# You'll never crawl alone: Neurophysiological evidence for experience-dependent motor resonance in infancy

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## ARTICLE INFO

## ABSTRACT

Lately, neuroscience is showing a great interest in examining the functional and neural mechanisms which support action observation and understanding. Recent studies have suggested that our motor skills crucially affect the way in which we perceive the actions generated by others, by showing stronger motor resonance for observation of actions that are established in one's motor repertoire. In the present study we extend previous findings that were based on expert motor skills in adults to the natural development of actions in infants. To investigate the effect of natural motor experience on motor resonance during action observation, 14- to 16-month-old infants' EEG was recorded during observation of action videos. Stronger mu- and beta-desynchronizations were found for observation of crawling compared to walking videos and the size of the effect was strongly related to the infant's own crawling experience. This suggests that already early in life one's own action experience is closely related to how actions of others are perceived.

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## Introduction

It is an intriguing question how infants represent and understand the surrounding world in relation to their own capabilities. An infant at the playground, for example, may observe other children playing and running around, while he himself still is unable to walk. However, when the infant gradually learns to walk, do his representations of the others' walking behavior thereby change? Recent studies in adults suggest that this may indeed be the case. Several studies have shown that acquisition of expert motor skills affects how actions are perceived and processed by the brain (Calvo Merino et al., 2005; Haslinger et al., 2005). More specifically, stronger activation of the motor cortex has been reported during observation of actions that are well established in one's motor repertoire. In addition, Cross et al. (2006) found that in adults learning a novel dance sequence over a 5-week period was related to an increase in motor resonance during observation of the same action.

Together, these studies suggest a strong link between action experience and motor resonance during action observation. The neural mechanism underlying this strong coupling between action and perception is likely provided by the mirror neuron system that becomes activated both during observation and execution of the same action (Rizzolatti and Craighero, 2004; Rizzolatti et al., 2001). Thus, when one observes someone else performing an action, comparable brain

areas are activated that are involved in the execution of that same action. This mirroring process is highly automatic and is thought to support action recognition and interpretation by providing an internal motor representation of the observed action. Thus far, however, effects of motor experience on action observation have been tested in experts who were highly over-trained in specific motor skills (e.g. ballet dancers). The question arises if the same principle might accompany the natural acquisition of new motor skills (e.g. an infant learning to crawl or walk). The natural variability in infants' motor development provides an excellent opportunity to investigate this question as it allows studying the relation between the acquisition of new actions and the processing of these actions performed by others.

At a behavioral level, developmental studies suggest a close link between action production and action perception in infants (Sommerville and Woodward, 2005; Sommerville et al., 2005). For example, 10-month-old infants who successfully managed to retrieve a toy by pulling a cloth were better able to interpret an observed action as goal-directed than age-matched children who were not able to perform the action (Sommerville and Woodward, 2005). Furthermore, at a neural level, motor resonance in 6-month-old infants has been examined by measuring spectral power decreases in the mu-frequency band (4–10 Hz) of infants' EEG (electroencephalogram) in response to the observation of actions (Nystrom, in press). Desynchronization in both the mu- and the beta-frequency bands in adult EEG has been found both during action execution and action observation and likely reflects activation of the primary motor cortex downstream to mirror neuron areas in parietal and frontal cortices

(Caetano et al., 2007; Muthukumaraswamy and Johnson, 2004). Accordingly, spectral power changes in infants' EEG provide a direct way to investigate motor resonance in infancy.

In the present study, we investigated whether infants' own motor experience (crawling and walking) is related to the activation of their motor system during the perception of these actions carried out by others. To this end we presented 14- to 16-month-old infants with short videos, which displayed crawling and walking infants (see Supplementary Videos 1 and 2 for stimulus examples). Infants' EEG, eye movements, and leg- and arm-movements were continuously measured during the experiment to obtain trials in which the infant continuously looked at the screen and did not move his or her limbs. In addition, we assessed the infants' motor skills and their amount of experience with different motor skills by asking parents since when their infant was able to crawl and/or walk.

## Methods

### Participants

Twelve 14- to 16-month-old full term infants (mean age: 483 days, range 436–489 days, 4 females) participated in the experiment. Eleven additional infants were tested but excluded from further analysis due to loss of eye movement data (6 infants) or due to insufficient artifact-free trials per condition (5 infants). The parent(s) gave informed consent for participation of their infant in the study.

### Stimuli

The stimulus material consisted of videos of walking and crawling infants which had been recorded at the Baby Research Center Nijmegen. Parents of the infant models were informed about the purpose of the experiment and gave their consent for use of the videos as stimulus material in the present study. Videos were recorded against a neutral background while the infant walked or crawled for a distance of circa 2 m from the left to the right side of the visual scene. Each movie was flipped horizontally in order to obtain both left- and rightward movements. In this way a total number of 64 movies (16 walking videos and 16 crawling videos presented in 2 different directions) was included in the experiment. Two example videos are available as supplementary material online (Supplementary Videos 1 and 2).

### Experimental setup and procedure

During the experiment, the infant was seated in a baby car seat slightly tilted backwards in front of a computer screen. Videos were presented on a Tobii 1750 eye-tracker 17" screen (Tobii Technology, Sweden) at a viewing distance of approximately 60 cm. Eye movement data were continuously sampled at 50 Hz and processed online using custom-made software implemented in Presentation 11.07 (Neurobehavioral Systems, USA). When the infant looked at a designated part of the screen at which the action was presented during video presentation for more than 1000 ms, a marker was sent to the EEG computer. Two tilt sensor modules (CW60A/30; Comus Group of Companies, Belgium) were placed on the infant's arm and leg to measure the movements during the experiment. Markers indicating movement of the infant and markers indicating the beginning and end of each video were sent to the EEG computer. Crawling and walking movies were randomly presented in blocks of approximately 10 s in which right- and leftward locomotion were alternated in a systematic fashion. During the experiment the infant's behavior was continuously monitored via a control monitor in the control room.

Parents provided information about the motor skills of their infant and also indicated the age at which the baby started crawling and/or walking. "Crawling" was defined as locomotion using the hands and knees while lifting the belly, whereas "walking" meant walking independently without external help for more than 5 steps. If possible, parents were asked to refer to baby diaries or agendas to indicate the moment at which their infant started crawling or walking. From this information it was calculated how many months of experience the infants had with crawling and/or walking.

### Eye movement data

For analysis of eye movement data, first, the relative looking times were calculated with respect to the total duration of video presentation. In addition, the absolute duration of looking time (in seconds) was calculated for crawling and walking videos. For a first indication of infants' looking behavior, eye position data was averaged across infants relative to video-onset. Next, in order to quantify looking behavior to crawling and walking videos, the area in which the video was presented was divided into four parts (upper left, upper right, lower left, lower right). For each of the designated parts the percentage of looking time was calculated for walking and crawling videos using a 2 (Video: Crawl vs. Walk)×2 (UpLow: Upper vs. Lower visual field)×2 (LeftRight: Left vs. Right visual Field) repeated measures ANOVA.

### EEG recording and analysis

EEG was recorded using an infant-size BrainCap with 29 Ag/AgCl electrodes (Montage No. 17, Easycap, Germany). All electrodes were referenced to the left mastoid online and re-referenced offline to the linked mastoids. EEG was recorded with a BrainAmp AC amplifier using a band-pass of 0.1–80 Hz at a sampling rate of 250 Hz. Impedances were kept below 50 kΩ. EEG data was analyzed using Brain Vision Analyzer (Brain Products, Germany) and FieldTrip (open source software, developed at the FC Donders Centre for Cognitive Neuroimaging; http://www.ru.nl/fcdonders/fieldtrip/).

Based on the eye movement data, the EEG data was segmented into 1000 ms time frames during which the infant continuously looked at the screen for both crawling and walking videos. Segments that were preceded by a movement or during which a movement of the infant's leg or arm was detected were excluded from analysis. Trials with artifacts were rejected on the basis of careful visual inspection. In this way, 13% of all trials for walking videos and 12% of all trials for crawling videos were excluded from further analysis, leaving on average 34 trials per infant per condition (crawling vs. walking). For each infant an estimate of the spectral power for observation of walking and crawling videos was obtained by analyzing individual segments using Welch's method with Hanning tapers and the resulting power values were averaged across trials for each condition.

Cluster-level randomization tests were applied to identify clusters of channel-frequency pairs that differed significantly between conditions (Maris and Oostenveld, 2007). The cluster-level randomization test identifies clusters of adjacent channel-frequency pairs, whose $t$-statistic exceeds a critical threshold ($p<.05$, two-sided). To control for multiple comparisons, the maximum cluster-level test statistic (sum of $t$-values) is evaluated against the null distribution. To this end, the observed data is 1000 times randomly assigned to both conditions and the Monte Carlo $p$-value expresses the proportion of the randomized null distributions exceeding the observed maximum cluster-level statistic. Cluster-level randomization tests applied from 4 to 30 Hz revealed significant differences between crawling and walking videos in the mu-frequency band (7–9 Hz) and in the beta-frequency band (17–19 Hz), $p$-values<.05 (corrected for multiple comparisons).

In an additional analysis, we used conventional repeated measures ANOVAs to assess differences between crawling and walking videos. For both the mu- and the beta-frequency bands, two electrodes were selected on the basis of significant clusters identified by means of the cluster-level randomization tests (electrodes are highlighted in the

topographic maps in Fig. 3). For statistical analysis of the difference in the mu-frequency band (7–9 Hz) between crawling and walking videos, a 2 (Video: crawling vs. walking)×2 (Electrode: FCz and Cz) repeated measures ANOVA was applied. The effect in the beta-frequency band (17–19 Hz) between crawling and walking videos was analyzed using a 2 (Video: crawling vs. walking)×2 (Electrode: RP and LP) repeated measures ANOVA. The relation between motor experience and effects in the mu/beta-frequency band was investigated by calculating the correlation (using Pearson's $r$) between the absolute difference in power between crawling and walking conditions and the amount of crawling experience. In order to control for natural maturation effects, the partial correlations between crawling experience and the mu- and beta-effects were calculated after controlling for age.

## Results

### Locomotor experience

Overall, the infants of our sample had more experience with crawling (average duration of crawling experience at the time of the study: 6.1 months, standard deviation=2.1 months) than with walking (1.8 months, standard deviation=2.1 months), $t(11)=8.5$, $p<.0001$. At the time of study, three infants could still not walk; three infants had started walking within three weeks preceding the study and six infants had experience with walking for longer than 1 month.

### Eye movement data

Analysis of eye movement data revealed that reliable data about the infants' eye position was obtained in 50.1% of the time during which videos were presented. The average duration of absolute looking time was slightly longer for walking videos (64 s), compared to crawling videos (56 s), $t(11)=2.4$, $p<.05$.

Next, differences in looking behavior between infants with relatively more walking experience (>1.5-month walking experience) compared to the novice walkers (<1.5 months of walking experience) were investigated. Averaged looking times indicated that infants with relatively long walking experience tended to look longer at crawling videos (64 s) compared to walking videos (54 s). In contrast, infants with relatively little walking experience tended to look longer at walking videos (75 s) compared to crawling videos (48 s). However, analysis of the difference between looking times to walking and crawling videos with high or low walking experience as a between-subjects factor did not reveal a significant interaction ($F<1$). Furthermore, locomotor experience did not interact with any of the subsequent analyses (see below; all $F$'s<1).

Averaged horizontal and vertical eye movement data are represented in Fig. 1. Horizontal eye movement data indicate that infants smoothly pursuit the observed actions and vertical eye movement data indicate that for walking videos infants tended to look to the upper part of the screen, whereas for crawling videos infants looked at the lower part of the screen.

To investigate differences in looking behavior between crawling and walking videos we segmented the screen in four different areas of interest (left vs. right and upper vs. lower visual field). The relative looking times to areas of interest for crawling and walking videos are represented in Fig. 2. The relative looking times were analyzed using a 2 (Video: Crawl vs. Walk)×2 (UpLow: Upper vs. Lower visual field)×2 (LeftRight: Left vs. Right visual Field) repeated measures ANOVA. Locomotor experience was introduced as a between-subjects variable but did not interact with any of the other variables ($F$'s<1). A significant main effect for UpLow indicates longer relative looking times towards the lower part of the videos compared to the upper part, $F(1,11)=10.1$, $p<.01$. No other significant main effects were found ($p$-values>.12). A highly significant interaction was found between Video and UpLow, $F(1,11)=137.3$, $p<.0001$, indicating that for crawling videos infants tended to look longer at the lower part compared to the upper part, whereas for walking videos infants looked longer at the upper part compared to the lower part of the videos. Finally, a three-way interaction was found between Video, UpLow and LeftRight, $F(1,11)=5.4$, $p<.05$, indicating that for walking videos infants looked longer at the right side of the upper visual field and longer at the left side of the lower visual field whereas for crawling videos the opposite pattern was found.

### EEG analysis

For the main analysis of the EEG, the data was group averaged across all infants, independent of their walking or crawling experience. Grand averaged EEG power for walking videos and crawling videos at different electrode sites is represented separately for the mu-frequency band (Fig. 3a) and the beta-frequency band (Fig. 3b). Analysis of the group averaged EEG revealed a stronger desynchronization in the mu-frequency band (7–9 Hz) for observation of crawling compared to walking, $F(1,11)=5.4$, $p<.05$, which was found to be maximal over central sites (Fig. 3c). In addition, a stronger bilateral desynchronization was found in the beta-frequency band (17–19 Hz) for observation of crawling compared to walking $F(1,11)=7.0$, $p<.05$ (Fig. 3d).

Previous studies have suggested that sensorimotor activity is most likely to occur around the standard C3 and C4 electrode positions (Babiloni et al., 2002; Muthukumaraswamy and Johnson, 2004). Accordingly, an additional analysis investigated differences in mu-
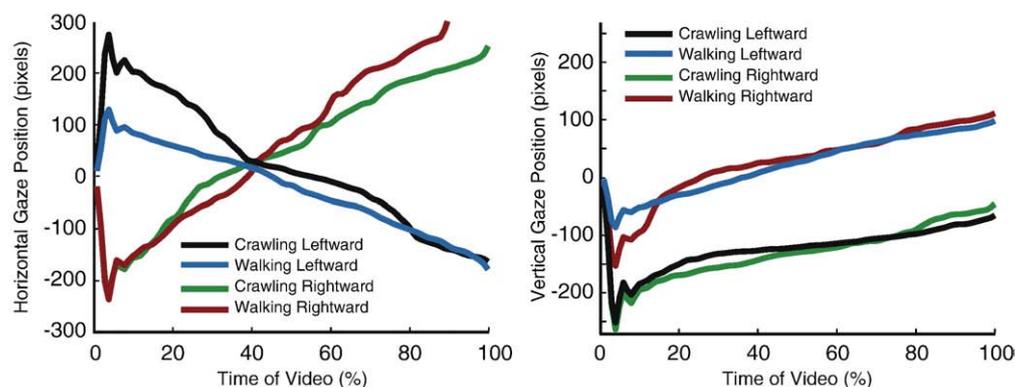


**Fig. 1.** Averaged eye position data for observation of walking videos (red and blue lines for rightward and leftward movements respectively) and crawling videos (green and black lines for rightward and leftward movements respectively). The left graph represents horizontal gaze position (in pixels) and the right graph represents vertical gaze position (in pixels). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
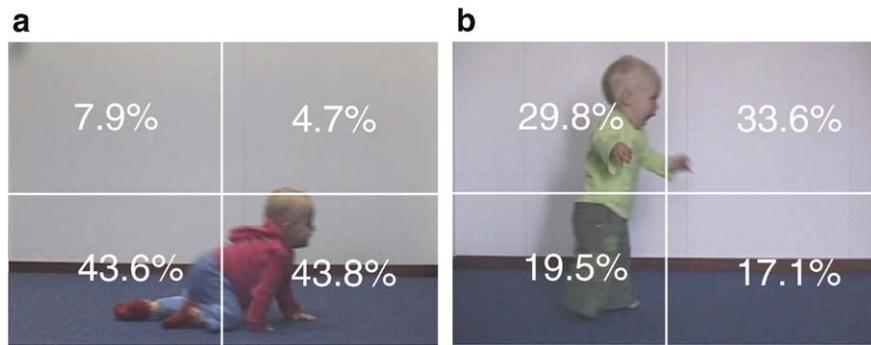
**Fig. 2.** Relative percentage of looking time for designated areas of interest for crawling (left graph) and walking videos (right graph). Upper values indicate looking times for observation of leftward videos and lower values indicate looking times for rightward videos.

and beta-powers around C3 and C4 electrode positions, using a 2 (Video: crawling vs. walking)×2 (Electrode: C3 vs. C4) repeated measures ANOVA. For the mu-frequency band, the difference between walking and crawling videos did not reach statistical significance, $F(1,11)=2.2$, $p>.17$. For the beta-frequency band a significant difference was found between crawling and walking videos, $F(1,11)=9.1$, $p<.05$, reflecting stronger beta-desynchronization for crawling compared to walking. In addition, a main effect of electrode is reflected in stronger beta-power at C4 (right hemisphere) compared to C3 (left hemisphere), $F(1,11)=5.2$, $p<.05$. As can be clearly seen in Fig. 3b, the absolute beta-effect is stronger at parietal sites (difference between crawling and walking=1.4 μV) than at central sites (difference between crawling and walking=0.4 μV). However, post-hoc analysis of the size of the beta-effect at central and parietal sites using a 2 (Central vs. Frontal sites)×2 (Video: crawling vs. walking)×2 (Left vs. Right

hemisphere) did not reveal significant interactions between Video and electrode site ($p>.18$) These findings suggest that although the beta-effect was found maximal at parietal sites, the difference between crawling and walking in the beta-frequency band is broadly distributed across parietal and central motor areas.

Next, the relation between the infant's locomotor experience and desynchronization in the mu/beta-frequency band was investigated. To this end the difference in mu/beta-power between walking and crawling videos was correlated to the infants' own experience with crawling and walking. The size of both the mu- and the beta-effects (difference in power between observation of crawling and walking) was highly correlated with the amount of infants' crawling experience, $r=-.60$, $p<.005$ and $r=-.42$, $p<.05$ for respectively the mu- and the beta-effects (Fig. 4). After controlling for age the partial correlations remained highly significant, $r=-.57$, $p<.005$ for the mu-effect
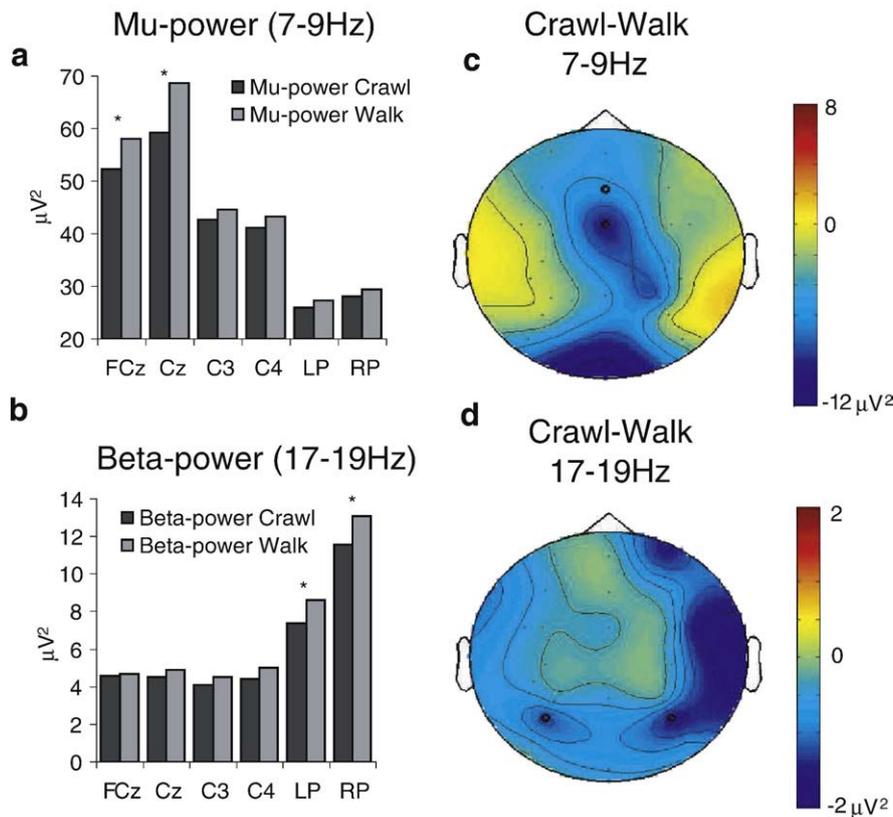


**Fig. 3.** (Left) Grand averaged EEG power for walking videos (dark bars) and crawling videos (light bars) at different electrode sites for the (a) mu-frequency band (7–9 Hz) and the (b) beta-frequency band (17–19 Hz). (Right) Topographic maps, representing the difference in the infant EEG power spectrum between observation of crawling and walking videos (c) in the mu-frequency band (7–9 Hz) and (d) in the beta-frequency band (17–19 Hz). Blue colors indicate stronger desynchronization for crawling compared to walking. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
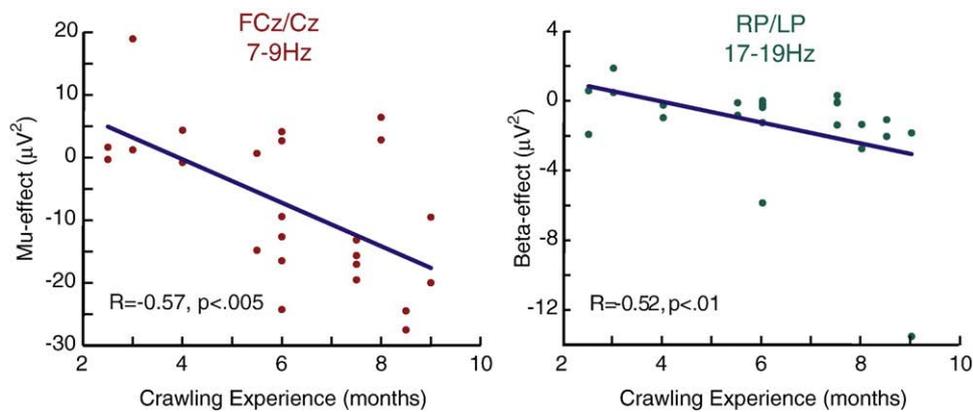
**Fig. 4.** Correlations between crawling experience and the mu- and beta-effect sizes. The left graph represents the correlation between crawling experience and the difference in mu-power between crawling and walking videos. The right graph represents the correlation between crawling experience and the difference in beta-power between crawling and walking videos. Pearson's r reflects the partial correlation between the mu/beta-effect and crawling experience, after controlling for age (The correlation in the beta-frequency band (right graph) remained significant after removal of possible outliers at 2.5, 6 and 9 months, $r=-.70$, $p<.001$).

and $r=-.52$, $p<.01$ for the beta-effect, thereby minimizing the possibility that correlations between crawling experience and mu/beta-desynchronization can be attributed to solely maturational changes. In contrast, no significant correlations were found between the size of the mu- and beta-effects and the amount of walking experience ($p$-values$>.25$).

To investigate the possibility that effects in the mu- and beta-frequency bands are related to the observation of specific parts of the stimuli (e.g. observation of legs), correlations were calculated between the relative looking times to different parts of walking and crawling videos (as represented in Fig. 2) and the mu- and beta-effects. However, no significant correlations were found between relative looking time to designated areas of crawling and walking videos and the amount of mu- and beta-desynchronizations ($p$-values$>.20$).

**General discussion**

In the present study, we relied on the natural variability in infants' motor development to directly investigate the relation between the acquisition of new motor acts and the perception of other's actions. Two main findings suggest that the infants' motor system is more strongly activated during observation of actions with which the infant has relatively much experience.

First, a stronger desynchronization in both the mu- and the beta-frequency bands was found for observation of crawling compared to walking. Modulations of the beta-frequency band have been localized to the primary motor cortex in both humans in monkeys (Koelewijn et al., 2008; Ritter et al., 2008; Sanes and Donoghue, 1993), whereas modulations in the rolandic mu-rhythm likely originate from sensorimotor areas, such as the primary somatosensory cortex (Caetano et al., 2007; Hari et al., 1997; Salmelin and Hari, 1994). Activation of these regions is directly modulated by activity in core areas of the human mirror neuron system, such as the inferior frontal gyrus, the superior temporal sulcus and the inferior parietal lobule (Caetano et al., 2007; Nishitani and Hari, 2000, 2002). Accordingly, desynchronization in both the mu- and beta-frequency bands likely reflects activation in the motor system downstream to mirror neuron areas in parietal and frontal cortices (Babiloni et al., 2003; Muthuku-maraswamy and Johnson, 2004). As the infants in the present study had more experience with crawling than with walking, these findings suggest stronger motor resonance for actions that are already established in one's motor repertoire.

Second, the amount of crawling experience was directly related to the degree of mu- and beta-desynchronizations. The correlation between motor experience and mu- and beta-desynchronizations was not affected by chronological age as a confounding variable. Therefore, the strong correlation between crawling experience and mu- and beta-desynchronizations provides support for the view that motor resonance during action observation is directly related to infants' natural developing action abilities.

Analysis of the eye movement data showed that infants looked longer at walking compared to crawling videos. It is possible that infants tend to look more at actions which they cannot yet perform themselves or with which they have relatively little experience. According to this interpretation, it is unlikely that effects in the mu- and beta-frequency bands can be attributed to attentional or motivational differences, because then a stronger desynchronization would have been expected for walking compared to crawling videos. Inspection of the eye movement data furthermore confirmed that infants looked more at the lower part of the screen for observation of crawling and more at the upper part of the screen for walking videos. This looking pattern confirms that infants were closely following the two actions. Importantly, no significant correlations were found between relative looking times towards the upper or lower visual field and the amount of mu- or beta-desynchronization, thereby minimizing the possible confound that stronger mu- and beta-desynchronizations might be attributable to infants focusing more on moving body parts (e.g. the legs) for observation of crawling compared to walking videos. Rather than being attributable to attentional, motivational, or perceptual differences, the stronger mu- and beta-desynchronizations for crawling compared to walking thus likely reflects effects of action experience on motor resonance.

Neural correlates of motor resonance in infancy have previously been reported only for the mu-frequency band of the infant EEG (Cochin et al., 2001; Lepage and Theoret, 2006; Nystrom, in press). In the present study we found a desynchronization in both the mu- and the beta-frequency bands of the EEG, which is in line with findings from studies on action observation in adults (Babiloni et al., 2002; Caetano et al., 2007; Lahav et al., 2007). For example, a strong suppression in the beta-frequency band has been reported for adults observing a goal-directed action with a tool and the amount of beta-suppression was directly related with the frequency of subjects' use of the observed object (Jarvelainen et al., 2004).

In the present study, the electrodes at which the beta-effect was found to be maximal were located above parietal sites. Comparable modulations of the beta-frequency band above parietal sites have been associated with both action observation and movement preparation (Koelewijn et al., 2008; Wheaton et al., 2005a,b). The involvement of the parietal lobe in action observation is in line with previous studies that have reported a strong activation of parietal areas in imitation and

observation of human bodily movements (e.g. Buccino et al., 2004; Fogassi et al., 2005; Stevens et al., 2000). Recently, several studies have suggested an important role for posterior parietal cortex in the control of goal-directed locomotion such as walking and especially in the visuomotor transformations required for obstacle avoidance (for review, see: Drew et al., 2008). Due to its widespread connections to both visual and frontal motor areas, the parietal lobe is a core-region for perception-action coupling (Wise et al., 1997). Accordingly, the strong relation between the beta-effect and motor experience suggests that the beta-frequency band may be a useful correlate of motor resonance and perception-action coupling in infancy, to be further investigated in future studies.

One well-known concern in studies using EEG with infants is the small number of trials that can be recorded during an experimental session (for methodological considerations, see: deBoer et al., 2007). Typically, in infant studies a minimum number of 10 trials per condition or even less is used for calculating an averaged evoked brain response (for comparison, see: Bell, 2002; Reid et al., 2007). Accordingly, the low number of trials in infant EEG studies compared to adult EEG studies may potentially limit the interpretation and generalizability of the results. In the present study, however, for each condition on average 34 trials per infant were included in the averaged power spectra. Furthermore, the effects observed in the power spectra are in line with previous findings from both adult and children studies (Nystrom, in press; Lepage and Theoret, 2006; Muthukumaraswamy and Johnson, 2004). Therefore, we suggest that the mu- and beta-effects observed in the present study reliably reflect the activation of the infant's motor system during action observation.

Previous studies have shown that increased crawling experience is accompanied by neural changes, resulting in a more efficient cortical organization as crawling becomes more routine (Bell and Fox, 1996). The current findings show that longer crawling experience also affects the way in which an infant perceives other infants crawling, suggesting that action production and action perception are deeply intertwined already early in life. Interestingly, a recent study using near-infrared spectroscopy in 6- to 7-month-old infants found a comparable activation of motor areas both during action execution and action observation (Shimada and Hiraki, 2006). Although in the present study we did not collect enough movement data to directly relate mu- and beta-effects during action execution and action observation, the correlation between crawling experience and the modulation of the mu- and beta-frequency bands suggest a strong relation between action experience and motor resonance during action observation. Thereby, the present findings are in line with previous studies, that have reported an experience-dependent modulation of the motor system in skilled experts (e.g. such as ballet dancers or piano players; Calvo Merino et al., 2005; Haslinger et al., 2005).

The mu- and beta-effects in the present study were significantly correlated only with the amount of crawling experience and not with walking experience. The infants in this study had relatively little experience with walking and much longer experience with crawling. One explanation of this finding could be that it takes a considerable amount of experience before novel action representations are grounded strongly enough to become activated during observation of a similar action. Developmental studies support the idea that the acquisition of novel goal-directed locomotion (e.g. walking and crawling) takes considerable time to develop. For example, walking proficiency was found to improve considerably during the first 4–5 months of locomotor experience, with an increase in walking frequency and a reduction in the physiological contribution of the body (Breniere and Bril, 1998; Bril and Breniere, 1992). These behavioral changes are likely accompanied by changes in the neural organization of motor behavior, such as a more efficient communication between different brain areas (e.g. Bell and Fox, 1996). In adults, effects of learning novel actions on motor resonance have been reported to occur even after 5 weeks of training (Cross et al., 2006). However,

Cross et al. (2006) tested expert dancers who learned a novel dance sequence that consisted of basic action elements that the dancers could already perform. In contrast, the present study focused on the learning of novel motor primitives rather than combining existing primitives in novel action sequences (cf. Mussa-Ivaldi and Bizzi, 2000). Given that the acquisition of novel locomotion takes considerable time to develop, it might be interesting to investigate in future studies how long it takes before infants with relatively long walking experience show a stronger desynchronization for walking compared to crawling.

The present findings provide an important argument for the view that motor resonance in infancy is experience-dependent. An intriguing question is how this view relates to the idea that the mirror neuron system could also support observational learning of novel actions via imitation (Lepage and Theoret, 2007; Meltzoff and Decety, 2003). One possible explanation for the apparent discrepancy between both views is that the supposed function of motor resonance in observational learning may depend on combining existing motor acts in new combinations, rather than directly learning motor primitives (Mussa-Ivaldi and Bizzi, 2000). Although at present it is unclear whether motor resonance is differentially involved in the learning of new motor primitives compared to more complex actions, this suggestion opens interesting avenues for future research.

## Conclusions

The present findings suggest that the acquisition of new motor skills by infants, such as learning to crawl, is accompanied by a stronger motor resonance during observation of similar actions. Apparently, the infant brain automatically transforms visual information into a motor representation that is already established in the infant's own motor repertoire (Rizzolatti and Craighero, 2004). In sum, from very early in life, the skills that we naturally acquire are closely related to how we represent the behaviors of others.

## Acknowledgments

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2008.07.057.

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