How learning to shake a rattle affects 8-month-old infants' perception of the rattle's sound: Electrophysiological evidence for action-effect binding in infancy

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A R T I C L E   I N F O

Article history:
Received 18 February 2011
Received in revised form 23 April 2011
Accepted 21 May 2011

Keywords:
Action-effect binding
Sensorimotor learning
Motor resonance
Mirror neuron system
Ideomotor principle
Action training

A B S T R A C T

Bidirectional action-effect associations play a fundamental role in intentional action control and the development of the mirror neuron system. However, it has been questioned if infants are able to acquire bidirectional action-effect associations (i.e., are able to intentionally control their actions). To investigate this, we trained 8-month-old infants for one week to use a novel rattle that produced a specific sound when shaken. Infants were also presented with another sound, which was not related to an action. Thereafter, infants' EEG responses to these two sounds and to an additional, unfamiliar sound were recorded. Infants displayed a stronger mu-desynchronization above cortical motor sites (i.e., motor resonance) when listening to the action-related sound than when hearing other sounds. Our results provide therefore electrophysiological evidence that infants as young as 8 months are able to acquire bidirectional action-effect associations and parallel findings of audiovisual mirror neurons in the monkey brain.

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As adults we quickly learn that an action we perform, such as for instance hitting a drum, produces a specific effect, in our example a characteristic sound pattern. When we encounter the same sound at a later occasion, we can infer that it probably has been the consequence of this specific action. Theories have proposed that such associations between actions and their distal effects (i.e., bidirectional action-effect associations) play an important role in action control (Hommel et al., 2001) and the processing of others’ actions (Kohler et al., 2002).

In the nineteenth century, Lotze (1852) and James (1890) already suggested that actions are controlled through bidirectional action-effect associations (see also Prinz, 1997). According to this ideomotor theory of action control, action knowledge is acquired through the repeated co-occurrences of actions and their sensory effects and represented in terms of these action effects (Elsner and Hommel, 2001; Hommel et al., 2001; Kunde et al., 2002; Paulus et al., in press-a; Topolinski, in press; for a recent review see also Nattkemper et al., 2010). As the intention to elicit a particular sensory effect is assumed to directly activate the motor program that is associated with this effect, acquired action-effect associations underlie the voluntary control of actions (Elsner and Hommel, 2001; Hommel, 2009).

In a similar vein, the discovery of audiovisual mirror neurons in the monkey brain suggests a close link between an action’s typical effect and the associated motor program (Kohler et al., 2002). In particular, it was observed that neurons in the monkey’s premotor cortex show an increased rate of activation not only when the monkey performs an action himself, but also when he perceives the typical...
auditory effect of this action. To explain the acquisition and development of mirror neurons, Heyes and colleagues (Catmur et al., 2007, 2009; Heyes, 2001, 2010; Heyes and Ray, 2000) as well as Keysers and colleagues (Del Giudice et al., 2009; Keysers and Perrett, 2004) proposed that mirror neurons might be the product of an acquired association between sensory and motor codes, that is, based on sensorimotor learning.

Even though the acquisition of bidirectional action-effect associations is thought to play an important role in human action control (e.g., Hommel et al., 2001) and the development of mirror neurons (e.g., Del Giudice et al., 2009; Heyes, 2010), little is known about infants’ ability to acquire bidirectional action-effect associations. Research has shown that from early on infants are sensitive to the contingencies between their actions and the effects of these actions in the environment (e.g., Bahrick and Watson, 1985; Mast et al., 1980; for a review see Moore, 2006). Furthermore, it has been suggested that infants use these contingencies to guide and intentionally control their actions (e.g., Elsner and Aschersleben, 2003; Hauf et al., 2004; Hauf and Aschersleben, 2008; Verschoor et al., 2010). However, it has been argued that some of these results could also be explained by instrumental learning, as infants just repeated the actions that had been rewarded with an interesting effect (instead of having an expectation that the action leads to a particular effect). In other words, it has been suggested that infants’ action control is merely based on stimulus–response (S–R) learning and operant conditioning rather than on acquired action-outcome associations (Kenward et al., 2009; Klossek et al., 2008). Accordingly, more research is needed to investigate if infants can acquire bidirectional action-effect associations that can later be employed to intentionally control actions (e.g., Hommel et al., 2001) or to process other people’s actions (e.g., Kohler et al., 2002).

To address the question whether infants are able to acquire bidirectional action-effect associations and whether they indeed “mirror” others’ actions (i.e., activate the corresponding motor program when they perceive another person’s action) within their own motor repertoire when they perceive the effects of these actions, we examined infants’ brain responses to the perception of distal action effects with electroencephalography (EEG). Research with adults has repeatedly shown that spectral power decreases in the mu-frequency band above cortical motor sites provide a direct way of assessing activation in the motor system (e.g., Caetano et al., 2007). Frequency band analysis has thus become a reliable method to investigate cortical motor activation also in infants (Marshall et al., 2011; Nyström et al., 2010; Reid et al., 2011; Stapel et al., 2010; van Elk et al., 2008; for a review see Marshall and Meltzoff, 2011). To investigate infants’ acquisition of bidirectional action-effect associations, we trained 8-month-old infants for one week with a novel rattle that produced a specific sound effect when shaken. After the training period, infants’ electrophysiological responses to the sound were measured. Our main interest was to identify power-changes related to the presentation of the rattle’s sound. Typically, power-changes are expressed with respect to a pre-stimulus baseline period or as the difference between conditions. In the present study we used two other conditions to determine power-changes in the mu-frequency band: Infants’ brain responses to a likewise familiar, but non-action related sound (presented through a voice recorder during the training period) and to an unfamiliar auditory stimulus were recorded. If infants built bidirectional action-effect associations during their rattle training, perceiving the auditory stimulus that had been the effect of the infants’ own actions should activate the associated motor program. This should be reflected in a stronger desynchronization of power in the infants’ mu-frequency band above cortical motor areas for the action-related sound compared to the two other sounds that were not action-related.

1. Method

1.1. Participants

The final sample consisted of 15 8-month-old infants (age range: 7 months, 8 days to 8 months, 30 days; average age: 250 days; 6 boys). Four infants were tested but not included in the final sample because of equipment failure (n = 1) or fussiness (n = 3). The participants were recruited from public birth records and were healthy, full-term infants without any pre- or perinatal complications. Informed consent for participation was given by the infants’ parents. The families received a baby book or monetary compensation for their participation.

1.2. Stimuli

The stimulus material of the training phase consisted of three identical cylindric objects (d = 4.5 cm; h = 6 cm; see Fig. 1) made out of red plastic, as well as voice recorders (Voicetracer 600, Philips, Germany). When shaken, the objects produced three different sounds (due to their
content which could be a bell, a couple of tambourine disks fixed on a stick, or loose metal screws) and could thus be used as rattles. Additionally, the same three sounds were recorded and put on a voice recorder, so that they could be played to the infants. Each of the voice recorders contained recordings from only one of the three sounds. Cylindrical plastic boxes, in which the voice recorders could be inserted, served as containers so that the voice recorders could be put on the table in a stable position (see Fig. 1).

The stimulus material of the test phase and the sounds of the voice recorder consisted of recordings of the same three sounds, which lasted for 2000 ms each. Stimuli were recorded digitally using an AKG-3000 condenser microphone and a MOTU 828ml2 audio interface on a MacPro computer in an acoustically isolated room at 16-bit, 44,100 KHz quality and were controlled for pitch and loudness. Additionally, we used geometric shapes as background pictures on a computer screen while the sounds were presented in the test phase to maintain the child’s attention and to avoid head movements.

1.3. Procedure and design

1.3.1. Training phase

For the first appointment, infants and parents were visited at home by the experimenter. The experimenter handed over one of the rattles and one voice recorder to the parents. Parents were instructed verbally about the training procedure. They also received a written training schedule, which indicated that they had to train with their infant every day for about one week (the number of training days varied between 6 and 8). Parents were asked to give their infants 5 min of training with the rattle and let the infant listen to the voice recorder for 5 min each day. In particular, they were asked to offer the rattle to the infant and let him play with the rattle for this time period. Additionally, Velcro was provided with the rattle. In case infants had difficulties grasping and holding the rattle, parents were asked to attach the rattle to the infants’ wrist. For the training period with the voice recorder, the parents were instructed to activate the replay function of the recorder and then insert it into the container and place it in front of the infant approximately 1.5 m away (i.e., out of reach). During the training with the rattle and the voice recorder, parents were instructed to remove any other toys and to avoid any other sounds in the background (e.g., radio).

It was counterbalanced between days with which object parents were supposed to start the training (i.e., rattle or voice recorder). To ensure compliance with the instructions, parents were asked to write down the exact training times every day on the training schedule and provide information, how their infant reacted to the stimuli. It was balanced between participants which of the three sounds was the action-related sound (AS; caused by shaking the rattle), the non-action related sound (NAS; played automatically from the voice recorder), and control sound (CS; not experienced during the training phase; see Table 1).

1.3.2. Test phase

The test session was scheduled one day after the last training session in the infant EEG lab of the Donders Institute, Radboud University Nijmegen. During the experiment, the infant was seated in an infant seat in front of a computer monitor. The child’s parent was sitting out of view behind the infant. A loudspeaker was located behind the screen. The software Presentation 11.07 (Neurobehavioral Systems, USA) was used to present the three auditory stimuli (i.e., AS, NAS, CS) in a pseudo-randomized order so that the same stimulus was never presented more than two times in a row. At the same time, pictures of geometrical figures were displayed on the screen in a random order that was unrelated to the sound presented. The experiment was conducted until the child lost interest in the sound stimuli, as evidenced by yawning, crying, or falling asleep. The study was set up as a within-subjects design, as the participants were presented with all three auditory stimuli.

1.4. EEG recording and analysis

EEG was recorded using an infant-size cap with 30 Ag/AgCl active electrodes (EasyCap, Germany) with a layout following the 10/20 system. All electrodes were referenced to a central reference electrode. EEG was recorded with a BrainAmp AC amplifier using a band-pass filter of 0.1–125 Hz at a sampling rate of 500 Hz. EEG data was analyzed using Brain Vision Analyzer (Brain Products, Germany).

The EEG data was segmented into 2200 ms time frames per trial, including a 200 ms baseline before stimulus onset and the 2000 ms, during which the stimuli were presented. By means of a filter, frequencies below 0.0159 Hz and above 120 Hz were cut off. A baseline correction was performed employing the 200 ms time frame before stimulus onset. Trials with artifacts were rejected by means of the automatic artifact rejection function of Brain Vision Analyzer, employing the individual channel rejection mode (maximum difference of values in a segment 250 μV). On average, 24.8% of all trials were excluded from further analysis, leaving on average 27 trials per infant and per condition. Per infant, on average 27.3 trials for condition AS (range: 10–49), 27.2 trials for condition NAS (range: 9–46), and 26.7 trials for condition CS (range: 9–47) were used in the analysis. A two-way repeated measures analysis of variance (ANOVA) with the within-subject factors Hemisphere (C3, C4) and Sound Condition (AS, NAS, CS) and number of

| Table 1 The allocation of the three different sounds (1: bell; 2: metal screws; 3: tambourine disks) to the three experimental conditions (AS, NAS, CS) and the number of participants in each of the six different conditions. |
|---|---|---|---|
| AS | NAS | CS | Number of participants |
| 1 | 2 | 3 | 2 |
| 1 | 3 | 2 | 3 |
| 2 | 3 | 1 | 3 |
| 2 | 3 | 1 | 2 |
| 3 | 1 | 2 | 3 |
| 3 | 2 | 1 | 2 |
included trials as dependent variable revealed no significant differences (all ps > .44).

For each trial, fast Fourier transformations (FFTs) were conducted over the 2000 ms time period beginning with stimulus onset and grand averages of the FFTs were calculated for all three conditions. To investigate motor activation during infants’ perception of the three different sounds, we focused on the C3 and C4 electrodes, as they are located above the left and right hemispherical cortical motor regions where we expected an effect (cf. Bablioni et al., 2003; Reid et al., 2011). To analyze the average strength of mu-desynchronization for the three sounds, mu-frequency power was averaged over the 6–8 Hz frequency band (cf. Stapel et al., 2010). Data were entered into a two-way repeated measures analysis of variance (ANOVA) with the within-subject factors Hemisphere (C3, C4) and Sound Condition (AS, NAS, CS).

2. Results

It was the aim of the study to investigate whether the power of the EEG signal in the mu-frequency range was more strongly suppressed during the perception of the action-related sound (AS) compared to a similarly familiar, but not action-related sound (NAS) or an unfamiliar sound (CS). An ANOVA revealed a significant main effect of Sound Condition, $F(2,28) = 3.344$, $p < 0.05$, $\eta_p^2 = .19$ (see Fig. 2). No significant effect of Hemisphere and no interaction effect were found (all ps > .21). So, to further analyze the effect of Sound Condition, we averaged the data across hemispheres. Post hoc t-tests revealed that the amount of mu-desynchronization in condition AS differed significantly from condition NAS and CS, $t(14) = 2.498$, $p < .05$ and $t(14) = 2.424$, $p < .05$, respectively, whereas no significant difference was found between the latter two conditions, $t(14) = 0.697$, $p = .50$.

To further analyze whether the strength of mu-desynchronization was related to the duration of training, we calculated the correlation between mu-desynchronization and the number of training days. To this end, we computed for each participant a learning score defined as average difference in mu-desynchronization between AS and NAS (AS-NAS-score) as well as AS and CS (AS-CS-score) over the 6–7 Hz frequency band, where we found the largest effect. The analysis revealed a significant correlation between the number of training days ($M = 6.9$ days, SD = 0.64) and the AS-CS-score ($r = -.69$, $p < .05$), suggesting that infants showed more motor activation for AS the more they trained with the novel objects. The negative correlation for the AS-NAS-score did not reach significance ($r = -.34$, $p = .21$).

Finally, to ensure that the effect of mu desynchronization was restricted to central areas and not widely distributed (i.e., spreading from central over frontal and parietal sites), we performed an additional analysis. To this end, we selected for each hemisphere an additional frontal (Fp1, Fp2) and parietal electrode (P3, P4) and investigated differences between these electrodes for these three electrodes. Data were entered into a three-way repeated measures ANOVA with the within-subject factors Hemisphere (left, right), Side (frontal, parietal) and Sound Condition (AS, NAS, CS). The analysis revealed only a main effect of Side, $F(1,14) = 17.020$, $p = .001$, $\eta_p^2 = .55$ (all other ps > .10), which shows that power was smaller over parietal sites ($M = 5.19$, SE = .67) than over frontal sites ($M = 9.76$, SE = 1.55). Importantly, there was no effect of Sound Condition, $F < 1$, no interaction effect of Sound Condition with Side, $F < 1$, or Hemisphere, $F(2,28) = 7.549$, $p = .19$, $\eta_p^2 = .11$, and no three-way interaction between the factors was found, $F < 1$, suggesting that the effect of Sound Condition on the infant mu frequency band was restricted to central sites.

3. Discussion

This study investigates the acquisition of bidirectional action-effect associations in infancy. To this end, infants were trained for one week to use a novel rattle that produced a specific sound when shaken. At the same time, infants were familiarized with another, not action-related sound. After this training phase, infants’ EEG responses to these two sounds and to an additional, unfamiliar sound were recorded. Our results show that infants displayed stronger mu-desynchronization when listening to the action-related sound than when hearing the other two sounds. Interestingly, the strength of this effect was related to the duration of training. Our results provide therefore electrophysiological evidence that infants as young as 8
months of age can acquire bidirectional action-effect associations.

Following the ideomotor theory, we interpret these findings as evidence that through the repeated co-occurrence of an action and its auditory effect the motor code and the perceptual code (i.e., of the perceived effect) became related to each other, and thus, infants acquired an action-effect association. When infants subsequently perceived the auditory stimulus, the perception of this sound led to an activation of the perceptual code and the associated motor code (cf. Del Giudice et al., 2009; Elsner and Hommel, 2001; Heyes, 2010). Accordingly, the perception of the auditory effect resulted in an activation of cortical motor areas (cf. Elsner et al., 2002) and thus a desynchronization in the mu-frequency band.

It is important to emphasize that our results cannot be explained by differences between the three auditory stimuli. First, the stimuli were carefully recorded and were controlled for pitch and loudness. Second, the use of the stimuli as action-related sound, non action-related sound and control sound was counterbalanced between participants, rendering it unlikely that our effects were merely due to specific stimulus characteristics. Furthermore, the desynchronization was significantly stronger for the action-related sound compared to another familiar and to an unfamiliar sound, whereas no difference was found between the familiar, but not action-related sound and the unfamiliar sound. This excludes the possibility that the desynchronization was merely due to a familiarity or a novelty effect.

Interestingly, our analysis did not reveal any difference between the hemispheres, suggesting that the effects were comparably pronounced for both the left and right cortical motor areas. Assuming that the infants did always train with one hand, this finding could suggest that the infants associated a rather abstract motor code (i.e., of hand action in general instead of a, for example, right hand action) with the rattle’s sound effect. Therefore motor areas of both hemispheres become activated upon hearing the rattle’s typical sound. Alternatively, it might be the case that the infants did not have a strong hand preference during the training phase, but trained sometimes with their left and sometimes with their right hand. This explanation is supported by research on infants’ handedness, which provided evidence for lateral fluctuations in infants’ hand preferences (e.g., Corbetta and Thelen, 1999, 2002). As a consequence, infants might have associated left- and right-hand actions with the sound effect and, when perceiving this sound again, showed an activation in cortical motor areas of both hemispheres. Further research, carefully controlling for infants’ left- and right-hand use, is necessary to investigate this issue in more detail.

Previous research has suggested that infants are sensitive to the effects of their own actions from early on and use these effects to guide their actions (e.g., Hauf et al., 2004; Mast et al., 1980; for a review see Elsner, 2007). Hauf and Aschersleben (2008), for example, demonstrated to 7- and 9-month-old infants that pressing one of two buttons led to a salient action effect. Subsequently, infants could play with the buttons. In their experiment, the infants tended to press the button first and longer that led to the salient action effect in the demonstration phase. Although these findings provide evidence for an impact of action effects on infants’ subsequent action execution, it was unclear if the effects were due to an acquisition of bidirectional action-effect contingencies. Alternatively, merely reinforcement learning of habitual responses can also explain the results (e.g., Klossek et al., 2008; Kenward et al., 2009). Our study, however, provides direct evidence that already 8-month-old infants are able to acquire bidirectional action-effect associations and is in line with other recent findings that employed response latency measures with 9-month-old infants (Verschoor et al., 2010). Following the ideomotor theory (cf. Hommel et al., 2001), these associations might provide the neurocognitive basis of infants’ ability to voluntarily control their actions (cf. Gibson and Pick, 2000; von Hofsten, 2007).

Recently, cortical motor activation during action observation (i.e., motor resonance) has been reported in several developmental studies (e.g., Marshall et al., 2011; Meyer et al., 2011; Nyström et al., 2010; Reid et al., 2011; Stapel et al., 2010), and it has been suggested that motor resonance is related to infants’ own action experience (van Elk et al., 2008). In the study by van Elk et al. (2008), however, infants were presented with recordings of human actions and infants’ ability to perform these actions was not experimentally manipulated. Our study is the first to systematically manipulate infants’ active action experiences and provide electrophysiological evidence that motor resonance is directly modulated by action-experience. Furthermore, supporting the theoretical models proposed by Hommel et al. (2001) and Heyes (2010), our results show that motor resonance can be elicited not only through the observation of an action itself, but also through the perception of the distal effects of this action (cf. James, 1890).

Some studies have shown that the perception of an action leads to activation in the observer’s motor cortex (e.g., Marshall and Meltzoff, 2011; Nyström et al., 2010). Other studies have provided evidence that such motor activation is measurable on a muscular level (e.g., Cattaneo et al., 2007) or in overt behavior (e.g., Kilner et al., 2003). In the present study, the relation of mu-desynchronization to overt behavior and covert motor activation remains an open question. Further research is thus necessary to investigate whether infants’ motor activation upon hearing the auditory effect, which has previously been caused by their own action, is restricted to covert motor activation or can also lead to behaviorally measurable consequences (i.e., the child making sub-threshold or small arm movements during the hearing of the sound).

Our results parallel findings on audiovisual mirror neurons in the monkey brain (e.g., Keysers et al., 2003; Kohler et al., 2002). In particular, it has been found that the perception of an action’s specific auditory effect (e.g., cracking a nut) activates the same neurons in the monkey’s premotor cortex that are activated when the monkey performs the action himself. The results of our EEG study show cortical motor activation in response to a specific auditory action effect. It has been suggested that activation in these cortical areas during action perception probably reflects the working of a human mirror neuron system (Kilner and Frith,
2007; see also Caetano et al., 2007). Our findings are thus in line with the suggestion that a mirror neuron system (MNS) might also exist in the human brain (e.g., Rizzolatti and Craighero, 2004). Supporting this notion, we found stronger motor activation for the perception of a sound that was previously the effect of the infants’ own actions than of sounds that were either unfamiliar or familiar, but not related to infants’ actions. Furthermore, the strength of this effect was partly dependent on the number of training days. In other words, the more active action experience infants had, the more motor activation they showed for the rattle’s sound compared to an unfamiliar sound. If we assume that motor activation for the rattle’s sound reflect the activation in a human mirror neuron system, then our results provide empirical support for the notion that the development of the MNS is experience-dependent and the consequence of sensorimotor learning experiences (Catmur et al., 2007; Del Giudice et al., 2009; Heyes, 2010) rather than based on an innate matching system (cf. Ferrari et al., 2006). Our results are therefore informative with respect to the question of how the mirror neuron system changes in the course of development (cf. Kilner and Blakemore, 2007).

Our results have implications for current theories on infants’ action understanding and imitation, as it has been argued that infants’ own action capabilities and experiences are related to these abilities (e.g., Meltzoff, 2007; Paulus et al., in press-a,b; Sommerville and Woodward, 2005). For example, it has been argued that the perception of an action or action effect is automatically mapped onto infants’ own action system (cf. Heyes, 2010; Ray and Heyes, 2011) and that this mapping process plays an important role in infants’ understanding of this action (e.g., Falck-Ytter et al., 2006). In particular, it has been proposed that such a mapping mechanism enables humans to employ their own motor system to predict the goal of an ongoing action. This suggestion is in line with recent theoretical approaches that stress the embodied nature of infants’ action perception and action understanding (e.g., Daum et al., 2009). Infants’ growing experience with different actions and their effects should thus enable them to gradually understand more of other people’s intentional action (Barresi and Moore, 2008). Our results provide clear evidence for cortical motor activation during the perception of the effects of well-known actions and are thus in line with suggestions that infants map others’ actions onto their own motor repertoire.

Acknowledgements

We thank Angela Khadar and Evelien Akker for their support in the Baby Lab, Janny Stapel and Marlene Meyer for support in data acquisition, Alex Brandmeyer for help with stimulus recording and the families, who participated in this study.

References


