERPs) during the observation of grasping actions. The mu rhythm signal becomes clearly measurable from the age of 6–8 months (Strogonova *et al.*, 1999; Marshall *et al.*, 2002), rendering ERP components a more robust way to categorize neural correlates of action perception in younger infants. The ERP component that we aim to investigate is the posterior temporal P400. The infant P400 ERP is mainly known to index socially relevant stimuli. It has been

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reported to indicate the congruency of pointing hands and object locations (Gredebäck et al., 2010) with higher amplitudes for congruent vs incongruent pointing. A similar effect has been found in the study by Senju et al. (2006) where the P400 was modulated by gaze direction in relation to previously presented object (gaze directed towards or averted from the object) and expressed in amplitude difference between the conditions. Another socially relevant stimuli that influences deflection of the P400 are faces (de Haan et al., 2002) and facial emotional expressions with more positive amplitudes to angry compared with fearful facial expressions (Hoehl and Striano, 2008) and fearful when compared with happy or neutral faces (Leppänen et al., 2007). Last but not least, the P400 was weaker when infants were presented with distorted faces and bodies' configuration compared with the intact original images (Gliga and Dehaene-Lambertz, 2005).

In Experiment 1, we measured the infants' ERP response to power grasping actions at an age at which infants learned to perform accurate power grasp (6-month-olds) and compared this with another age group that had not yet mastered grasping (4-month-olds; von Hofsten, 1980). In Experiment 2, we focused on the interrelation between perception and action by testing infants that are in a transitional phase (5-month-olds). Finally, in Experiment 3, we tested the generalizability or specificity of this link by looking at a second kind of grasping, precision grasp, for which 6-month-old infants develop particular competence at a later age (~9 months; Halverson, 1931; Butterworth et al., 1997). In all experiments, infants were presented with sequences of pictures depicting hands performing grasps towards or away from objects. In half of the trials, the orientation of the grasping hand was directed towards the prior location of an object (congruent trials); in the other half, the hand was directed towards the opposite direction (incongruent trials). The same paradigm has been used previously to investigate how covert attention modulates reactive saccades during the observation of grasping hands in 3- to 7-month-old infants (Daum and Gredebäck, 2011). It was also used to investigate neural correlates of shifts in covert attention as a function of pointing (Gredebäck et al., 2010) and gaze direction in 8-month-old infants (Senju et al., 2006).

According to previous research that suggests a close relation between infants' sensitivity of observed actions and their own ability to produce such actions (Sommerville et al., 2005; Falck-Ytter et al., 2006; van Elk et al., 2008; Gredebäck and Melinder, 2010), we expected a differential activity to be in synchrony with infants' grasping skills. More specifically, infants that were able to produce proficient power grasps should demonstrate larger amplitudes of P400 for congruent than incongruent grasping actions. This should be the case for the older infants in Experiment 1 and for proficient graspers in Experiment 2, since these experiments present infants with power grasps. However, no differential amplitudes of P400 are expected in Experiment 3 where precision grasps are presented. The difference between the predictions from the first two studies and the third study is motivated by the fact that infants develop power grasps between 4 and 6 months of age (von Hofsten, 1980), whereas the ability to perform precision grasps develop much later, around 9 months of age (Butterworth et al., 1997).

EXPERIMENT 1

In Experiment 1, we presented 4- and 6-month-old infants with sequences of pictures of a human hand and an object; these sequences depicted either a congruent or an incongruent grasping action. The aim of the experiment was to investigate the neural correlates of grasping perception. We chose these age groups because grasping perception reportedly develops during this time window (von Hofsten, 1980); we were particularly interested in differences between the two age groups.

Methods

Participants

Fourteen 4-month-olds (8 girls, mean age 128 days, s.d. = 6 days) and fourteen 6-month-olds (7 girls, mean age 186 days, s.d. = 3 days) were included in the final sample. Four additional 4-month-olds and eight 6-month-olds were tested but excluded from the final analysis owing to fussiness or an insufficient number of artefact-free trials ($n < 15$ trials/condition). Before the experimental session started, participating families were informed about the purpose of the study and signed a consent form. Parents received a gift voucher of €10 value. The study was conducted in accordance with the standards specified in the 1964 Declaration of Helsinki and approved by the local ethics committee.

Stimulus and procedure

The stimulus material was presented on a 17-inch computer screen that was rotated 90°. Each session contained both congruent and incongruent conditions presented in randomized order. In both conditions, each trial began with two rectangles (6 horizontal × 5 vertical degrees) presented at the upper and lower part of the computer screen with 13 vertical degrees apart. After 100 ms, a fixation cross was presented at the centre of the screen for 1300–1750 ms. The fixation cross was removed and a target appeared inside one of the two rectangles for 240 ms. The final picture in the trial sequence depicted a grasping hand performing a power grasp (duration of 1000 ms) directed either towards (congruent condition) or away from (incongruent condition) the rectangle where the target had previously been present (Figure 1). This design allowed us to measure the brain responses to the congruency between the grasping hand and the target. The target was presented before the hand; this provided context for the functionality of the hand. Stimuli were presented using the software E-Prime 2.0, E-Studio (Psychology Software Tools, Inc., Pittsburgh, PA).

During the EEG recording, infants were placed on the parent's lap in front of the computer screen at a distance of 60 cm. To minimize visual distraction, light conditions were kept low and a curtain separated the experimenter and EEG equipment from the child/parent. The experimenter monitored the infant's gaze direction on an additional computer screen used to display the infant's face. When the infant did not attend to the presentation, the experimenter paused the experiment. During those pauses, an attention-grabbing picture with a sound was presented until the infant was attentive again. If necessary, the infant was turned away from the computer screen to take a break and play

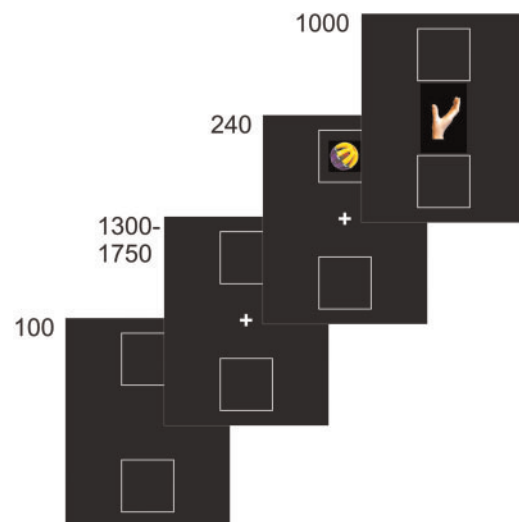


Fig. 1 Stimulus sequence in the congruent condition for Experiment 1 and 2.

for a moment. The experiment was terminated when an infant was no longer interested in the stimulus.

EEG recording and analysis

We used a 128-channel HydroCel Geodesic Sensor Net to record infants' EEGs and electrooculography. The vertex-referenced signal was amplified (EGI Net Amps 300 amplifier, Electric Geodesic, Eugene, OR) with a low-pass filter of 100 Hz sampled at 250 Hz and stored for off-line analysis. The EEG signal was digitally filtered (0.5–25 Hz) and segmented from 550 ms before the appearance of the hand (including the last 160 ms of the empty rectangles with the fixation cross and 240 ms of the target with the fixation cross) until 900 ms after the hand was presented. The electrodes from the most anterior and posterior areas were not included in the final analysis because of high noise caused by poor contact with the scalp. In total, 38 electrodes were excluded from the final analyses. Furthermore, the data were inspected manually, and those electrodes contaminated with artefacts were rejected. The data from the missing channels were interpolated from the surrounding electrodes. The trials included in the final data contained no more than 10% of the artefact-contaminated electrodes. The data were baseline corrected and averaged. The grand average was created from the individual averages of data that met the criteria for inclusion. Further analyses were performed on five areas—lower occipital (electrode number 74, 75 [Oz], 82), left posterior temporal (electrode number 65, 66, 67, 69, 70 [01], 71), right posterior temporal (electrode number 76, 77, 83 [02], 84, 89, 90), left central (electrode number 35, 29, 30, 36, 41, 42, 37) and right central (electrode number 87, 93, 103, 104 [C4], 105, 110, 111)—with a focus on a time interval ranging from 300 to 600 ms (labelled P400) after the onset of the stimulus. The choice of the electrodes was based on a similar procedure used in the study by Gredebäck *et al.* (2010). The average amplitudes within a selected time window were statistically compared in a $2 \times 2 \times 2$ repeated measures analysis of variance (ANOVA), with condition (congruent, incongruent) and lateralization (left, right) as within-subject factors and age (4 and 6 months) as a between-subject factor.

RESULTS AND DISCUSSION

The average number of presented trials for both conditions was 88 for 4-month-olds and 78 for 6-month-olds. The minimum criteria

for inclusion in the final sample were 15 artefact-free trials per condition. On average, the included 4-month-olds provided 60 artefact-free trials: 31 (range: 22–43) for the congruent and 29 (range: 19–39) for the incongruent condition. On average, the included 6-month-olds contributed 58 artefact-free trials: 24 (range: 17–58) for the congruent and 26 (range: 16–44) for the incongruent condition.

The analysis revealed a significant interaction between condition and age ($F(1, 26) = 5.60, P = 0.026, \eta^2 = 0.17$). For the 6-month-old infants, the post hoc analysis showed a significant P400 amplitude difference between congruent and incongruent trials in the posterior temporal area. More specifically, the amplitude was higher in the congruent (12.3 μ V) condition than in the incongruent (8.3 μ V) trials ($t(13) = 2.32, P = 0.037, d = 0.61$). Congruent and incongruent trials did not differ significantly in the group of 4-month-olds ($t(13) = 0.70, P = 0.491$). Differences between congruent and incongruent conditions were only observed in the posterior temporal area. There were no significant effects found in other tested regions (lower occipital, left central and right central regions, all $P > 0.05$). There was no significant difference within the posterior temporal area between the hemispheres ($F(1,13) = 0.65, P = 0.433$). The spatial distribution of grand-average ERPs for posterior temporal channels for 4- and 6-month-olds is presented in Figure 2.

These results demonstrate a pronounced differential neural activity during the observation of congruent and incongruent grasping actions performed by hands shaped as power grasps. The onset age of this differential neural activity (between 4 and 6 months) corresponds well with the onset of grasping as described in the literature (von Hofsten, 2004) and with the onset of the perception of the directionality of grasping hands (Daum and Gredebäck, 2011; Wronski and Daum, 2014). This finding is consistent with prior behavioural studies demonstrating a relation between the production and the perception of manual actions (Sommerville *et al.*, 2005; Gredebäck and Kochukhova, 2010; Kanakogi and Itakura, 2011). However, more solid conclusions require that both action production, that is the infant's own ability to grasp, and neural correlates of action perception, here the P400, be investigated in two groups of age-matched infants with different grasping proficiency. Experiment 2 focused on 5-month-old infants divided into two subgroups with more proficient *vs* less proficient grasping skills.

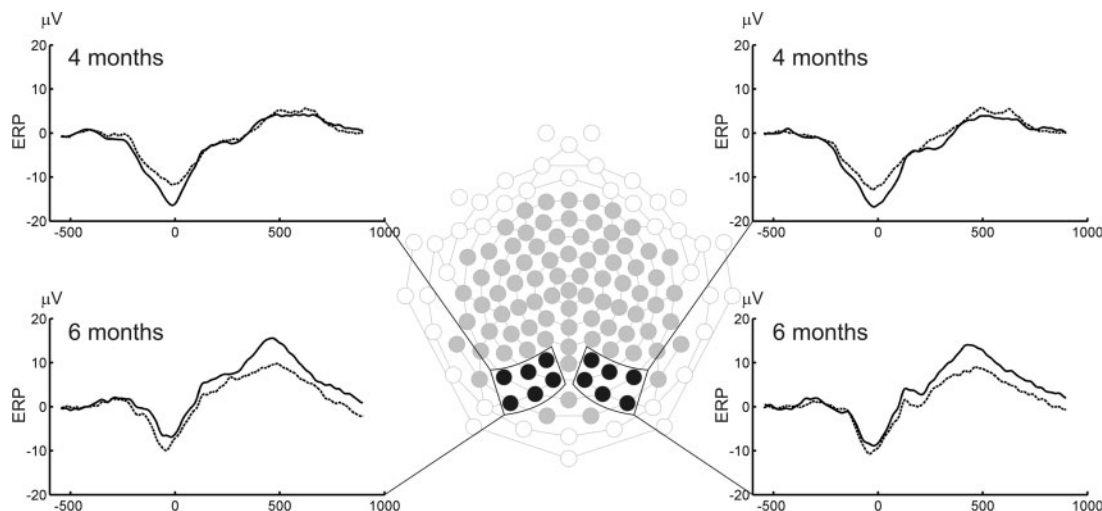


Fig. 2 Grand-average ERP of left and right regions of interest over posterior temporal sites (channels of interest are marked in black). Averages of the 4-month-olds are displayed at the top, 6-month-olds at the bottom. Dotted line represents the incongruent and solid lines the congruent condition.

EXPERIMENT 2

The infants were presented with the same stimulus material as in Experiment 1. To assess the direct connection between infants' grasping skills and their perception of grasping actions, we measured infants' grasping skills. This design provided us with the unique opportunity to compare the neural activity of infants that are able to grasp in a functional manner vs infants that are less successful graspers. Based on the results from Experiment 1, we hypothesized that infants that demonstrated proficient grasping skills would differentiate between congruent and incongruent grasping to a larger degree than less proficient graspers.

Methods

Participants

We tested 31 infants at the age of 5 months. Seven infants were not included in the final analysis owing to an insufficient number of artefact-free trials ($n < 15$). The final sample included 24 infants (12 girls, mean age 154 days, s.d. = 6 days). As in Experiment 1, participating families were informed about the purpose of the study and signed a consent form before participation. The parents received a voucher with a value of €10.

Stimulus and procedure

In addition to the EEG recording, we assessed infants' manual grasping skills. The grasping test was designed to evaluate grasping skills in a controlled objective setting. The total duration of the grasping test did not exceed 5 min. During this time, we registered the performance of up to three grasps. The grasps were video recorded and scored afterwards. On average, each infant performed two grasps. The child was presented with one of three rubber toys (5 × 5 cm; two black and white ducks and a green frog). The experimenter verbally offered one toy while passing it to the child. The experimenter's hand movement stopped in front of the child at a distance that made it possible for the child to grasp the toy. The experimenter waited ~10 s for the child to begin a grasping motion. The timing began as soon as the child's attention was on the toy held by the experimenter. If the grasping motion did not start within a 10 s time window, the toy was withdrawn and the experimenter started the procedure again with a different toy (up to three trials were conducted). To avoid that children became fussy, the grasping test was always performed before EEG data collection. We scored three components of the grasp: the extension of the infant's arm towards the object, the grip of the object and the ability to hold the object. For each component the child could receive 0 (not performing any movement or action that would help to accomplish the goal), 0.5 (the child initiates to perform the correct action but is not able to complete it; for instance, the child wanted to grasp the toy, touched it and tried to adjust the hand to the object and, in the end, grasped the toy but with incorrect hand aperture) or 1 point (child performed the action successfully, for example by adjusting the hand aperture correctly to the object and grasping the toy). The maximum attainable score was therefore 3 points. The caregiver was asked to score the child's everyday production of grasping with a scale of 0–3 points. This way we were able to detect infants that, despite of being generally good at grasping, did not perform the action in the laboratory setting. Each infant could receive a maximum of 6 points in total. The scores between our grasping test and the score given by the caregiver were strongly correlated ($R^2 = 0.78$). Subsequently, we divided the infants into two groups. Infants that scored a total of 0–3 points were assigned to the 'non-proficient graspers' group ($n = 12$, 5 girls, mean age 152 days, s.d. = 6 days) and those with 3.5–6 points were allocated to the 'proficient graspers' group ($n = 12$, 7 girls, mean age

150 days, s.d. = 6 days). The two groups did not differ in age ($t(11) = 0.79$, $P = 0.444$).

EEG recording and analysis

The stimuli and procedure for the EEG recording were the same as in Experiment 1. The grand average was created from individual averages of data that met our criteria for inclusion. The analyses were performed on identical electrodes and time interval (300–600 ms) as applied in Experiment 1. The average amplitudes within a selected time window were statistically compared in a $2 \times 2 \times 2$ repeated measures ANOVA, with condition (congruent, incongruent) and lateralization (left, right) as within-subject factors and grasping proficiency (good graspers, non-graspers) as a between-subject factor.

RESULTS AND DISCUSSION

On average, we presented 63 trials (both conditions) to the group of proficient graspers and 71 trials to non-proficient graspers. A minimum of 15 trials had to remain in each condition after artefact rejection to include a participant in the final analysis. On average, included proficient graspers provided 49 artefact-free trials: 25 (range: 20–54) for the congruent and 25 (range: 16–36) for the incongruent condition. Included non-proficient graspers contributed, on average, 51 artefact-free trials: 26 (range: 16–42) for the congruent and 25 (range: 17–38) for the incongruent condition.

The analysis revealed no significant effects for condition, lateralization, or grasping proficiency. However, a significant interaction between conditions and grasping performance was observed ($F(1,22) = 8.65$, $P = 0.008$, $\eta^2 = 0.282$). Post hoc analysis showed that, for the group of proficient graspers, there was a significant P400 amplitude difference between congruent and incongruent trials over posterior temporal sites ($t(11) = 2.93$, $P = 0.014$, $d = 0.84$). Amplitudes were larger in the congruent (4.95 μV) than in the incongruent (1.40 μV) condition. We did not observe a significant difference between congruent and incongruent trials among non-proficient graspers ($t(11) = 1.38$, $P = 0.194$). Differences between congruent and incongruent conditions were only observed in the posterior temporal region, and there were no significant differences within this brain area between the hemispheres ($F(1, 22) = 0.04$, $P = 0.827$). No significant effects were found in other tested regions (lower occipital, left central, and right central regions; $P > 0.05$).

These findings demonstrate that the perception of power grasps is emerging at the same time infants start to perform power grasps in a functional and efficient manner. The results of the influence of grasping ability on the neural data for all previously tested age groups (Experiments 1 and 2) are presented in Figure 3. Although our findings

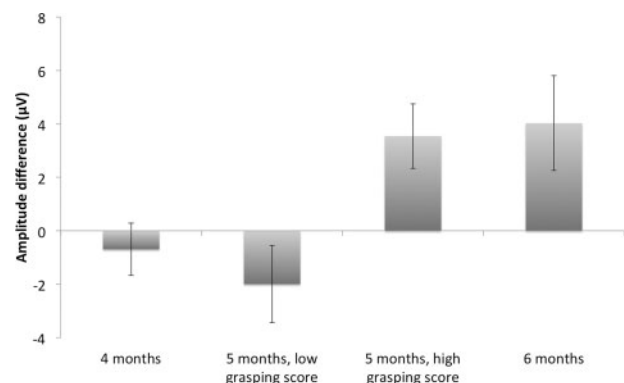


Fig. 3 Averaged P400 amplitude difference between the congruent and incongruent condition for all age groups (Experiment 1 and 2). Error bars represent standard error.

show that grasping ability is closely related to the neural processing of other people's power grasps, it is unclear whether these results depend on the grasping action that was used in the experiment. The next step of the current investigation was to establish whether differential activation between proficient and less proficient graspers is related to the specific action under investigation (grasping actions performed with a power grasp) or whether the effect generalizes to other hand actions that infants are unable to perform (e.g. precision grasps). It is also necessary to determine whether the observed effect is related to previous experience with a presented action or whether the co-emergence of P400 differentiation and grasping ability is driven by an underlying third variable, such as developmental maturity. Experiment 3 addressed these two issues.

EXPERIMENT 3

We presented 6-month-olds with similar stimuli as in Experiments 1 and 2. The main difference between the previous and the current stimuli was that the hand performing a power grasp was replaced with a hand performing a precision grasp. Additionally, object size was adjusted to the distance between the thumb and index finger. This way, the aperture of congruent grasping actions maintained the same functional relation to object size and finger separation as in Experiments 1 and 2. The choice of action was based on prior studies demonstrating that infants are not able to perform the precision grasp until 9–12 months of age (Halverson, 1931; Butterworth *et al.*, 1997). This assumption was validated by tests in the lab. All tested infants performed three valid power grasps, but none performed any precision grasps. Infants' behavioural abilities might suggest that when observing a power grasp, they should be able to encode the relation between the object and the hand. If this encoding is specific to the skill that they are able to perform themselves, then it should disappear when infants are presented with a precision grasp. Based on the argument from Experiment 1, that grasping ability is closely related to the neural processing of other people's power grasps, we could expect that the neural pattern is specific to the action that can already be performed. This implies that manual actions that are outside the manual repertoire should not cause a differential neural response. As such, we hypothesized that infants would not differentiate between congruent and incongruent precision grasping actions.

Methods

Participants

The final sample consisted of fourteen 6-month-old infants (9 girls, mean age 181 days, *s.d.* = 4 days). Four infants were not included in the final analysis owing to an insufficient number of artefact-free trials ($n < 15$). As in Experiments 1 and 2, participating families were informed about the purpose of the study and signed a consent form before participation. The parents received a voucher of ~€10 value.

Stimulus and procedure

The stimulus and procedure were similar to those described for Experiment 2, regarding both the tests of each infant's grasping ability and the subsequent EEG sessions. The main difference was that, in addition to the power grasp test, infants were tested regarding their ability to perform the precision grasp. When tested for the precision grasp, infants had to reach for three small objects (1×1 cm) that would require a precision grasp to pick them up. The precision grasp was scored as valid if the child was able to lift up the object using the index finger and the thumb.

EEG recording and analysis

The procedure for the EEG recording was exactly the same as in Experiments 1 and 2. The analyses were performed on identical electrodes and time intervals as applied in Experiments 1 and 2. The average amplitudes within a selected time window were statistically compared in a 2×2 repeated measures ANOVA, with condition (congruent, incongruent) and lateralization (left, right) as within-subject factors.

RESULTS AND DISCUSSION

On average, 52 trials were presented in both conditions. To be included in the final analysis, infants had to reach a minimum of 15 artefact-free trials per condition. On average, we recorded 42 artefact-free trials: 21 (range: 15–32) for the congruent and 21 (range: 15–41) for the incongruent condition. The analysis revealed no significant differences between conditions in the region of interest, that is, over posterior temporal sites ($t(13) = 0.19$, $P = 0.852$). There were no significant effects in the other investigated areas (lower occipital, left central and right central regions; $P > 0.05$).

The results show that infants are not able to encode congruency of a hand and its goal when the observed action is outside their own grasping abilities. This suggests that the findings documented in Experiments 1 and 2 are not caused by general maturation. More importantly, our result shows that the action–perception link is highly specific, operating solely for actions that are consistent with the infants' own action repertoire.

GENERAL DISCUSSION

The current study is the first to demonstrate a neural correlate of the action–perception link at the age when grasping skills develop and emerge. Experiment 1 revealed that 6-month-old infants' P400 ERP components differ between congruent and incongruent conditions when observing power grasps. The same pattern was observed in proficient 5-month-old graspers (Experiment 2). By contrast, the less proficient graspers among the 5-month-olds and the 4-month-olds did not exhibit differential ERP responses between the two conditions. Interestingly, Experiment 3 revealed that the ERP responses do not extend to other (visually similar) grasping actions that infants are not yet able to perform (e.g. precision grasps). These findings suggest that the P400 specifically encodes the relation between hands and goals when observing hand configurations that match infants' behavioural repertoire. The high specificity of the results suggests that the age effect demonstrated in Experiment 1 and the proficiency effect demonstrated in Experiment 2 cannot be attributed to general maturation.

Next, we discuss the details of the action–perception link and what we think our findings contribute to the developmental literature. We also look at the P400 from two additional perspectives. First, as our current design is based on the Posner attention paradigm, we will discuss attentional changes in relation to the P400 component. Second, we will relate the current findings to known neural networks dedicated to action perception and action production.

Action-Perception link

The core of our findings is the correlation between action production and action perception at the age when grasping ability emerges. The action–perception link is not new in the developmental literature, as it has been previously captured with a habituation paradigm (Sommerville *et al.*, 2005, 2008), predictive eye movements during action observation and action production (Flanagan *et al.*, 2003; Rosander and von Hofsten, 2011) or the connection between own experience with the observed actions and their prediction (Falck-Ytter *et al.*, 2006; Gredebäck and Kochukhova, 2010; Gredebäck and

Melinder, 2010; Cannon *et al.*, 2012). A similar link has been observed in studies of neural activity: amplitudes of the mu-desynchronization during action observation have been linked to the observer's own experience with the same actions (Lepage and Theoret, 2006; van Elk *et al.*, 2008; Southgate *et al.*, 2009; Nyström *et al.*, 2010). Additionally, the authors of a recent functional near-infrared spectroscopy study on infants reported a correlation between the perception of manual actions and the level of the own fine motor skills; they attributed the cortical activation of this link to the posterior superior temporal sulcus-temporoparietal junction region (Lloyd-Fox *et al.*, 2013). It is important to highlight that our current work extends those findings by capturing a (time-locked) neural underpinning (P400) of the grasping action–perception link. Furthermore, we demonstrate that action proficiency does not facilitate processing of a wide range of similar actions. Instead, being proficient in performing power grasps helps young infants encode the relation between power grasps and objects, an effect that does not extend to precision grasps. This finding goes beyond what has previously been demonstrated, suggesting that experience exclusively facilitates the processing and subsequent understanding of highly similar actions performed by others. In other words, a baby proficient at performing power grasps does not process or understand observed precision grasps better than infants that are less able to perform power grasps.

One, admittedly speculative, possibility is that we capture a neural correlate of the early behavioural experience-dependent process known as 'sticky mittens training' (Sommerville *et al.*, 2005). In their study, 3-month-old infants developed the ability to encode the goal of perceived manual actions (Woodward, 1998) if they received grasping training before viewing another person's grasp for similar objects. More specifically, infants in this study were not yet able to grasp; therefore, the training was performed while the infants wore mittens furnished with Velcro. The mittens allowed infants to make contact with Velcro-covered objects and lift them up. This training enabled infants to encode the goal of other people's manual actions in a manner unprecedented by untrained infants of the same age. Perhaps both studies (the current investigation and Somerville *et al.*, 2005) provide independent evidence for the same experience-dependent process.

Based on the findings above, we argue for the presence of an action–perception link early in development. One limitation of our findings is that the applied correlational design does not allow us to draw any conclusions about the directionality of this link. It is possible that, to be successful in online action processing, well-organized motor skills are needed to perform the same action. On the other hand, it is possible that we must possess clear goal concepts before being able to engage in the production of the same action. To find an answer to these open questions, additional studies are needed to investigate the directionality of the action–perception link.

How is attention related to the P400 effect?

In a typical Posner paradigm, a central visual stimulus cues attention to the periphery (e.g. an arrow or a grasping hand). The priming effect is measured through reaction times to peripheral targets that appear along the cued direction (congruent trials result in shorter reaction times) or another non-cued direction (incongruent trials result in longer reaction times; Posner and Cohen, 1984; Daum and Gredebäck, 2011; Daum *et al.*, 2013). Unlike prior spatial-cueing studies (e.g. Posner and Cohen, 1984), in the current study we reversed the order of the target and cue presentation. In our case, a peripheral target (a ball) appears and disappears, followed by a centrally located cue (grasping hand; for similar procedures see Senju *et al.*, 2006; Gredebäck *et al.*, 2010). This switch was implemented to elicit an

ERP response to the hand, which was directed towards the target (congruent trials) or away from the target (incongruent trials). Therefore, the target served as context for the stimulus of interest, the hand. Despite these differences, we argue that similar attentional processes are measured irrespective of presentation order. In the current paradigm, we suggest that when participants look at the peripheral target their attention to the targets' location is heightened. Once the peripheral target disappears, participants' attention is moved to the central cue (the hand). After the properties of the central cue (the hand grasping in one direction) are processed, participants' covert attention is shifted to the direction indicated by the grasping hand. If the shift of covert attention from the hand overlaps with the previous location of the target (congruent trials), the P400 amplitude is heightened. No such overlap of attention exists during incongruent trials. In other words, we argue that the enhanced P400 for congruent trials is generated by the summation of covert attention derived from the target's prior location and the extension of the grasping hand. Additionally, in the current study, infants' differential P400 amplitudes are linked to their own grasping ability. We suggest that being able to perform proficient grasping action allows infants to perceive the directionality of the hand. Once the direction is detected, infants shift their attention covertly towards the location indicated by the hand. Infants that cannot yet grasp in a proficient manner are not able to encode the directionality of the hand. Therefore, the shift of the covert attention does not occur or occurs to lesser degree. This results in low degrees of overlap in both congruent and incongruent trials and a lack of differentiation between P400 amplitudes.

What are the possible underlying neural structures?

The spatiotemporal properties of the P400 are highly similar to the neural activity previously demonstrated while observing facial expressions in 7-month-olds (Leppänen *et al.*, 2007), gaze shifts (Senju *et al.*, 2006), and biological motion in 8-month-olds (Reid *et al.*, 2006). It has been argued that the infant P400 activity is functionally related to the adult N170 (de Haan *et al.*, 2002; Nelson *et al.*, 2006). Additionally, co-registration of functional magnetic resonance imaging (fMRI), as well as source localization of ERP data, revealed that the adult N170 has been linked to activation in the superior temporal sulcus (STS; Puce *et al.*, 1998; Itier and Taylor, 2004; Dalrymple *et al.*, 2011). Previous work by Gredebäck *et al.* (2010) suggested the same link between the adult N170, the infant P400 and the STS in relation to spatial priming or manual gestures. In line with this argumentation, we propose that the posterior temporal P400 in infants may originate within the STS.

Previous research has found the STS to be involved in face processing, gaze direction and detection of biological motion (Allison *et al.*, 2000). A more recent review of the STS literature also reveals that the area becomes active during the perception and the production of goal-directed actions (Keysers and Perrett, 2004). The findings reported in the present study suggest, first, that the STS might also be involved in processing grasping actions early in development and, second, that its activity is functionally related to motor development. However, the current findings also leave room for alternative interpretations about the role of the P400 and the putative involvement of the STS in the link between action and perception during the observation of others' actions.

One possible interpretation is in agreement with Iacoboni *et al.* (1999), who claim that the main function of the STS (relative to the MNS) is to provide input to the primary MNS located around the inferior frontal and superior parietal cortex (Iacoboni *et al.*, 1999). From this perspective, the link between one's own grasping ability and grasping understanding originates in an area that is supposed to

feed forward to the primary MNS circuitry. In light of this, it is possible that the present findings capture an initial process for action perception that is first coded in the STS and then feeds information into the MNS for more advanced processing (e.g. the ability to predict others' action goals; [Elsner et al., 2013](#)).

Another interpretation is in line with a recent meta-analysis of fMRI studies on social cognitive mechanisms ([van Overwalle and Baetens, 2009](#)) that identifies the adult STS as an area with mirror properties. In light of this literature, the current findings might indicate that the MNS is more distributed than previously believed, as it has classically been assumed in the inferior frontal and inferior parietal regions ([Rizzolatti and Craighero, 2004](#)). These findings allow for the possibility that the P400 is generated by a feedback loop from inferior frontal and/or superior parietal areas that originally map observed actions onto the observer's own motor plans. This feedback loop starts to become operational at an age when infants have acquired a considerable amount of experience in both the perception and the production of the same action ([Kanakogi and Itakura, 2011](#); [Melzer et al., 2012](#)). For simple grasping actions such as those in the current study, the MNS circuitry might respond and send information to the STS in individuals that have developed sophisticated grasping skills. In fact, more studies in infants and adults need to target the pathways that connect the STS with inferior frontal and superior parietal areas. Finding out whether the mapping between own and others' actions originates within the STS or the recorded activity has its origin within the primary MNS is an important challenge for future research.

CONCLUSIONS

The current study brings to light a neural component that links production and perception of grasping actions. We captured this neural underpinning at the onset of grasping, which gave us a unique opportunity to compare the perception of two different grasping skills (power grasp and precision grasp). We found that the P400 located over posterior parietal sites is a neural correlate of infants' sensitivity to the congruency of a grasping hand and the object at a detailed perceptual level that tightly corresponds to infants' own grasping repertoire. Additionally, our study represents a potential involvement of the STS in the link between grasping production and perception of other people's grasping action.

Conflict of Interest

None declared.

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