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Action priming with biomechanically possible and impossible grasps: ERP evidence from 6-month-old infants

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ABSTRACT

Coding the direction of others' gestures is a fundamental human ability, since it allows the observer to attend and react to sources of potential interest in the environment. Shifts of attention triggered by action observation have been reported to occur early in infancy. Yet, the neurophysiological underpinnings of such action priming and the properties of gestures that might be crucial for it remain unknown. Here, we addressed these issues by recording electro-encephalographic activity (EEG) from 6-month-old infants cued with spatially non-predictive hand grasping toward or away from the position of a target object, i.e., valid and invalid trials, respectively. Half of the infants were cued with a gesture executable by a human hand (possible gesture) and the other half with a gesture impossible to be executed by a human hand. Results show that the amplitude enhancement of the posterior N290 component in response to targets in valid trials, as compared to invalid trials, was present only for infants seeing possible gestures, while it was absent for infants seeing impossible gestures. These findings suggest that infants detect the biomechanical properties of human movements when processing hand gestures, relying on this information to orient their visual attention toward the target object.

Introduction

Understanding the direction of human gestures (i.e., grasping and pointing), as well as that of eye gaze, head, and body orientation, reveals to the observer where other people are directing their own attention, providing important clues for detecting the sources of potential interest in the environment. Behavioral evidence suggests that the capability to detect these social signals and use their directionality as a cue to shift attention in space is present early in development (see review by Gredebäck & Daum, 2015). Indeed, humans are remarkably sensitive to gaze direction and goal-directed action since birth (e.g., Craighero, Leo, Umiltà, & Simion, 2011; Farroni, Csibra, Simion, & Johnson, 2002), and overt eye and head orienting responses in the direction of others' gaze develop long before the end of the first year of life (Gredebäck & Kochukhova, 2010; Gredebäck, Theuring, Hauf, & Kenward, 2008; Senju & Csibra, 2008; Szufnarowska, Rohlfing, Fawcett, & Gredebäck, 2014; Vecera & Johnson, 1995). Moreover, studies using a modified version of the well-known Posner paradigm (Posner, 1980) were able to demonstrate that infants can benefit from their sensitivity to

others' gaze and gestures in orienting attention across space. The general procedure devised in these studies involves presenting an attention getter to drive infant's attention to the center of a screen, where the action is subsequently displayed, followed by a target stimulus at a peripheral location congruent or incongruent with the direction of the action (i.e., valid and invalid trials, respectively). Typically, the action is not predictive of the location of the impending target, which can appear with equal likelihood at either position. By using this procedure it was shown that infants perform faster saccades to peripheral targets displayed at the spatial position congruent with the direction of the action, i.e., valid trials, than to targets located at the incongruent position, i.e., invalid trials (Bardi, Di Giorgio, Lunghi, Troje, & Simion, 2015; Bertenthal, Boyer, & Harding, 2014; Daum & Gredebäck, 2011; Daum, Ulber, & Gredebäck, 2013; Farroni, Johnson, Brockbank, & Simion, 2000; Farroni, Mansfield, Lai, & Johnson, 2003; Hood, Willen, & Driver, 1998; Rohlfing, Longo, & Bertenthal, 2012; Wronski & Daum, 2014). This behavioral effect (action priming) has been interpreted by assuming that the directionality of the action cue triggers a covert shift of attention (i.e., a movement of the attentional focus without

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corresponding eyes and head movement) in the direction of the cue, yielding a facilitation in reacting to target stimuli at the attended location, as revealed by faster saccades (i.e., overt orienting responses) to those stimuli. Vice versa, a cost is paid in responding to targets at the non-attended location, since attention must disengage from the attended position, move and engage to the stimulus at the incongruent location, resulting in slower saccades to incongruent targets compared to congruent ones.

Action priming might be less effective if the target stimulus is presented when the action cue is still visible, as disengaging attention from a salient stimulus (i.e., action) can be difficult in infancy (Hood et al., 1998). Crucial to the priming effect would be a reflexive, rather than strategic, orienting of attention in the direction of the cue, favored by short onset asynchrony between cue and target (Bertenthal et al., 2014). The effectiveness of the action priming can also depend on other factors. In particular, although the priming effect can be observed with static images of a referential action (Bertenthal et al., 2014; Daum & Gredebäck, 2011; Hood et al., 1998), it is enhanced by the observation of dynamic, more ecological gestures (Farroni et al., 2000, 2003; Rohlfing et al., 2012; Wronski & Daum, 2014). Finally, early action priming in infancy seems to be confined to hand gestures that are present in the infant's motor repertoire (Bakker, Daum, Handl, & Gredebäck, 2015; Daum & Gredebäck, 2011). Despite the wealth of research focusing on functional aspects of action priming, much less research has been devoted to the investigation of its neural underpinnings.

As first demonstrated by Richards (2000) using electroencephalography (EEG) and electrooculography (EOG), infants are capable of shifting attention to the location indicated by a spatially non-predictive cue both overtly and covertly. By measuring infants' saccadic responses to peripheral targets preceded by non-social cues displayed at either the same or the opposite location as the target (i.e., valid and invalid trials, respectively), Richards (2000) found that, when attending overtly (i.e., gazing) to the target, 3-, 4.5-, and 6-month-old infants showed shorter saccadic latency to stimuli in valid than invalid trials. Thus, the priming effect of an exogenous, non-social, cue on infants' saccadic orienting response to the target is analogous to the effect generated by the direction of a centrally displayed human action. The two effects are likely mediated by a common functional mechanism, namely a covert shift of spatial attention triggered by the cue, increasing the efficiency and speeding up processing of stimuli at the attended location. Richards explored the possible neural basis of the priming effect by analyzing event-related potentials (ERPs) in response to the target onset during trials in which infants covertly attended to the target without gazing at it. He reasoned that, if covert orienting occurs with the cue biasing the analysis of target stimuli, as reflected at the behavioral level, then ERP responses to the target should be modulated by trial validity, which would affect early or late ERP components according to the stage of information processing at which the priming effect would arise. Following milestone EEG studies on visual-spatial attention in adult participants (see Hillyard & Anllo-Vento, 1998 for a review), ERP responses were analyzed over occipital sites ipsilateral and contralateral to the hemifield of target presentation. Two early components – P100, peaking at about 135 ms, and N1, peaking at about 260 ms – were observed in response to target onset, with the P100 over contralateral sites being larger in valid than in invalid trials for 4.5- and 6-month-old infants, but not for 3-month-olds. The P1 validity effect shown by older infants was comparable to that found in EEG studies with adult participants. Importantly, this effect indicated that, like in adults (e.g., Heinze et al., 1994; Hillyard & Anllo-Vento, 1998), also in infants a shift of attention to a cued location automatically yields a facilitation in reacting to targets on valid trials, which reflects increased efficiency at early (sensorial and perceptual) stages of processing at the attended location. On the other hand, the facilitation of the saccadic localization responses found in 3-month-olds, which was not associated with ERP evidence of validity effect, may be simply due to a combination of cue-elicited reflexive saccadic planning and target-elicited saccades (Richards, 2000).

In light of the above ERP evidence, one might ask whether and to what extent infants' ability to interpret social signals, like gestures, might have developed as a means to shift attention in space and increase efficiency of sensory processing of potentially relevant information. As far as we know, this hypothesis still needs to be investigated.

The issue of how infants use the direction of other's eye gaze to process information has been addressed by Reid and colleagues (Reid, Striano, Kaufman, & Johnson, 2004) in an EEG study with 4-month-old infants, who were shown an adult face gazing toward or away from objects. When presented with the objects a second time, infants showed differences in a slow wave ERP observed at fronto-temporal sites, which was smaller in response to previously cued, as compared to uncued, objects, indicating that objects cued by the direction of other's gaze were perceived as more familiar than uncued objects. This important evidence proves that the direction of other's eye gaze is used to covertly

shift attention and that this enhances the processing of the object at the cued location. However, the ERP study by Reid et al. (2004) leaves open the question of how visual-spatial attention may enhance information processing at the attended location, which could only be addressed by measuring ERP responses to objects directly displayed at that location (Richards, 2000).

Another line of research investigating infants' attentional responses to social signals used EEG and a procedure in which, unlike the Posner paradigm, the peripheral target preceded the gesture. ERPs in response to the onset of the gesture were then analyzed to unravel the neurophysiological correlates of comprehension of referential actions (Bakker et al., 2015; Gredebäck, Melinder, & Daum, 2010; Melinder, Konijnenberg, Hermansen, Daum, & Gredebäck, 2015; Senju, Johnson, & Csibra, 2006). Senju et al. (2006) found that object-incongruent gaze shifts elicited an enhanced posterior ERP component (N290), as compared to object-congruent gaze shifts, in 9-month-old infants; instead, object-congruent gaze shifts enhanced ERP components over frontal scalp sites (anterior N200 and N400). More recent studies have shown that, in infants aged 4–13 months, the posterior P400 component is involved in the encoding of the relationship between hand (grasping and pointing) gestures and object position, with larger amplitude in response to congruent than incongruent gestures in older infants (i.e., older than 12 months; Bakker et al., 2015; Gredebäck et al., 2010), and a reversed pattern in younger infants (i.e., younger than 12 months; Melinder et al., 2015). In addition, the effect was modulated by infants' motor skills, as it could only be observed for actions proficiently performed by the infant himself (Bakker et al., 2015; Melinder et al., 2015).

Overall, this evidence indicates that the object–action link in infancy is indexed by ERP modulation that undergoes substantial development in infancy. Indeed, the emergence of differential ERP responses to congruent and incongruent gestures at about 400 ms after the onset of the action (Bakker et al., 2015; Gredebäck et al., 2010; Melinder et al., 2015), and the presence of slightly delayed saccadic localization responses to targets cued by congruent versus incongruent actions (Daum & Gredebäck, 2011) is intriguing. However, given the substantial differences between the paradigm employed in ERP and eye-tracker studies, the possibility to link the behavioral priming effect to the P400 ERP effect remains speculative.

Beside the neurophysiological aspects of the priming effect, a second issue, which still needs to be explored, relates to the properties of human gestures that are critical in triggering action priming effects. Available evidence indicates that, with static stimuli, action priming is triggered by social cues (i.e., actions performed by a human agent), whereas it is less likely to occur for pseudo-social cues (i.e., foils; Bertenthal et al., 2014), or non-social cues (i.e., mechanical claws; Daum & Gredebäck, 2011). Dynamic actions can prime orienting responses toward congruent targets even in young (i.e., 4.5–5-month-old) infants, who do not show response facilitation with static stimuli (Rohlfing et al., 2012; Wronski & Daum, 2014). Indeed, the static image of an action contains information about directedness of the action goal, whereas a dynamic hand movement delivers information about directedness of both the goal and the motor component of the action. It has been proposed that younger infants might need both these information to rapidly detect the directionality of the action, and in turn to shift covert attention accordingly, whereas older infants may be able to efficiently use each of the two cues in isolation (Wronski & Daum, 2014).

One key aspect of the motor component of an action lies in the biomechanical properties of the action itself. Geangu and colleagues (Geangu, Senna, Croci, & Turati, 2015) have shown that, by 6 months of age, infants can discriminate between reaching-to-grasp hand movements that respect the biomechanical properties of the human hand and movements that violate such properties. Like adults (e.g., Avenanti, Bolognini, Maravita, & Aglioti, 2007), they show increased looking time to biomechanically impossible grasping actions as compared to biomechanically possible grasping actions, whereas 4-month-olds fail to do so. This indicates that 6-month-olds can detect violation of hand biomechanics and appreciate biomechanical properties while processing the action, a function relevant for the anticipation of action goal. However, this study leaves open the question of whether biomechanical properties may act as a cue priming orienting responses toward targets congruent with the direction of the action.

In the present study, we aimed at addressing this question by taking advantage of the EEG technique and the classical Posner paradigm (Richards, 2000). We tested 6-month-old infants, showing them a grasping hand as a central cue and measuring ERPs in response to the onset of the target subsequently flashed at a peripheral location, which could be congruent or incongruent with the grasp direction. The procedure was devised to foster the occurrence of an action priming effect: infants were presented with a whole hand grasp that they can proficiently perform at 6 months (e.g., Bakker et al., 2015; Daum & Gredebäck, 2011). Videos of a dynamic grasping hand action, rather than static

images, were used to deliver information about direct-edness of both the goal and the motor component of the gesture, which can be suitably used to rapidly detect the directionality of the action, and shift covert attention accordingly (Wronski & Daum, 2014). Our main purpose was to verify whether, and to what extent, ERP responses may reflect facilitation in reacting to the cued target, as observed in eye-tracking studies (Bertenthal et al., 2014; Daum & Gredebäck, 2011; Daum et al., 2013; Rohlfing et al., 2012; Wronski & Daum, 2014). If the priming effect specifically arises from a sensory facilitation in processing visual information at the cued location, we should observe modulation of early posterior ERP components (i.e., increased P1 and/or N1 amplitude on congruent trials) reflecting sensorial analysis of visual information (Richards, 2000). Otherwise, the priming effect might merely reflect expectation based on the relation between object location and action direction, which may affect ERP responses in a relatively late, rather than early, time window.

Importantly, here we manipulated the biomechanical properties of the grasping, so as to have a condition in which the gesture was executable by a human hand and a condition in which the gesture was impossible to be executed by a human hand. It is worth noting that biomechanically possible and impossible grasps are both characterized by a movement direction, although impossible grasps do not meet anatomical constraints. Thus, one possibility might be that information about movement direction is necessary and sufficient to trig-ger a shift of attention. In this case, we would expect to find similar ERP modulation as a function of the validity of the trial, regardless of the biomechanical plausibility of the hand movement. On the contrary, if infants heavily rely on information about the biomechanical properties of human motion when processing action direction in order to orient attention accordingly, we would expect to observe ERP modulation as a function of the action–target congruency for biomechanically possible grasps, but not for impossible grasps.

Methods

Participants

Twenty-four healthy, full-term 6-month-olds (11 females, mean age = 6 months 4 days, range = 150–198 days) were randomly assigned to the two experimental condi-tions: 12 (6 females, mean age = 6 months and 5 days, range = 150–198 days) to the biomechanically possible hand action condition, and 12 (5 females, mean age = 6 months and 2 days, range = 167–196 days) to

the biomechanically impossible hand action condition. An additional 28 infants were also tested, but were not included in the final sample due to fussiness and no completion of an adequate number of trials to be con-sidered for data analysis (i.e., 10 trials per condition; N = 19 infants), or eye and body movements that resulted in excessive recording artifacts (N = 9 infants). The protocol was carried out in accordance with the ethical standards of the Declaration of Helsinki and approved by the Ethical Committee of the University of Milano-Bicocca. Parents gave their written informed consent.

Stimuli, apparatus, and procedure

Testing took place in an electrically shielded and dimly illuminated room. Infants were seated on a parent's lap approximately 60 cm from a 24-inch screen used for stimulus presentation. A video camera installed above the screen recorded a video of the infant, which was synchronized with stimulus presentation for offline cod-ing of eye and body movements occurring during each trial. As shown in Figure 1, the latter began with an animated fixation point, randomly selected among 16 different animations, which was displayed at the center of the screen. As soon as the infant looked at it, this was replaced by the visual-spatial cue, namely a dynamic gesture of a human hand randomly grasping either toward the left or the right side (subtending maximum 5° of visual angle along the horizontal axis and 15° along the vertical axis). The grasping action lasted for 1200 ms and, after a variable delay (range: 300–500 ms), a target stimulus was displayed for 200 ms. The target consisted of the static image of a colorful ball, which was randomly selected among 16 images of a colored ball (all 1.75 cm in radius), in order to have a different target for each trial within the trial block. The target could be randomly presented at a peripheral location (~10° of visual angle from the center of the screen) either congruent (i.e., valid) or incongruent (i.e., invalid) with the grasping direction.

Two types of grasping gesture were presented: a biomechanically possible hand action and a biomecha-nically impossible action. The biomechanically impossi-ble action was obtained by making the virtual hand's fingers bending in the opposite direction with respect to that in the possible grasp, that is toward the back of the hand. In the impossible grasping, all angular dis-placements were clearly beyond the natural limits of the metacarpophalangeal joints, thus clearly violating the biomechanical constraints of the phalanges. The two types of gestures were otherwise matched for low-level visual features as well as cinematic aspects,
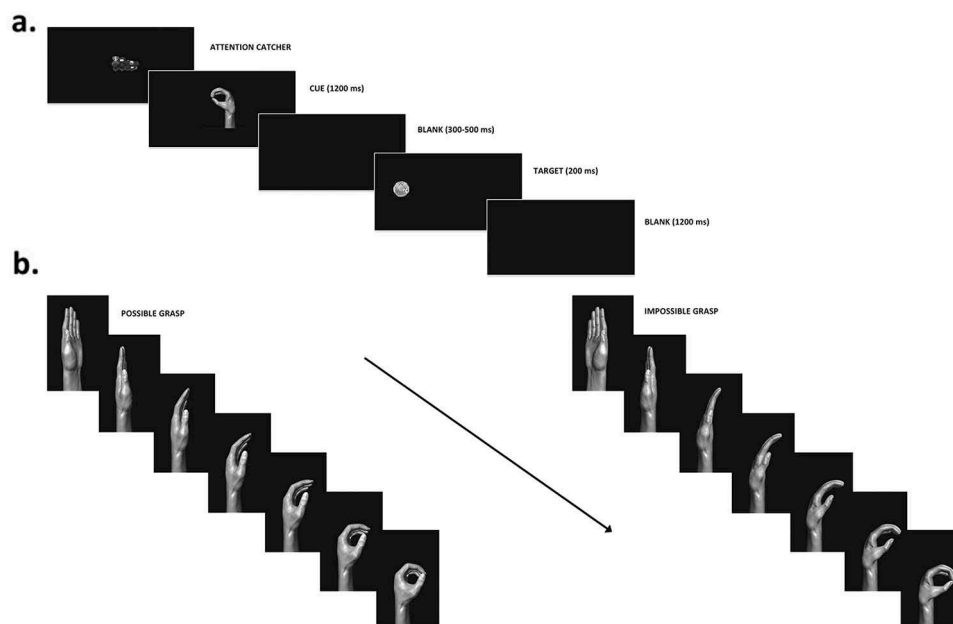
Figure 1. (a) A schematic representation of the sequence of events presented on each trial. This included a dynamic grasp displayed at the center of the monitor, which cued a peripheral target in either a valid way, as shown in example, or an invalid way. (b) A schematic representation of the crucial frames of the biomechanically possible and impossible hand gestures used as cue.

i.e., velocity and duration of the hand movement. In particular, the angle of fingers' and phalangeal joints' displacements was matched frame by frame between the two types of grasping; see Figure 1.

For each type of grasping, stimuli were presented in blocks of 16 trials, 8 valid (4 with left- and 4 with right-sided targets) and 8 invalid (4 with left- and 4 with right-sided targets). There was no restriction in number of blocks or trials shown, i.e., they could be played indefinitely. The experimental session terminated when infants looked away from the screen during five consecutive trials. On average, 48 trials (range = 33–72) were presented for the biomechanically possible grasping and 44 trials (range = 34–57) for the biomechanically impossible grasping. The total number of trials was not significantly different for the two types of action ($p > .43$). Also, there was no between- or within-group difference in the number of valid and invalid trials that were presented (possible action: 25 valid and 23 invalid trials; impossible action: 22 valid and 22 invalid trials; all ps > .11). The sequence and timing of the stimuli were controlled by E-prime 2.0 software.

ERP recording and analysis

Continuous scalp EEG was recorded from a 128-channel HydroCel Geodesic Sensor Net (Electrical Geodesic, Eugene, OR) that was connected to a NetAmps 300 amplifier (Electrical Geodesic, Eugene, OR) and

referenced online to a single vertex electrode (Cz). Channel impedance was kept at or below 100 kΩ and signals were sampled at 500 Hz. EEG data were pre-processed offline using NetStation 4.5 (Electrical Geodesic, Eugene, OR). The EEG signal was segmented to 1200 ms, post-stimulus onset, with a baseline period beginning 100 ms prior to target onset. Data segments were filtered using a 0.3–30 Hz bandpass filter and baseline-corrected using mean voltage during the 100 ms pre-stimulus period. Automated artifact detection was applied to the segmented data to detect individual sensors that showed >200 μV voltage changes within the segment period. The entire trial was excluded if more than 18 sensors (15%) overall had been rejected. Data were then inspected manually to mark as bad segments containing drift and eye blinks. We also manually marked as bad segments belonging to trials in which the infant did not look at the cue or did not keep central fixation at least until the target offset, as assessed by offline coding of the infant's video. Bad segments identified by either procedure, i.e., automatic and manual, were 36% of the total number of presented trials for the biomechanically possible grasp and 34% for the biomechanically impossible grasp, and they were excluded from further analysis. Of the remaining trials, individual channels containing artifacts were replaced using spherical spline interpolation. For each participant, average waveforms were generated within each experimental condition (valid and

invalid separately for left- and right-sided targets) only if at least 10 artifact-free trials were overall available per condition collapsed across the target-side. Averaged data were then re-referenced to the average reference. Overall, for the biomechanically possible grasp, each subject contributed with a mean number of 15 trials (range 13–24) to the valid condition average and a mean number of 15 trials (range 10–25) to the invalid condition average ($p > .5$), whereas for the biomechanically impossible grasp, each subject contributed with a mean number of 15 trials (range 12–20) to the valid condition average and a mean number of 13 trials (range 10–21) to the invalid condition average ($p = .01$). The mean number of trials per condition did not differ between the two groups (all $ps > .45$).

Inspection of the grand-averaged waveforms revealed that the two ERP components of interest, i.e., the P100 and N290, were elicited at the target onset over occipito-temporal scalp sites contralateral to the hemifield of stimulus presentation, but not over homologous ipsilateral sites (Figure 2). Thereby, ERP responses to the target were analyzed from posterior scalp sites of the contralateral hemisphere only. Based on visual inspection of both the grand-averaged and individual waveforms, 12 electrodes were identified for the ERP analysis: electrodes 71-70(O1)-66-65-64-58(T5) over the left hemisphere to analyze ERP in response to valid and invalid right-sided targets, and electrodes 76-83(O2)-84-90-95-96(T6) over the right hemisphere to analyze ERP in response to valid and invalid left-sided targets (Figure 2). For each participant, signal from homologous electrodes of the two hemispheres (71/76, 70(O1)/83(O2), 66/84, 65/90, 64/95, 58(T5)/96(T6)) was averaged to analyze ERP responses to valid and invalid targets across the whole visual field. Based on grand-averaged data and individual data, peak amplitude and latency of P100 and N290 were extracted within a time window of 100–230 ms and 200–330 ms, respectively. For each ERP component, a repeated-measures analysis of variance (ANOVA) was separately carried out on latency and/or amplitude (as
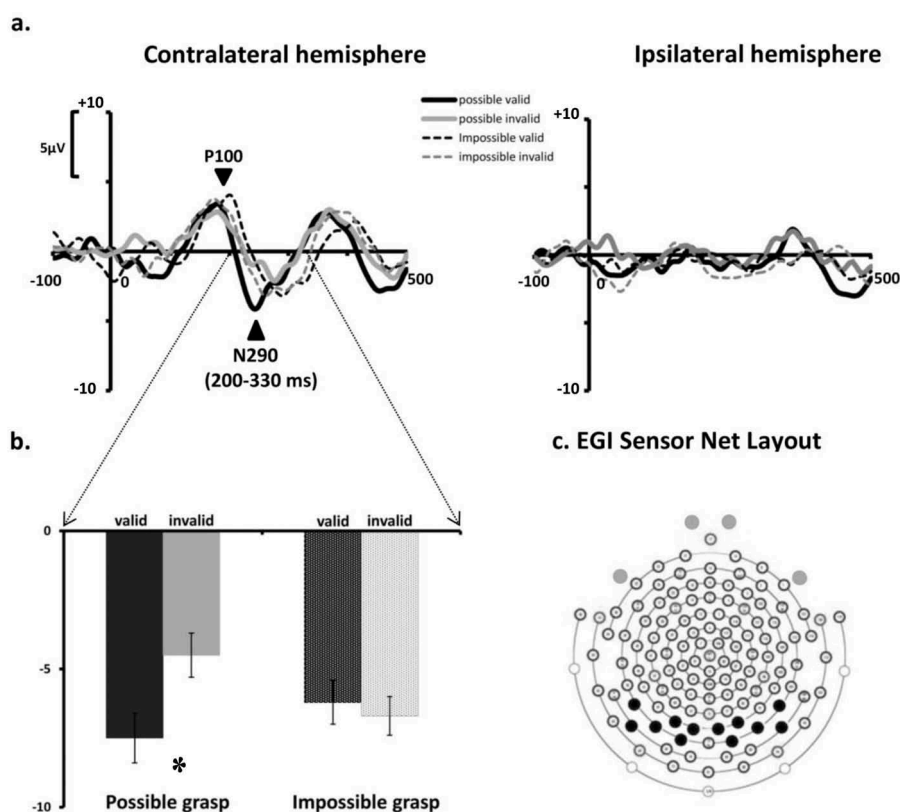

Figure 2. (a) ERPs waveforms elicited by the target cued by possible grasps (solid lines) and impossible grasps (dashed lines) on valid trials (black lines) and invalid trials (gray lines) in the hemisphere contralateral (left panel) and ipsilateral (right panel) to the hemifield of target presentation. ERPs were averaged across the hemifield of target presentation and the electrodes selected for the analysis. The number of trials going into the grand averages were 183 for the possible valid, 175 for the possible invalid, 182 for the impossible valid, and 161 for the impossible invalid condition. (b) Mean amplitude of the N290 component in response to valid and invalid targets cued by possible and impossible grasps. Error bars represent SEM; *$p < .01$. (c) The recording layout of the EGI sensor net. The two electrodes on the outside of the eyes (125, 128) and the two below the eyes (126, 127) were not used and are marked in gray in the layout. The posterior electrodes, marked in black, were selected for the ERP analysis.

obtained by collapsing together averaged amplitude and latency from each pair of homologous electrodes) with target validity (valid vs. invalid) as within-subjects factor and grasp type (biomechanically possible and impossible) as between-subjects factor.

Results

P100 (100–230 ms)

The ANOVAs did not reveal any significant main effect of grasp type and target validity as well as any no significant grasp type by target validity interaction for both the peak amplitude and latency of P100 (all ps > .13).

N290 (200–330 ms)

As for the peak amplitude of N290, the ANOVA revealed no main effect of grasp type (p > .65), a marginally significant main effect of target validity, $F(1,22) = 4.3$, $p = .051$, $\eta^2 = .16$, but a significant Grasp Type by Target Validity interaction, $F(1,22) = 9.1$, $p < .01$, $\eta^2 = .29$. Bonferroni post hoc test indicated that the amplitude of the N290 was larger in response to valid (-7.5 µV) than invalid (-4.5 µV) targets cued by a biomechanically possible grasp, $p < .01$, whereas there was no difference between the amplitude of the N290 in response to valid (-6.2 µV) and invalid (-6.7 µV) targets cued by a biomechanically impossible grasp, $p = .9$; see Figure 2. Bonferroni post hoc test also indicated that the amplitude of the N290 in response to valid and invalid targets did not differ between infants cued with biomechanically possible and impossible grasps, ps > .8.

As for the peak latency of N290, no main effects or interactions attained statistical significance (all ps > .09).

Discussion and conclusions

In the present study, 6-month-old infants were cued with spatially non-predictive hand grasping toward or away from the position of an impending target stimulus, i.e., valid and invalid trials, respectively. Participants were divided into two groups, one presented with biomechanically possible grasps, the other one with biomechanically impossible grasps. Scalp ERPs in response to target onset were analyzed as a function of the validity of the trial and the biomechanical properties of the cue. In line with previous EEG studies using the Posner paradigm with infant participants (Richards, 2000), we observed two ERP components in response to the target onset over occipital scalp sites contralateral to the hemifield of stimulus presentation, namely the P100, peaking at about 165 ms (slightly later than in previous studies; Richards, 2000) and the N290, peaking at about 270 ms. Although this latter component likely corresponds to the N1 reported by Richards (2000), we preferred to label it N290 in accord with the infant ERP literature (e.g., Nelson, Thomas, & de Haan, 2006). Results showed a modulation of the amplitude of N290 as a function of trial validity for infants presented with the possible gesture, but not for infants presented with the impossible gesture: for biomechanical possible grasps the amplitude of N290 was larger in response to targets at the cued than at the uncued location.

The ERP validity effect found in the present study using the direction of a human action to cue the position of the impending target is analogous to that reported in previous ERP studies employing a spatial cuing paradigm with exogenous, non-social cues (Hillyard & Anllo-Vento, 1998; Richards, 2000). In both cases, the spatial cue affected an early ERP component related to the sensorial analysis of the target stimulus and was significant over posterior scalp sites contralateral to the hemifield of target presentation, where attention was presumably driven by the cue. Therefore, our results can be interpreted as being driven by the shift of visual-spatial attention triggered by the valid cue, which enhanced sensorial analysis of stimuli at the attended location. Our findings show for the first time that early in development the direction of social signals related to other's actions can affect neural processing of targeted stimuli similarly as other, non-social spatial cues. This leads to the suggestive hypothesis that early sensitivity to the direction of social signals might have developed as a means to select potentially relevant information in the environment and facilitate sensory processing of that information. This hypothesis is supported by ERP evidence indicating enhanced processing of objects previously displayed at a peripheral location and gazed by the central adult face (Reid et al., 2004) as well as by behavioral evidence showing faster localization responses to targets displayed at the spatial position congruent with the direction of a human action than to targets located at the incongruent position (Bardi et al., 2015; Bertenthal et al., 2014; Daum & Gredebäck, 2011; Daum et al., 2013; Farroni et al., 2000, 2003; Hood et al., 1998; Rohlfing et al., 2012; Wronski & Daum, 2014).

Unlike previous studies on infants' covert spatial attention showing ERP validity effect at the level of the early P100 component (Richards, 2000), here we observed a modulation restricted to N290. Although several methodological differences might explain this discrepancy, the one concerning the nature of the cue (i.e., social in the present study, non-social in the

previous study) appears to us as the most relevant. Indeed, the N290 component is specifically sensitive to social information in infancy (Csibra, Kushnerenko, & Grossman, 2008; de Haan, Johnson, & Halit, 2003; Luyster, Powell, Tager-Flusberg, & Nelson, 2014; Nelson et al., 2006). Moreover, over posterior scalp regions the N290 is the earliest reported component to reflect object–action links (Senju et al., 2006). Thus, it is reasonable to hypothesize that the modulation of the N290 amplitude observed in the present study reflects the facilitation of sensory analysis triggered by social cues. On this ground, the current findings suggest that the modulation of the N290 amplitude could be taken as a hallmark of sensory, as well as higher perceptual-cognitive, processes elicited by social information.

Nonetheless, it is important to consider that in developmental studies the N290 and the P400 have been identified as a pair of components with topographical and functional analogies: indeed, both components are recorded over roughly the same topographical locations and are thought to be precursors of the adult face-sensitive N170 (Csibra et al., 2008; de Haan et al., 2003; Luyster et al., 2014; Nelson et al., 2006). This leaves open the possibility that the current modulation of N290 might reflect the encoding of the relationship between the hand gesture and the stimuli that potentially represent the action goal, which in previous studies with a different paradigm was found to modulate P400 (Bakker et al., 2015; Gredebäck et al., 2010; Melinder et al., 2015). In this perspective, differences in the temporal window in which peak effects were observed in the present and previous studies might depend on the different types of action (dynamic versus static) that were used as cue. Dynamic hand grasps, as used in the present study, may trigger earlier ERP effects compared to those elicited by static actions, as used in previous studies (Bakker et al., 2015; Gredebäck et al., 2010; Melinder et al., 2015), similar to the overall speeding-up of saccadic localization responses observed when targets were preceded by dynamic as compared to static action (Rohlfing et al., 2012).

A critical aspect of the current findings is that, unlike infants who were shown biomechanically possible hand gestures, those who saw biomechanically impossible gestures showed no significant modulation of ERP responses as a function of trial validity. This is also in line with previous evidence showing no ERP modulation when the hand gesture was not part of the infant's motor skills (Bakker et al., 2015; Melinder et al., 2015). Indeed, an action impossible to be executed cannot be part of the infant's motor repertoire. Thus, our findings extend previous evidence indicating that the neural responses that accompany infants'

comprehension of referential actions are modulated by the infant's motor skill and undergo substantial development.

Unlike in previous studies (Bakker et al., 2015; Melinder et al., 2015), which included multiple age groups and showed participants an action that could be proficiently performed by the older, but not the younger infants, here we showed participants with a grasping action, which all infants were capable to perform. The finding that action priming effects were observed only for the possible gesture converges with recent demonstrations that 6-month-olds discriminate between biomechanically possible and impossible hand movements, as they make more anticipatory gaze shifts toward the goal of the possible, as compared to the impossible, action (Geangu et al., 2015). The current results are the first to demonstrate that the ability to detect violations of hand biomechanics during observation of gestures, included in the infants' motor repertoire, can interfere with the possibility of using the direction of the gestures as a cue to shift attention in space.

Two hypotheses can be proposed to explain the influence of biomechanical plausibility on the action priming effect. One possibility is that infants quickly discriminate between possible and impossible actions; the outcome of this first evaluation allows them to extract information about directionality from the possible, but not the impossible, action. Alternatively, hand actions that violate biomechanical properties may represent more salient or complex visual stimuli than actions that respect biomechanical properties of human movements. This would in turn yield greater difficulty in disengaging attention from the impossible than the possible action, preventing infants from showing any ERP validity effect with the former as compared to the latter.

Overall, the present findings indicate that information about goal and movement direction conveyed by a grasping action modulates ERP responses in 6-month-old infants. This information is used to drive attentional shifts in space, select potentially relevant information and enhance efficiency at early (sensorial and perceptual) stages of information processing at the attended location. Importantly, action priming effects can only be observed in infants when biomechanical properties are respected, and not when they are violated. This novel result highlights the relevance of biomechanical properties of a human movement for the effective shifting of attention based on directional information conveyed by human hand gestures and, on a broader perspective, for perceptual-cognitive processes taking place during observation of goal-directed actions.

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