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SHORT REPORT

The early development of human mirror mechanisms: evidence from electromyographic recordings at 3 and 6 months

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Abstract

In primates and adult humans direct understanding of others' action is provided by mirror mechanisms matching action observation and action execution (e.g. Casile, Caggiano & Ferrari, 2011). Despite the growing body of evidence detailing the existence of these mechanisms in the adult human brain, their origins and early development are largely unknown. In this study, for the first time, electromyographic (EMG) measures were used to shed light on the emergence of mirror motor mechanisms in infancy. EMG activity was recorded while 6- and 3-month-old infants watched two videos displaying an agent reaching for, grasping and bringing an object either to the mouth or to the head. Results indicate that the motor system of 6-month-olds, but not 3-month-olds, was recruited and selectively modulated during observation of the goal-directed actions, favoring the idea that mirror mechanisms driving action understanding gradually emerge during early development.

Introduction

Neuroimaging and behavioral evidence suggests that adult humans and non-human primates possess a neurophysiological system enabling them to understand others' actions and intentions through mirror mechanisms that unify action observation and execution within the same observer's motor representation (e.g. Casile et al., 2011; Cattaneo & Rizzolatti, 2009). Yet, the origins of the mirror system in human ontogeny are largely unknown. The current study attempts to shed light on this issue, investigating whether the infant's motor system is recruited and selectively modulated during the observation of goal-directed actions.

Based mainly on pioneering studies of neonatal imitative behavior (Meltzoff & Moore, 1977, 1983), the hypothesis has been put forward that the capacity to match observed and executed actions is already available at the beginning of postnatal experience (Lepage & Théoret, 2007; Meltzoff & Decety, 2003). According to an alternative proposal, mirror mechanisms may represent a byproduct of associative learning that relies on sensorimotor experience (Heyes, 2010). Finally, within the neuroconstructivist framework, it has been proposed that innate predispositions to perform our own actions and to pay particular attention to them would promote active learning of the association between the execution and perception of an action (Del Giudice, Manera & Keysers, 2009).

Behavioral evidence supporting the early existence of mechanisms able to match an observed action with the observer's motor representation of the same action comes from studies investigating infants' ability to imitate others' actions (Meltzoff, 2007). Infant research has also documented the effects of action observation on action execution (Daum & Gredebäck, 2011), and, vice versa, the effects of action execution on action perception (Cannon, Woodward, Gredeback, von Hofsten & Turek, 2012; Libertus & Needham, 2010; Sommerville, Woodward & Needham, 2005). Finally, it has been shown that goal anticipation during action observation (Falck-Ytter, Gredebäck & von Hofsten, 2006; Kochukhova & Gredebäck, 2010) may be dependent on manual ability in both infants (Kanakogi & Itakura, 2011) and toddlers (Gredebäck & Kochukhova, 2010).

Fewer attempts have been made to explore the neurophysiological correlates of mirroring mechanisms early in development. Using near infrared spectroscopy

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(NIRS), Shimada and Hirachi (2006) showed that the motor cortical areas that were activated when 6- to 7-month-old infants performed hand actions were also active during the passive observation of an experimenter manipulating an object. However, the link between this activation and infants' understanding of goal-directed actions remained unclear because the motor cortex of infant participants was also activated by the observation of an object moving, without any goal-directed action being performed. By using electroencephalographic (EEG) or magnetoencephalographic (MEG) techniques, other studies observed a decrease in neural synchrony at central sites associated with both action execution and observation – i.e. *mu-rhythm desynchronization* – in infants from 8 months of age (Marshall & Meltzoff, 2011; Nyström, Ljunghammar, Rosander & von Hofsten, 2010; Southgate, Johnson, El Karoui & Csibra, 2010; Southgate, Johnson, Osborne & Csibra, 2009; Stapel, Hunnius, van Elk & Bekkering, 2010) as well as in children (Berchicci, Zhang, Romero, Peters, Annett, Teuscher, Bertollo, Okada, Stephen & Comani, 2011; Lepage & Théoret, 2006). In adults, modulation of the mu rhythm at central sites contingent upon action observation is considered as an index of action perception–execution overlap (Streltsova, Berchio, Gallese & Umiltà, 2010). However, to date neurophysiological indexes of the presence of mirror mechanisms in the first 6 months of life are still lacking.

Recently, Cattaneo and colleagues (Cattaneo, Fabbri-Destro, Boria, Pieraccini, Monti, Cossu & Rizzolatti, 2007) used electromyography (EMG) to show that 5- to 9-year-old children activate mouth-opening muscles while observing someone else grasping an object and bringing it to the mouth, but not while observing an agent grasping an object and placing it into a container located on the agent's shoulder. The demonstration that a specific action chain was activated up to the peripheral muscles provided direct evidence that, in children, the motor system can be recruited and selectively modulated during action observation, suggesting that, by the age of 5 years, others' actions are mapped onto the observer's motor representation of the same actions.

Here, we investigated whether and to what extent the motor system is recruited and selectively modulated during the observation of goal-directed actions early in development. To this end, we recorded surface EMG activity from the muscles responsible for mouth opening in healthy, full-term 6-month-old (Experiment 1) and 3-month-old (Experiment 2) infants watching two video-clips. The videos displayed an agent either reaching for an object and bringing it to the mouth or reaching for an object and placing it on the head. The two displayed actions had different goals, but were similar for biomechanical properties and other low-level characteristics. Thus, any dissociation in the modulation of infants' muscles activation would represent a direct index of the selective recruitment of the infants' motor system in response to the observation of these goal-directed actions (i.e. motor resonance).

Experiment 1

Method

Participants

Thirty healthy, full-term 6-month-olds (12 females, mean age = 6 months 9 days, range = 167–201 days) participated in the study. Sixteen additional infants were tested, but then discarded from the final sample because of fussiness and not completing the minimum number of trials required for data analysis. The protocol was carried out in accordance with the ethical standards of the Declaration of Helsinki (BMJ 1991; 302: 1194) and approved by the ethical committee of the University of Milano Bicocca. Parents gave their written informed consent.

Stimuli, apparatus and procedure

EMG activity was recorded from suprahyoid muscles (SM, a group of muscles used for mastication and swallowing) during the observation of videos depicting an actress reaching for, grasping and bringing either an object to the mouth (object-to-mouth action) or an object on to the head (object-to-head action) (Figure 1). Each infant was shown two different actions, each cued by a different object. As soon as the video started, the object provided a cue to understand which was the goal of the action. In order to control for possible effects of the displayed object, participants were assigned to two different groups: Group 1 (*N* = 17, seven females, mean age = 6 months and 9 days, range = 171–201 days) infants watched an agent bringing a pacifier to the mouth and a piece of lego on to the head, Group 2 (*N* = 13, five females, mean age = 6 months and 8 days, range = 167–200 days) infants were shown an agent bringing the piece of lego to the mouth and the pacifier onto the head.

The experiment took place in an audiometric cabin equipped with a Faraday cage, and participants were seated in an infant seat ~60 cm from a 24-inch screen. Each trial began with an animated fixation point and, when the infant looked at it, the experimenter started the video. Each video lasted 4 sec and consisted of 100

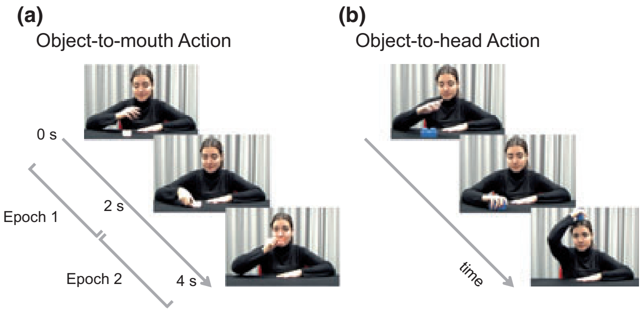

Figure 1 *A schematic representation of the trials diplayed, with the crucial frames of the (A) object-to-mouth action and (B) object-to-head action.*

frames, 40 ms each. In particular, for both actions, frame 51 (i.e. 2 s from the video onset) depicted the exact moment in which the actress's hand touched the object. Each phase of the actress's movement, i.e. reaching for, grasping and bringing, had the same duration across the two different actions. In the object-to-mouth action, the actress opened her mouth during the bringing phase, slightly before the object came into contact with her mouth. At the end of each video, a colored circle slowly expanding and contracting was displayed for 3.5 sec, followed by a 500 ms blank screen.

For each group of infants, the two types of action were presented in separate and counterbalanced blocks of trials. There was no restriction on number of blocks or trials shown, i.e. they could be played indefinitely. However, when infants reached the criterion of watching at least 70% of the video duration, across five trials, the block ended and the subsequent block of trials was shown. When infants looked away for at least 2 seconds during five consecutive trials, the experimental session ended. On average, 18.6 trials (range = 10–43) were presented for each action type. The number of presented trials was not significantly different for the two types of action ($p > .8$). The computer controlled the sequence and timing of the stimuli.

EMG recording, signal processing and data analysis

A Digitimer electromyograph was used to record the EMG signal from the infants' SM. Two surface electrodes for pediatric use were placed 2 cm apart under the infant's chin symmetrically to the midline. The reference electrode was positioned ~2 cm above the nasion. The EMG signal was amplified (gain 1000), filtered (band-pass: 10–1000 Hz), sampled at 1 kHz, and stored for offline filtering (150 Hz; high-pass: 30 Hz). Impedance was between 5 and 10 kΩ. The EMG signal was then rectified for analysis.

Infants' looking time toward the stimuli was coded on-line. Trials in which infants looked at the video for less than 70% of its duration were discarded on-line. Looking time was also coded off-line by a second observer. Pearson correlation revealed a high degree of agreement between the two coders on the trials to be discarded based on the looking time criterion, r (30) = .99, $p < .0001$. In order to avoid any spurious effect produced by infants' movements while watching the videos, trials were also discarded off-line whenever signal noise and motion artifacts contaminated the recordings. As a consequence, about 40% of object-to-mouth and object-to-head action trials were excluded from data processing. Only infants with at least four trials per action type were included in the analyses. On average, each infant contributed to the analyses with 10 trials (range = 4–29) for each action type. The number of trials included in the analysis was not significantly different for the two types of action (all ps > .4).

The EMG signal recorded during the 4-sec video presentations was segmented into two epochs, one corresponding to the first half (Epoch 1, 2 sec of duration) and the other to the second half (Epoch 2, 2 sec of duration) of the video-clips. The area under the curve of the rectified EMG activity was computed on a trial by trial basis, normalized (z-scores) and averaged separately for each type of action and epoch.

Recordings of infants' facial movements were coded off-line to explore the presence of mouth-opening movements during action observation. To this end, we considered the duration of mouth-opening movements (i.e. how long the mouth remained opened during the observation of the video-clips) in each trial of the two experimental conditions. A mouth-opening movement was defined as a movement of mouth opening leading to a variation in the mouth's shape along the horizontal and vertical plane, so as to depict an 'O', followed by the closing of the mouth. Similar to the EMG analysis, the behavioral analysis included only those trials with at least 70% of looking time. However, unlike the EMG analysis, trials were not discarded because of motion artifacts. Therefore, the trials used for EMG and behavioral analyses did not perfectly match. To calculate inter-coder reliability, a second observer coded mouth-opening movements in a sample of eight participants. Pearson correlation revealed a high degree of agreement between the two coders, r (8) = 0.99, $p < .0001$.

Results

A repeated-measures analysis of variance (ANOVA) on the EMG signal with group (group 1 vs. group 2) as the between-subjects factor, and type of action (object-to-mouth vs. object-to-head action) and epoch (epoch 1 vs. epoch 2) as within-subjects factors revealed a significant Type of Action × Epoch interaction, $F(1, 28) = 12.81$, $p = .001$, $\eta p^2 = .31$. Post-hoc comparisons (Newman-Keuls test) indicated that observing an agent bringing an object to the mouth produced an increase of SM activity, which was greater in epoch 2 as compared to both epochs 1 and 2 of the object-to-head action (all $ps < .01$). Importantly, for the object-to-mouth action SM activity also showed a significant increase between epoch 1 and epoch 2 ($p < .01$). Finally, SM activity during epoch 1 of the two actions did not differ ($p = .8$; see Figures 2a and 3a).

Off-line inspection of the data indicated that only 13 (out of 30) infants showed mouth-opening behavior during the observation of the video-clips. For these infants, duration of mouth-opening movements was entered into a repeated-measures ANOVA with type of action (object-to-mouth vs. object-to-head action) and epoch (epoch 1 vs. epoch 2) as within-subjects factors. The ANOVA did not reveal any significant effect (all $ps > .1$). Behavioral and EMG scores were also correlated. Behavioral scores were calculated by subtracting the duration of mouth-opening behavior in epoch 1 from the duration of mouth opening behavior in epoch 2. EMG scores were calculated by subtracting SM activity recorded in epoch 1 from SM activity in epoch 2. To calculate the EMG score, we used the same trials as for the EMG signal analysis (i.e. trials without motion artifacts). Correlational analysis revealed that overt mouth-opening behavior and SM activity were positively correlated in the object-to-mouth action ($r_s = .53$, $p = .03$), but not in the object-to-head action ($r_s = .43$, $p = .07$) (Figure 4).

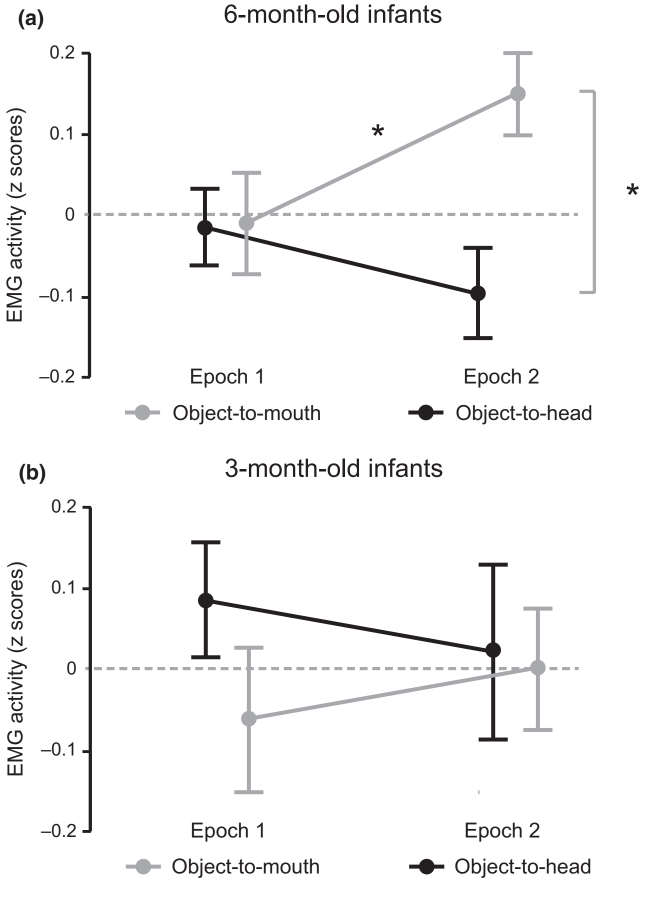

Figure 2 *SM activation during the object-to-mouth (grey lines) and object-to-head (black lines) actions in (A) 6-month-old and (B) 3-month-old infants. Error Bars = SEM; * = p < .05.*

Discussion

Results showed that SM activity recorded while infants looked at an adult agent performing a grasping action was modulated by the action goal. A greater activation of the SM muscle for object-to-mouth action as compared to object-to-head action during the bringing epoch

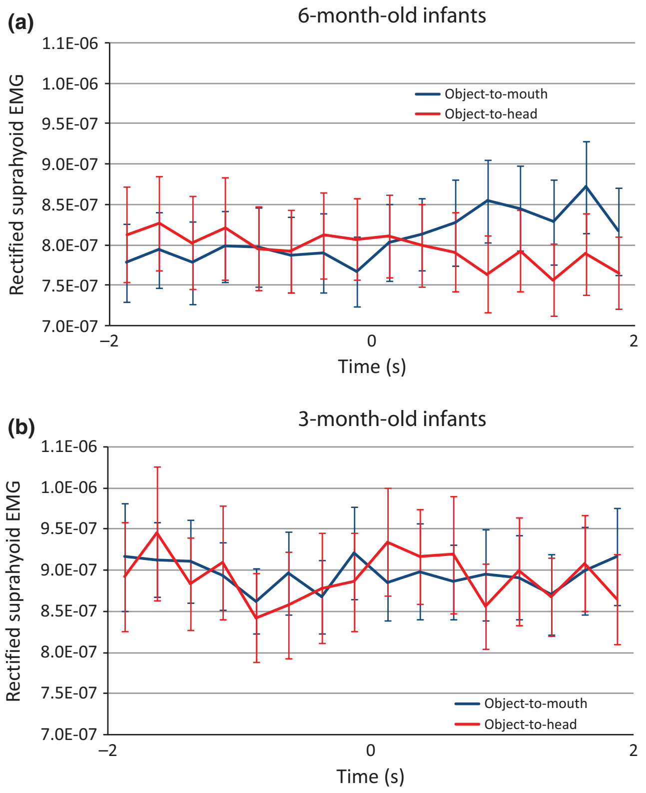

Figure 3 *Time-course of the rectified EMG activity of SM muscles during the observation of the object-to-mouth (blue lines) and object-to-head (red lines) actions in (A) 6-month-old and (B) 3-month-old infants. Error Bars = SEM.*

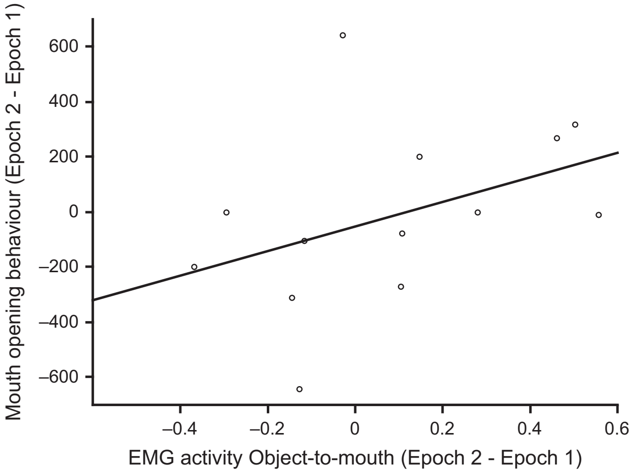

Figure 4 *Correlation between SM activity and overt mouth-opening behavior during the object-to-mouth action.*

was observed, suggesting a motor resonance-related effect arising only in the final stage of the agent's action.

The observed EMG modulation did not lead to a corresponding modulation of overt behavior, as suggested by the lack of any significant effect of the type of action on infants' mouth-opening behavior in the two epochs. Nevertheless, SM muscle activation and mouth-opening overt behavior were positively correlated, indicating that the EMG modulation observed in the current study is a reliable measure of sub-threshold motor activation.

Experiment 2

Methods

Participants

Nineteen healthy, full-term 3-month-olds (six females, mean age = 3 months and 11 days, range = 87–111 days) were tested. Ten additional infants were excluded from the final sample because of fussiness and not completing the minimum number of trials required for data analysis. The protocol was carried out in accordance with the ethical standards of the Declaration of Helsinki (BMJ 1991; 302: 1194) and approved by the ethical committee of the University of Milano Bicocca. Parents gave their written informed consent.

Stimuli, apparatus and procedure

These were the same as in Experiment 1. However, since no effect of the type of object was found in Experiment 1, in Experiment 2 all participants were presented with the video in which the actress performed the object-to-mouth action by bringing the pacifier to the mouth and the object-to-head action by bringing the lego to the head. These were the same experimental conditions as for Group 1 in Experiment 1. We used the object-action pair that could be thought of as having more chances to modulate infants' SM motor activity, that is pacifier to the mouth and lego onto the head. On average, 14.6 (range = 10–28) and 12.9 (range = 5–22) trials were presented for the object-to-mouth and the object-to-head action, respectively. The number of presented trials was not significantly different for the two types of action (p = .29).

EMG recording, signal processing, and data analysis

These were the same as in Experiment 1. Thus, for the EMG analysis trials were discarded on-line when the infant's looking time was shorter than 70% of the total video duration and off-line whenever signal noise and motion artifacts contaminated recording. As in Experiment 1, only infants with at least four trials per action type were included in the analyses. On average, the analyses were performed on 5.8 (range = 4–10) and 6.6 (range = 4–11) trials for the object-to-mouth and the object-to-head action, respectively. The number of trials included in the analysis did not differ for the two types of action (p = .14). As in Experiment 1, Pearson correlation revealed a high degree of agreement between the two coders on the trials to be discarded based on the looking time criterion, r (19) = 0.99, $p < .0001$. Inter-coder reliability calculated in a sample of eight participants was high also for overt mouth-opening behavior, Pearson correlation, r (8) = 0.99, $p < .0001$.

Results

A repeated-measures ANOVA on SM activation with type of action (object-to-mouth *vs.* object-to-head) and epoch (epoch 1 vs. epoch 2) as within-subjects factors did not attain any significant result (all ps > .3, $\eta p^2 = 0.05$) (see Figures 2b and 3b). As for the behavioral analysis, mouth-opening behavior was observed in 9 out of 19 infants. A repeated-measures ANOVA on the duration of mouth-opening behavior did not show any significant main effect or interaction (all ps > .19).

In order to substantiate possible age effects on SM activity found in the two experiments, we compared the EMG responses exhibited by the 3-month-old infants tested in Experiment 2 and those manifested by the 6-month-olds in Group 1 of Experiment 1. A repeated-measures ANOVA on SM activation with type of action (object-to-mouth vs. object-to-head) and epoch (epoch 1 vs. epoch 2) as within-subjects factors and age (3 vs. 6 months) as the between-subjects factor revealed a significant Age × Type of Action × Epoch interaction, $F(1, 34) = 7.3$, $p = .01$, $\eta p^2 = 0.18$.

General discussion

EMG recordings (mostly combined with transcranial magnetic stimulation) have been widely used to investigate mirror mechanisms in adults (e.g. Fadiga, Craighero & Olivier, 2005), whereby the demonstration that a specific action chain is activated up to the peripheral muscles provides evidence that others' actions are mapped onto the observer's motor representation of the same actions. In the present study, EMG was employed for the first time to investigate mirror mechanisms in infancy. The activity of muscles responsible for mouth opening (i.e. suprahyoid muscles, SM) was recorded while 3- and 6-month-old infants watched videos displaying an adult agent reaching for, grasping and bringing an object either to the mouth or to the head. We found that SM activity changed with the goal of the observed grasping action in 6-month-old, but not in 3-month-old, infants.

Six-month-olds' SM activity increased during observation of the action involving mouth-opening muscles as compared to the observation of the action not involving the muscles. This indicates the presence, at 6 months of age, of a motor resonance-related effect and suggests that the motor system is recruited during the observation of others' actions. Importantly, such an effect was selectively found for the latest phase of the action, that is the bringing phase, during which the action goal was achieved. This finding differs from the results obtained with older children by Cattaneo and colleagues (2007), who observed a modulation of mouth-opening muscles already during the earlier phases of the grasping action in 5- to 9-year-old children.

The delay in EMG modulation observed in infants as compared to children might be explained in at least two ways. One may claim that infants process information more slowly than children, resulting in a delay of the effect. Both behavioral and neurophysiological studies typically report a decrease in latency of responses during development (e.g. Nelson & Monk, 2001). Another possibility would be that a developmental trend exists from a motor resonance effect arising only during the observation of the actions' final goal to a motor resonance effect driving anticipation of the goal. Accordingly, using EEG measures, Stapel *et al.* (2010) demonstrated that, at 12 months, infants capitalize on their motor system to generate predictions about grasping-to-mouth actions. This explanation would imply that the ability to visually anticipate object-directed actions that infants manifest at 6 months in anticipatory eye-movement paradigms (Kochukhova & Gredebäck, 2010) may not originate directly and/or exclusively from motor resonance mechanisms triggered within the infants' motor system by action observation. Indeed, recent evidence questions the interpretation of adults' proactive goal-directed eye movements as reflecting mirror mechanisms (Eshuis, Coventry & Vulchanova, 2009). Similarly, infants' anticipatory eye movements might not be related to mirror motor simulation but rather to an interpretation of the observed action in terms of goals (i.e. teleological reasoning; see Csibra, 2003; Csibra & Gergely, 2007). Moreover, it is important to note that the specific nature of the action modulates infants' ability to show proactive goal-directed eye movements. In Kochukhova and Gredebäck's (2010) study, 6-month-olds anticipated the goal of a familiar action such as feeding, but not the goal of an unfamiliar action such as combing. Similarly, in Falck-Ytter *et al.*'s (2006) study, 6-month-old infants, unlike 12-month-olds, did not anticipate the goal of placing actions. Future studies may directly investigate whether individual differences in 6-month-olds' familiarity with an action might affect motor resonance, with infants familiar with the action showing greater and earlier motor resonance than infants not familiar with the same action.

Although the analysis of mouth-opening behavior did not show any motor resonance effect during action observation, at 6 months of age the modulation of motor activity correlated with overt mouth-opening behavior. We interpret this finding as evidence that the infants' motor system simulates under-threshold the observed action in a congruent fashion, and that EMG is a powerful measure for capturing subtle changes occurring during sensorimotor processing in infants.

Different interpretations for the lack of motor resonance effects in 3-month-old infants might be advanced. Recently, several studies have emphasized the role of sensorimotor experience related to action execution on infants' perception of others' actions (e.g. Libertus & Needham, 2010; Sommerville *et al.*, 2005). Accordingly, one possibility is that, at 3 months of age, motor grasping abilities are not sufficiently mastered in order to contribute to infants' action understanding. More specifically, the mirror system hypothesis predicts that only motor acts that are present in the motor repertoire of the observer are effective in activating the mirror system (Cattaneo & Rizzolatti, 2009). Therefore, 3-month-old infants are not expected to mirror a reach-for-grasping action, as it is not within their repertoire at this age. However, further studies with young infants of similar age are needed to corroborate this claim and disentangle the relative contribution of general maturational processes and sensorimotor experience in the early emergence of motor resonance effects.

Another possibility is that, in preverbal infants, the early development of a linkage between action perception and action production may be associated with the emergence of imitation capacity (Saby, Marshall & Meltzoff, 2012). Imitation abilities have been observed in newborn infants (Meltzoff & Moore, 1977, 1983; but see Anisfeld, Turkewitz, Rose, Rosenberg, Sheiber, Couturier-Fagan & Ger, 2001; Jones, 1996), and decline by 2–3 months of age (Abravanel & Sigafoos, 1984; Fontaine, 1984). Thus, it would be interesting to investigate also whether motor resonance effects are present at birth and decline between birth and 3 months of age.

Overall, the present evidence favors the idea that the development of mirror resonance mechanisms, that may support infants' ability to understand others' actions, undergoes a process of gradual refinement during development, rather than being already available at the beginning of postnatal experience. In particular, it seems that mirror mechanisms are functional at 6 months of age, but, unlike in older children, they are activated only when the action is concluded and the goal is achieved. Future studies might address the issue of whether and when, as found by Cattaneo and colleagues (2007) in 5- to 9-year-old children, motor resonance can be observed from action outset, allowing the observer to anticipate the goal of the agent.

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