



Rhythmic neural activity indicates the contribution of attention and memory to the processing of occluded movements in 10-month-old infants



Cathleen Bache^{a,*}, Franziska Kopp^a, Anne Springer^{b,1}, Waltraud Stadler^{b,2},
Ulman Lindenberger^a, Markus Werkle-Bergner^{a,*}

^a Center for Lifespan Psychology, Max Planck Institute for Human Development, Lentzeallee 94, 14195 Berlin, Germany

^b Department of Psychology, Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstraße 1a, 04103 Leipzig, Germany

ARTICLE INFO

Article history:

Received 2 May 2015

Received in revised form 17 July 2015

Accepted 11 September 2015

Available online 14 September 2015

Keywords:

Action perception

Occlusion

Attention

Memory

Sensorimotor simulation

EEG

ABSTRACT

Infants possess the remarkable capacity to perceive occluded movements as ongoing and coherent. Little is known about the neural mechanisms that enable internal representation of conspecifics' and inanimate objects' movements during visual occlusion. In this study, 10-month-old infants watched briefly occluded human and object movements. Prior to occlusion, continuous and distorted versions of the movement were shown. EEG recordings were used to assess neural activity assumed to relate to processes of attention (occipital alpha), memory (frontal theta), and sensorimotor simulation (central alpha) before, during, and after occlusion. Oscillatory activity was analyzed using an individualized data approach taking idiosyncrasies into account. Results for occipital alpha were consistent with infants' preference for attending to social stimuli. Furthermore, frontal theta activity was more pronounced when tracking distorted as opposed to continuous movement, and when maintaining object as opposed to human movement. Central alpha did not discriminate between experimental conditions. In sum, we conclude that observing occluded movements recruits processes of attention and memory which are modulated by stimulus and movement properties.

© 2015 Elsevier B.V. All rights reserved.

1. Introduction

In everyday life, moving targets frequently disappear from sight for a moment. Maintaining an internal representation of moving targets across gaps of visual input is crucial for efficient movement processing that, in turn, enables understanding and prediction of actions observed in others as well as coordination of one's own actions with the environment (cf. Hommel et al., 2001). It is therefore a fundamental question how infants process moving targets in their visual world.

Movement perception evolves rapidly during the first year of life (Blake and Shiffrar, 2007; von Hofsten, 2004). From the age of 3 to 4 months, infants form an internal representation of object movements that are briefly occluded from view (e.g., Bremner et al., 2005;

Rosander and von Hofsten, 2004). Behavioral and neural activity has often been interpreted as providing a mental representation of the continued existence of temporarily hidden objects (i.e., object permanence; e.g., Kaufman et al., 2003; see also Piaget, 1937/1959). Such theoretically postulated high-level cognitive competencies ignore domain-general processes such as learning, memory, or perception (cf. Heyes, 2014; see also Santiesteban et al., 2014) that are potentially involved in internal representation during occlusion. To date, the cognitive and neural processes that allow infants to internally represent occluded movement remain underspecified.

From a domain-general perspective, previous findings on action perception and movement observation in both adult and infant populations suggest the contribution of cognitive processes that relate to *attention* (Kaduk et al., 2013; Rohenkohl and Nobre, 2011; Tan et al., 2013; Thompson and Parasuraman, 2011; Warreyn et al., 2013), *memory* (Cruikshank et al., 2012; Reid et al., 2009; Stadler et al., 2011; Urgen et al., 2013), and *sensorimotor simulation* (Marshall et al., 2011; Muthukumaraswamy and Johnson, 2004; Nyström et al., 2011; Paulus et al., 2012; Southgate et al., 2009; Stapel et al., 2010; Urgen et al., 2013). Although a widespread cortical activation has been indicated during movement observation in adults (Babiloni et al., 2002; Perry et al., 2011; Urgen et al., 2013) and infants (Marshall et al., 2011), most recent studies have focused on only one of these cognitive

* Corresponding authors.

E-mail addresses: bache@mpib-berlin.mpg.de (C. Bache), kopp@mpib-berlin.mpg.de (F. Kopp), anne.springer@unibas.ch (A. Springer), waltraud.stadler@tum.de (W. Stadler), lindenberger@mpib-berlin.mpg.de (U. Lindenberger), werkle@mpib-berlin.mpg.de (M. Werkle-Bergner).

¹ Present address: Department of Clinical Psychology and Psychiatry, University of Basel, Missionstrasse 60/62, 4055 Basel, Switzerland.

² Present address: Human Movement Science, Department of Sports- and Health Sciences, Technical University Munich, Georg-Brauchle-Ring 60/62, 80992 München, Germany.

domains. There is an increasing awareness that a better understanding of movement processing requires the consideration of interactions among multiple brain systems (e.g., Marshall and Meltzoff, 2011, p. 110; see also Press et al., 2006; Springer et al., 2013). Therefore, the simultaneous analysis of the abovementioned neural mechanisms is a promising approach to identify the processes involved in infants' internal representation of occluded movement. Importantly, neural mechanisms might differentially contribute to the processing of various movement types.

1.1. Target and movement properties

Human and object motion naturally differ on various dimensions. Whereas human movement is rather smooth – with a non-linear relation between path and velocity – and self-propelled, object movement is more linear and usually externally initiated and stopped. Moreover, human movement provides multiple cues on the evolving locomotion. For instance, the motion direction can be extracted from the body orientation, and changes in velocity are accompanied by adjustments of the extremities. In addition to the perceptual analysis based on external cues, observers can also utilize rich internal sources of information originating from memory or sensorimotor representations of the observed movement. Indeed, normally developing infants have been shown to readily discriminate biological from non-biological and distorted movements, demonstrating a remarkable capacity for socially relevant stimuli (see Grossmann and Johnson, 2007 for a review). Hence, movement properties (i.e., continuous vs. distorted movement) and target characteristics (i.e., human agent vs. abstract object) are presumably crucial factors influencing internal representation during occlusion.

The majority of previous studies presented occlusion events during abstract object motion to identify infants' reasoning about common-sense physical principles such as continuity (e.g., Spelke et al., 1994) or unity of form (e.g., S. P. Johnson et al., 2002). For instance, after being habituated to a ball rolling behind a screen, infants looked longer towards a linear final position than to a non-linear one, which indicates knowledge of an object's continued motion pathway during occlusion (Spelke et al., 1994). Moreover, there is substantive evidence that infants aged 6 to 12 months follow occluded object motion in a predictive manner, that is, they look at the location where the object is supposed to reappear after occlusion ahead of time (e.g., Bertenthal et al., 2007; Gredebäck and von Hofsten, 2004; Grönqvist et al., 2006; Hespos and Rochat, 1997). Correspondingly, infants predictively track un-occluded object-directed human movement (i.e., grasping or transporting action; e.g., Falck-Ytter et al., 2006; Hunnius and Bekkering, 2010). Together, these findings suggest that infants learn about trajectories (e.g., S. P. Johnson et al., 2003; von Hofsten et al., 2000) independent of target characteristics and, therefore, are able to internally represent ongoing movement over occlusion.

Comparative studies highlighting commonalities and differences in the processing of occluded human, object, and distorted movement are surprisingly scarce and inconclusive. Infants apparently assume some physical constraints to apply to humans and objects (e.g., solidity principle, Saxe et al., 2006), but also recognize the specific self-propelled properties of human behavior (Kuhlmeier et al., 2004; Legerstee, 1994; Spelke et al., 1995). A systematic comparison of target characteristics and movement properties is required to further our knowledge on internal representation of various movement stimuli as well as its neural basis in infancy.

1.2. Neural markers of movement observation in infants

In the present study, we investigated the processing of occluded human and object movement, presented in both continuous and distorted fashion, by measuring EEG in 10-month-old infants in a within-subjects design. We derived measures of rhythmic neural activity

taken to reflect *attention*, *memory*, and *sensorimotor simulation* based on empirical findings and theoretical considerations.

1.2.1. Posterior alpha activity as an indicator for attention and perception

Traditionally, increased occipital alpha oscillations have been considered as a passive consequence of lacking visual stimulation in both adults (Niedermeyer, 1999; Pfurtscheller and Lopes da Silva, 1999) and infants (Marshall et al., 2002; Stroganova et al., 1999). However, recently, occipital alpha modulations have been ascribed a major role in internally controlled information processing (cf. Klimesch, 2012; Orekhova et al., 2001).

Both synchronization and de-synchronization in the alpha range have been linked to active processing (i.e., attention) in visual areas of the brain. On the one hand, enhanced alpha oscillations are theorized to reflect cortical inhibition supporting the precise timing of widespread cortical communication (Klimesch et al., 2007; Neuper and Pfurtscheller, 2001) and the selection of task-relevant information (Freunberger et al., 2011; J. S. Johnson et al., 2011; Klimesch, 2012). In accordance with the inhibition account, Orekhova et al. (2001) found more pronounced posterior alpha activity in infants who maintained anticipatory attention longer in a peek-a-boo game. On the other hand, a more recent notion argues that excitatory states (i.e. alpha de-synchronization) support the generation of enriched information in the brain (cf. Hanslmayr et al., 2012), for example preceding the recognition or reappearance of an object (Freunberger et al., 2011; Rohenkohl and Nobre, 2011).

Although occipital alpha activity related to mechanisms of attention has been reported in a variety of adult studies on movement processing, it has rarely been acknowledged in infants. In adults, oscillatory modulations were found to mirror the ongoing extraction and prediction of movement information (Rohenkohl and Nobre, 2011; Tan et al., 2013), particularly when participants had only little own experience in performing a movement (Diersch et al., 2013; Urgesi et al., 2012). Hence, occipital alpha oscillations could be regarded as an indicator for attentionally controlled processing of visual movement information.

Even when an infant finally masters a motor act such as crawling or walking, first-hand motor experience is still relatively restricted; hence, attentional mechanisms are likely to assist processing of various movement types in infancy. Furthermore, adults' perceptual processing reflected in oscillatory modulations is highly attuned to compensate for missing or distorted information (Freunberger et al., 2008; J. S. Johnson and Olshausen, 2005; Thompson and Parasuraman, 2011). Given infants' performance in movement tracking tasks as described above (Gredebäck and von Hofsten, 2004; von Hofsten et al., 2007), we investigated modulations of occipital alpha oscillations as a marker of controlled perceptual processing (i.e., attention) during the observation of various occluded movements here.

1.2.2. Frontal theta activity and its relation to cognitive demands and mnemonic operations

Rhythmic neural activity in the theta frequency range has often been linked to spatial, working, and long-term memory demands in adults (for recent reviews, see, e.g., Jacobs and Kahana, 2010; Lisman and Jensen, 2013; Nyhus and Curran, 2010). Recent studies suggested that fronto-central theta activity is generated by prefrontal-hippocampal interactions (Cohen, 2011; Guitart-Masip et al., 2013). Given the importance of these brain regions in *maintaining and integrating* information across time and space (e.g., Miller and Cohen, 2001; Simons and Spiers, 2003), fronto-central theta activity might form the implementation of a neural accumulator (e.g., Bland and Oddie, 2001; van Vugt et al., 2012).

In line with this assumption, there is evidence that infants recruit frontal theta networks in cognitively demanding situations (see Saby and Marshall, 2012 for a review). Orekhova and her colleagues (Orekhova et al., 1999; Orekhova et al., 2006; Stroganova et al., 1998) studied neural modulations in the theta range using a so-called

'internally controlled attention task', referring to a situation in which infants maintain attention to a social partner during peek-a-boo play. This game mimics a working memory task – in a broad sense: Only when infants are capable of extracting and actively keeping information on the evolving interaction, they respond to the reappearing adult with laughter. Comparing infants aged 8 to 12 months and preschool children, frontal theta activity during the game increased as compared to the passive observation of soap bubbles (Orekhova et al., 2006), indicating that frontal theta rhythms assisted the processing of the disappearing and reappearing adult. Furthermore, the relation between the magnitude of frontal theta and the duration of maintained attention to the game varied with age (Orekhova et al., 1999; Stroganova et al., 1998), showing that the cognitive demands of the attention task decreased with development.

The role of frontal theta activity in movement processing was recognized only recently. Presenting human, android, and robotic movement in a sample of adults, Urgen et al. (2013) found increased theta activity for non-human movements. The results suggest that demands on memory processing may be increasing when the observed movement deviates from biological movement. It has not yet been investigated whether frontal theta in infant brains is also sensitive to target and movement properties. With regard to occlusion events, movement information needs to be maintained during occlusion and integrated with the reappearing visual input following the occlusion. As both maintenance and integration are functions supported by theta activity in prefrontal–hippocampal circuits, we expected differences in frontal theta activity to reflect cognitive demands related to the processing of occluded movement under varying target and movement properties.

1.2.3. Central alpha activity and sensorimotor simulation

Decreased alpha and beta activity at central sites (also labeled sensorimotor, rolandic, or mu rhythm) has been associated with *sensorimotor simulation* during movement observation in adults (Cochin et al., 1999; Hari et al., 1998; Muthukumaraswamy and Johnson, 2004; Virji-Babul et al., 2007). More precisely, sensorimotor brain areas, particularly the premotor cortex, become active in a simulation mode as if the person were actually performing the action (for a review, see Rizzolatti and Craighero, 2004). A similar pattern has been demonstrated in infants and toddlers for central alpha activity only (see also Marshall and Meltzoff, 2011; for a review, see Marshall et al., 2011; Nyström, 2008; Southgate et al., 2009). Thus, sensorimotor simulation provides a link between perception and action (e.g., Pineda, 2005) that may promote social functions including observational learning (e.g., Brass and Heyes, 2005), understanding intention (e.g., Iacoboni et al., 2005; Meltzoff, 2007), or joint action (e.g., Knoblich and Sebanz, 2008).

Behavioral and neurophysiological data in adults suggest that sensorimotor simulation is continued or maintained in real-time when an action is temporarily hidden from view (Diersch et al., 2013; Graf et al., 2007; Saunier et al., 2012; Stadler et al., 2011; Stadler et al., 2012). Corresponding evidence was obtained for infants aged 6 to 12 months. It was shown that 9-month-old infants' central alpha activity was sensitive to the display of a hand reaching behind an occlusion (Southgate et al., 2010). Moreover, at the same age, sensorimotor simulation seemed to operate in a real-time manner (Southgate et al., 2009). Therefore, central alpha modulations might indicate the reliance on internally represented actions during transient occlusion.

It has been a matter of debate whether and to which extent sensorimotor simulation is sensitive to target and movement properties. On the one hand, it has been assumed that motor as well as perceptual experience in a given motor act is essential to automatically recruit the motor system during action observation (e.g., Aglioti et al., 2008; Casile and Giese, 2006; Heyes, 2010; Reid et al., 2006; van Elk et al., 2008). Investigating 14- to 16-month-old infants, van Elk et al. (2008) found that neural activity correlates with the duration of motor experience infants had with the observed crawling and walking movements. From this point of view, only movement within infants' motor

repertoire and daily perceptual experience would result in decreased alpha activity (see Heyes, 2010). On the other hand, there is accumulating evidence for motor activation elicited by motor acts that are outside of the observers' (current) motor abilities, such as for robotic motion (e.g., in infants, Grossmann et al., 2012; in adults, Stadler et al., 2012), or even beyond motor practicability, such as for non-imitable object and abstract movements (in infants, Virji-Babul et al., 2012; in adults, Zago and Lacquaniti, 2005). For instance, in a study presenting object movement as well as grasping and walking videos to 4- to 11-month-old infants, Virji-Babul et al. (2012) found sensorimotor simulation in response to all movement types. Consistently, Urgen et al. (2013) did not find differences in central alpha in adults watching human, android, and robotic movement. In line with these findings, continuous movement might result in central alpha decrease independent of the observed target.

To further specify the functioning of sensorimotor simulation in infants, we varied the degree of familiarity of the observed movements. Specifically, we compared a continuous human movement in which observing infants were experienced (i.e., crawling) to distorted versions of this movement as well as to continuous and distorted versions of an abstract object's movement.

1.3. The present study

The present study investigated neural mechanisms that allow infants to process and internally represent observed movement that is transiently occluded from view. Using EEG, we examined the oscillatory activity associated with cognitive processes of attention, memory, and sensorimotor simulation among 10-month-old crawling infants. A behavioral proxy measure of attention was derived from coding infants' gazing away from the monitor during stimulus presentation. The infants watched videos showing a human crawling movement and an abstract object's movement that were briefly occluded. Two perceptual conditions were implemented for both targets: The movement prior to the occlusion was presented either continuously or in a 'jumping' non-continuous fashion. The latter condition was intended to render movement tracking more difficult and thereby impede successful internal representation during occlusion.

We hypothesized the following: (a) In accordance with infants preference for social stimuli (see Section 1.1), we assumed more attention during the presentation of human compared to object movement as indicated by less gazing away from the monitor. (b) Likewise, we expected increased attentional demands during the observation of object compared to human, as well as distorted compared to continuous stimulus material, as reflected in modulations of occipital alpha activity (see Section 1.2.1). (c) We assumed distorted and object movement to result in higher cognitive demands in relation to the presentation of continuous human movement, as displayed by increased frontal theta activity (see Section 1.2.2). (d) We hypothesized that continuous human movement would recruit the neural networks related to sensorimotor simulation more strongly, resulting in decreased central alpha activity, than distorted or abstract movement would (see Section 1.2.3).

2. Methods

2.1. Participants

The study was conducted in the Baby Laboratory at the Max Planck Institute for Human Development, Berlin, Germany. The study was approved by the Institute's Ethics Committee in accordance with the Declaration of Helsinki. A total of 79 10-month-old infants (± 10 days) were recruited from the Institute's database of parents interested in participating in infant studies. Parents gave their written informed consent upon arrival. Study participants received 17 € for each test session. All infants were born at term (week of gestation ≥ 37 , birth weight ≥ 2500 g), healthy at the time of testing, and, according to

their parents, capable of crawling on hands and knees with their stomach lifted. Parents were encouraged to bring their own notes about their children's motor development to fill out a short checklist in the lab.

Twenty-three infants were excluded from analysis of gazing behavior for the following reasons: (a) the infant did not participate in two test sessions within 2–10 days ($n = 12$; e.g., due to illness); (b) the infant did not crawl a distance of 1.5 m in the lab at least once ($n = 4$); (c) the infant was too fussy to be properly tested ($n = 5$); or (d) occurrence of technical issues with video recording ($n = 2$). Further 31 infants were excluded from EEG analysis because (a) the infant did not produce sufficient artifact-free EEG data of at least 10 trials in all four conditions in both test sessions combined ($n = 29$) or (b) the EEG measurement failed due to technical issues ($n = 2$).

The final sample for the EEG analysis consisted of 25 infants, while gaze behavior could be analyzed in 56 infants. Table 1 presents descriptive information on the samples. In the EEG sample, all infants except one were capable of sitting independently and all infants except one were able to pull themselves into a standing position.³ None of the infants were able to walk at the time of testing.

High attrition rates are commonly observed in EEG studies with mobile infant populations (see de Haan, 2007). In the present study, EEG was collected concurrently with eye-movement recordings (not part of the current report). Furthermore, four conditions, presented in 4 s long trials, were compared in a within-subjects design, making two test sessions necessary. As a result, a considerable amount of EEG data (68%) had to be excluded from analyses.

2.2. Stimulus material and procedure

The experiment was conducted in an acoustically shielded room in which the floor was covered with an electromagnetically shielding mat. The testing area was surrounded by white curtains to minimize visual distraction. The infant sat on the parent's lap facing a 20.1" monitor at a distance of approximately 80 cm. To prevent extensive movement, the infant sat in a BabyBjörn® baby carrier.

2.2.1. Stimuli and design

Participants watched video clips displaying ongoing movement (2480 ms of *pre-occlusion*) that was occluded by a full-screen black occlusion (520 ms of *occlusion*) and continued subsequently (1000 ms of *post-occlusion*). Thus, each video comprised three phases, lasting a total of 4000 ms.

Stimuli were designed to vary the video's target (human vs. object), as well as the smoothness of the depicted movement during the pre-occlusion phase (continuous vs. non-continuous), resulting in four fully crossed conditions: *human continuous*, *human non-continuous*, *object continuous*, and *object non-continuous*.

The human stimulus featured a 10-month-old infant crawling from left to right in front of a neutral background (recorded in the lab). The object stimulus (designed with Adobe After Effects, Adobe Systems Software, Dublin, Ireland) depicted a constantly moving 2D-hexagon with rounded edges. While object and human stimuli shared perceptual features (i.e., size, color, and velocity), they differed in terms of dynamics, complexity, and morphology (see Fig. 1A).

Both object and human stimuli were presented in a continuous and a non-continuous manner during the pre-occlusion phase. To construct non-continuous movement, the continuous pre-occlusion video stream was cut into short snips and shuffled (duration of snips varied from 160 to 360 ms; a total of 9 snips was used for restructuring) resulting in jumping movement. Thus, non-continuous movements were less traceable than continuous movements during pre-occlusion (see Fig. 1B). Three versions of non-continuous human and object movements were

Table 1

Descriptive information on samples for Gaze and EEG analysis.

	Gaze sample		EEG sample	
	N = 56		N = 25	
	M	SD	M	SD
Number of boys/girls	23/33		14/11	
Age in days				
Session 1	299.8	6.4	298.6	6.0
Session 2	305.7	7.5	304.6	7.2
Delay between sessions in days	5.9	2.2	6.0	2.4
Week of gestation at delivery	40.2	1.4	40.2	1.4
Birth weight in grams	3552	411	3602	407
Onset age in months				
Crawling	8.3	0.9	8.3	0.9
Sitting	7.8	1.2	7.7	1.4
Standing	8.8	0.8	8.7	1.0
Number of trials				
Human continuous	54	15	23	9
Human non-continuous	57	13	26	8
Object continuous	56	14	20	7
Object non-continuous	54	14	19	7

Note. M = mean; SD = standard deviation. The EEG sample is a sub-sample of the Gaze sample. 300 days equals 10-month birthday. Samples did not significantly differ from each other ($t < 0.836, p > .405$) except for number of trials ($t < 3.6, p > .001$) due to different inclusion criteria for Gaze and EEG data (see Section 2.5 "EEG preprocessing"). The number of trials available for EEG analysis varied between human and object conditions ($t > 2.75, p < .011$).

generated, respectively. The final 200 ms of the pre-occlusion were identical for continuous and non-continuous movements.

During the occlusion phase, the visual input was identical for all conditions (i.e., black screen). During the post-occlusion phase, the visual input was identical for continuous and non-continuous conditions of both human and object movement. This design ensured that differences between the experimental conditions during the occlusion and post-occlusion cannot be attributed to differences in visual input during these phases, but rather to differences in the visual input between the conditions during the pre-occlusion phase. To avoid lateralization of brain activity, each condition was presented from left to right, and from right to left (i.e., flipped versions of the original videos were shown).

2.2.2. Procedure

Stimuli were presented using a customized program written in Microsoft Visual C++ (Microsoft Corporation, Redmond, USA). Each trial was preceded by a centered fixation object (i.e., colored pictures of toys; duration of 800–1300 ms) on a gray background. In repeated trial presentation, learning effects have been reported for the tracking of ongoing movement (e.g., Falck-Ytter et al., 2006). Therefore, trials of each condition were presented in blocks of six. Prior to each block a short attention-getter video was shown (2500–4500 ms). The order of blocks was quasi-randomized such that the same condition was never repeated immediately; infants were randomly assigned to one of four predefined orders. A maximum of 24 blocks (i.e., 144 trials) was presented.

An experimenter controlled the stimulus presentation from an adjacent room watching the infant via video-recording. If an infant became fussy or lost attention, the stimulus presentation was interrupted by an infant-appropriate video (Baby Einstein) or by interactive play with the experimenter. Trials interrupted due to such a pause were subsequently repeated. The session ended when the infant's attention could no longer be attracted to the monitor. To obtain sufficient data for EEG analysis, the same procedure was repeated within 2–10 days for each participant.

2.3. Video-recording and coding of gaze behavior

The experimental session was video-recorded in time-synchronized split-screen images including a frontal and lateral view of the infant as

³ Note that the exception was not the same child.

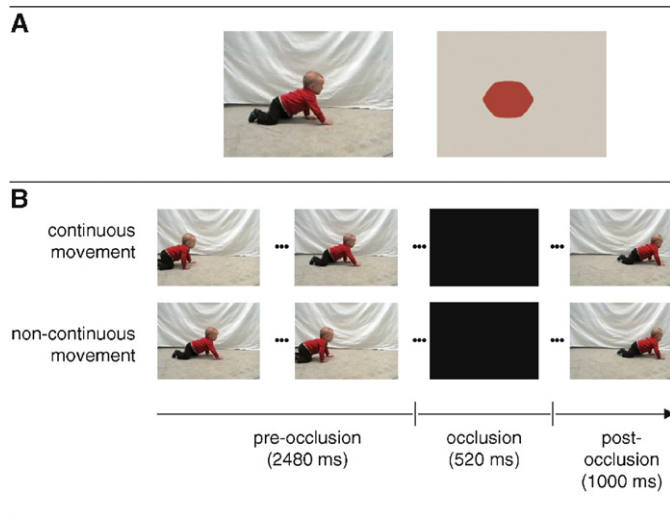


Fig. 1. Depiction of the stimulus material, (A) screenshot of human movement (left) and object movement (right), (B) screenshots of human movement at pre-occlusion, occlusion, and post-occlusion phases, for continuous movement (upper row) and non-continuous movement (lower row).

well as a running and condition trigger. For each participant, the *frequency of gazing away* was coded post-hoc from the video-recordings using Interact (Mangold International GmbH, Arnstorf, Germany) to derive a proxy measure of attention to the four presented movement types. Therefore, separately for each phase of the trial (i.e., pre-occlusion, occlusion, post-occlusion), it was determined whether and how often the participant gazed away from the monitor during the respective phase. Only uninterrupted trials were coded. The length of each phase of a trial and the number of trials presented to each participant varied. Therefore, the mean across trials per phase relative to the length of the phase (in frames) was calculated. For each condition, data were collapsed across movement directions.

2.4. EEG recordings

The EEG was recorded continuously with a BrainAmp DC amplifier (BrainProducts GmbH, Gilching, Germany) from 32 active electrodes (actiCap by BrainProducts) that were inserted into a soft elastic cap according to the 10–20-system (EASYCAP GmbH, Herrsching, Germany). During recording, the right mastoid electrode served as reference and the left mastoid was recorded as an additional channel. Ground was placed at location AFz. Impedances were kept below 20 k Ω during preparation. The EEG was recorded with an analog pass-band of 0.1 to 250 Hz and digitized with a sampling rate of 1000 Hz.

2.5. EEG preprocessing

Prior to EEG preprocessing and based on the coding of video-recordings as described above, trials were discarded in which infants showed one or both of the following behaviors: (a) they did not attend to the stimulus for the total duration of the trial; (b) they produced limb movement that could be seen as part of imitative crawling. The latter criterion was chosen because we were interested in brain activity related to action observation but not to overt imitation.

Using Vision Analyzer 2 (Brain Products), the remaining EEG data was segmented into 4700 ms long epochs (from -2700 ms to 2000 ms relative to the onset of occlusion). The extracted segments were visually inspected for broken channels and extreme or untypical artifacts (i.e., extensive movements), which were removed from further analyses. All subsequent preprocessing and EEG analyses were conducted using the FieldTrip software package (developed at the F.C. Donders Centre for Cognitive Neuroimaging, Nijmegen, The Netherlands; <http://>

fieldtriptoolbox.org, Oostenveld et al., 2011) and custom-made routines operated in MATLAB 7.10.0 (MathWorks Inc., Natick, MA, USA).

Independent Component Analysis (ICA; Jung et al., 2000) was performed to clean the EEG from further stereotyped artifacts, especially eye-movements and muscle-related ones. For this preprocessing step, all selected segments across all conditions were concatenated within subject, filtered (high pass 1 Hz, low pass 100 Hz, 6th-order Butterworth filter), and subjected to an extended infomax ICA (A. J. Bell and Sejnowski, 1995). A DFT filter as implemented in FieldTrip was used to suppress line-noise. ICs representing eye blinks, saccades, muscle activity, or instrumental noise were visually identified and discarded. All subsequent analyses were carried out in sensor space, based on the back-projection of the non-artifact ICs. Previously identified broken channels were interpolated after ICA cleaning. Cleaned data were re-referenced to the mathematically linked mastoids (Michel et al., 2004), filtered (high pass 1 Hz, low pass 30 Hz, 6th-order Butterworth filter), and segmented into 4000 ms epochs according to the onset of occlusion (-2480 ms to 1520 ms). For each single trial, the offset was removed by subtracting the average of the total epoch.

2.6. Extraction of individualized EEG measures

Traditional data aggregation presumes that observed interindividual differences originate from noise in the data obscuring the actual subject of investigation (e.g., Danziger, 1990). However, in the presence of true interindividual differences, such an approach may produce distorted results. Here, we pursued an individualized approach to EEG frequency analysis by identifying the individual peak frequency at the individual peak electrode in a given electrode cluster and frequency range (Doppelmayr et al., 1998; Werkle-Bergner et al., 2009). Such an approach is advisable as, in adults, individual differences in spectral characteristics of the EEG are sizeable and reliable (for a review see Klimesch, 1999), and some of them, such as alpha peak frequency, relate to cognitive functioning in a trait-like manner (e.g., Grandy, Werkle-Bergner, Chicherio, Lövdén et al., 2013; Grandy, Werkle-Bergner, Chicherio, Schmiedek et al., 2013). Interindividual differences in the alpha range have also been associated with cognitive performance in infants (M. A. Bell, 2001, 2012). At the same time, the electrodes best capturing a neural process of interest might differ between participants, due to differences in head shape or in convolution of the brain. From a methodological perspective, our approach corresponds to an “idiographic filter”, in which the indicators of a given construct are individualized to allow for more valid comparison across individuals and experimental conditions (cf. Nesselroade et al., 2007; Nesselroade and Molenaar, 2010).

In line with the literature on infant EEG, frontal theta band activity was defined as oscillatory activity within 4–6 Hz (Orehova et al., 1999; Orehova et al., 2006) and alpha band activity was defined as oscillatory activity within 6–9 Hz (Marshall et al., 2002; Stroganova et al., 1999). The *individual peak frequency* (IPF) was defined as the maximum peak within these frequency ranges. Given our interest in frontal theta band activity as well as alpha band activity over central and occipital regions, electrode clusters of interest (EOI) were chosen accordingly (Marshall et al., 2002; Marshall et al., 2011; Orehova et al., 1999; Saby and Marshall, 2012; Stroganova et al., 1999). The *frontal theta* cluster included electrodes F3, Fz, F4, FC1, and FC2. The *central alpha* cluster included electrodes FC1, FC2, C3, Cz, C4, CP1, and CP2. The *occipital alpha* cluster included electrodes O1 and O2. The *individual peak electrode* (IPE) was defined as the electrode within a respective EOI at which the IPF was detected. Note that we did not aim to investigate the distribution of IPEs but to identify reliable rhythmic neural activity in each individual (Aru et al., 2015; Doppelmayr et al., 1998; Klimesch, 1999).

To detect individual peak frequencies, the spectral power distribution between 1 Hz and 20 Hz at each electrode was estimated by means of fast Fourier transformation (FFT) across all trials and phases

(i.e., from –2480 ms to 1520 ms after occlusion onset). Each trial was zero-padded to 10 s and tapered with a Hanning window to achieve a frequency resolution of 0.1 Hz. The power spectra were corrected for the 1/f trend inherent in scalp EEG data to facilitate the detection of spectral peaks (Demanuele et al., 2007; He et al., 2010). When no IPF was detected, the missing values were interpolated with the mean of all detected peaks to preserve comparable samples for the EEG measures. There was one missing value for the frontal theta, four missings for the central alpha, and two missings for the occipital alpha activity; missings did not occur in the same participants across all EEG measures.

To analyze modulations in rhythmic neural activity, FFT was performed separately for each phase of the trial (i.e., pre-occlusion, occlusion, and post-occlusion). As the phases of each trial varied in length, the data were again zero-padded to 10 s prior to FFT calculation, resulting in a common frequency resolution of 0.1 Hz. Power values for each phase of the trial and experimental condition were extracted for each participant at the respective IPF and IPE after averaging across trials within participants. For each condition, data were collapsed across movement directions and sessions to obtain enough trials for statistical comparison.

2.7. Statistical analysis

Statistical analyses were done in SPSS 15.0 (SPSS Inc., 1989–2006, USA). For frequency of gazing away, a repeated-measures ANOVA with four within-subjects factors was calculated: Stimulus (human vs. object), Distortion (continuous vs. non-continuous), Phase (pre-occlusion vs. occlusion vs. post-occlusion), and Session (Session 1 vs. Session 2). Separately for each EEG measure, repeated-measures ANOVAs with three within-subjects factors were performed: Stimulus (human vs. object), Distortion (continuous vs. non-continuous), and Phase (pre-occlusion vs. occlusion vs. post-occlusion). As the distribution of power values was skewed, data were log-transformed prior to the analysis.⁴ Partial eta squared η_p^2 is reported as an estimate of the effect size. Greenhouse-Geisser and Bonferroni corrections were applied when indicated.

3. Results

3.1. Frequency of gazing away

For frequency of gazing away, a four-way repeated-measures ANOVA revealed the following significant effects, which were followed up by paired-sample *t*-tests: (a) Phase ($F_{(1.07, 58.71)} = 665.21, p = .000, \eta_p^2 = .92$), showing that infants gazed away more often during the occlusion compared to pre- ($t = -26.29, p = .000$) and post-occlusion ($t = 24.61, p = .000$), and also more often during post-occlusion compared to pre-occlusion ($t = -25.50, p = .000$), (b) Stimulus ($F_{(1, 55)} = 146.38, p = .000, \eta_p^2 = .73$), showing that infants gazed away more often during object movement than during human movement ($t = -12.10, p = .000$), (c) Session ($F_{(1, 55)} = 34.88, p = .000, \eta_p^2 = .39$), showing that infants gazed away more often during Session 2 than during Session 1 ($t = -5.91, p = .000$), (d) Phase and Stimulus ($F_{(1.21, 66.28)} = 97.81, p = .000, \eta_p^2 = .64$) and (e) Phase and Session ($F_{(1.15, 63.08)} = 22.28, p = .000, \eta_p^2 = .29$) could not be dissolved (all $t > |21.00|$ all $p < .000$). No further effects were observed ($F < 3.60, p < .063$). See Table 2 for details of the descriptive statistics.

Overall, the results confirmed that infants preferred human over object movement, which corresponds to previously published evidence (e.g., Grossmann and Johnson, 2007; Reid et al., 2008). Furthermore, infants' attention decreased over the two sessions as well as over the

⁴ Comparable results were obtained in non-log-transformed data after exclusion of outliers ($> \text{mean} \pm 3 \text{SD}$).

Table 2
Descriptive information on analysis of frequency of gazing away.

Phase	Condition	Session 1		Session 2	
		M	SE	M	SE
Pre-occlusion	Human continuous	.0057	.00032	.0072	.00032
	Human non-continuous	.0059	.00038	.0077	.00035
	Object continuous	.0093	.00046	.0104	.00037
	Object non-continuous	.0082	.00039	.0102	.00040
Occlusion	Human continuous	.0219	.00134	.0288	.00158
	Human non-continuous	.0228	.00153	.0293	.00145
	Object continuous	.0365	.00227	.0424	.00171
	Object non-continuous	.0333	.00179	.0409	.00172
Post-occlusion	Human continuous	.0125	.00080	.0166	.00081
	Human non-continuous	.0132	.00084	.0172	.00079
	Object continuous	.0192	.00118	.0234	.00085
	Object non-continuous	.0188	.00096	.0229	.00090

Note. M = mean; SE = standard error of mean. Gaze behavior was defined as gazing away from the monitor. Frequency of gazing away was calculated as the mean across presented trials relative to the length of the respective phase (in frames).

course of a trial. Particularly, occlusion seemed to have challenged infants' continued attention towards the movement.

3.2. Individual peak frequency: topography and variability

Table 3 and Fig. 2 summarize the results of the individualized peak detection. As can be inferred from the topographical plots in Fig. 2, theta and alpha IPFs demonstrate distinct spatial distributions: While theta IPFs are maximal over fronto-central regions, alpha IPFs are most strongly expressed over central and occipital regions. Furthermore, alpha IPFs are not only distinguishable by their topographical profile; the average occipital IPF has a slightly lower peak frequency compared to the central one (see Table 2). The mean frequencies corresponded to those reported in the existing literature (for frontal theta, Orekhova et al., 1999; Orekhova et al., 2006; for central and occipital alpha, Stroganova et al., 1999).

3.3. Occipital alpha activity

For occipital alpha power, a three-way repeated-measures ANOVA revealed significant main effects of Phase ($F_{(1.39, 33.3)} = 40.4, p = .000, \eta_p^2 = .63$), Stimulus ($F_{(1, 24)} = 30.92, p = .000, \eta_p^2 = .56$), and Distortion ($F_{(1, 24)} = 7.31, p = .012, \eta_p^2 = .23$). In addition, we found significant two-way interaction effects of (a) Phase and Stimulus ($F_{(2, 48)} = 28.85, p = .000, \eta_p^2 = .55$), and (b) Phase and Distortion ($F_{(2, 48)} = 12.13, p = .000, \eta_p^2 = .34$) as well as a three-way interaction of (c) Phase, Stimulus and Distortion ($F_{(2, 48)} = 3.20, p = .05, \eta_p^2 = .12$). Follow-up analyses using repeated measures ANOVAs separately per level of Phase yielded that:

- (1) mean occipital alpha power was higher in object compared to human movement during pre-occlusion ($M = 1.32, SE = .14$ and $M = .63, SE = .1$, respectively, $p = .000$) and post-

Table 3
Descriptive information on individualized EEG measures.

	Mean IPF in Hz \pm SD	Number of infants per IPE within each electrode region of interest
Frontal theta	4.6 \pm 0.6	Fz = 14, FC1 = 5, FC2 = 3, F3 = 2, F4 = 1
Central alpha	7.4 \pm 0.6	Cz = 17, FC2 = 3, C3 = 2, CP2 = 2, FC1 = 1, C4 = 0, CP1 = 0
Occipital alpha	6.9 \pm 0.4	O1 = 13, O2 = 12

Note. IPF = Individual Peak Frequency; IPE = Individual Peak Electrode. On an individual basis, no overlap observed for IPF or IPE across EEG measures.

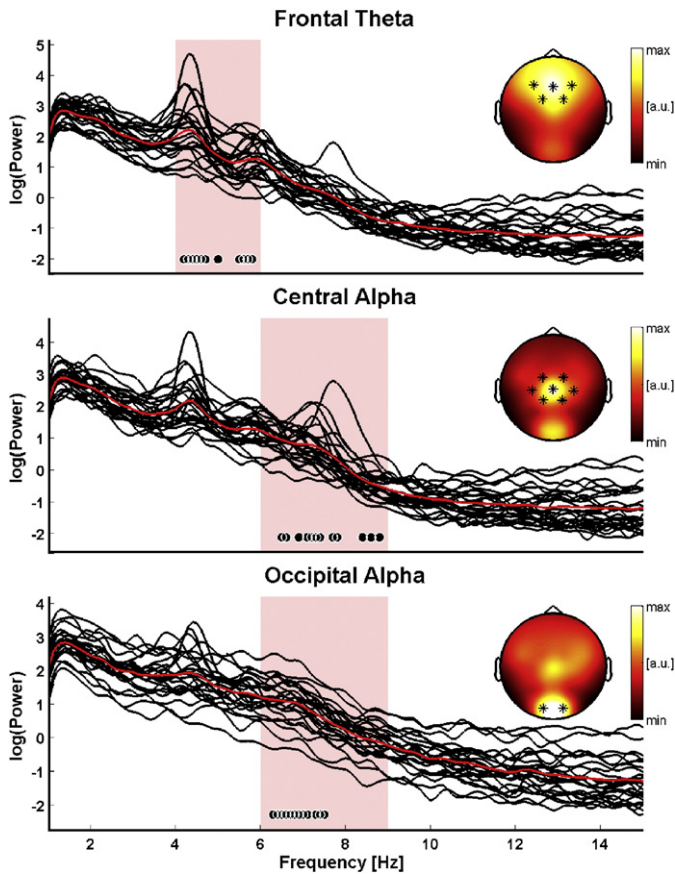


Fig. 2. Logarithmized single averaged power spectra of each individual at the individual peak electrode for EEG measures of frontal theta (upper line), central alpha (middle line), and occipital alpha (lower line) activity. The highlighted line indicates the grand average. The shaded area indicates the frequency range of each EEG measure. Individual peak frequencies (black circles) are plotted on the x-axis. Topography of grand averaged individual peak frequencies is included in the upper right. Note the differences between scaling of the EEG measures due to the $1/f$ trend inherent in scalp EEG data.

occlusion ($M = 1.26, SE = .12$ and $M = .97, SE = .1$, respectively, $p = .000$); there was no such difference during the occlusion ($M = 1.69, SE = .17$ and $M = 1.74, SE = .18$, respectively, $p = .493$);

- (2) mean occipital alpha power was higher in non-continuous compared to continuous movement during pre-occlusion ($M = 1.12, SE = .12$ and $M = 1.3, SE = .11$, respectively, $p = .000$); there were no such differences during the occlusion ($M = 1.74, SE = .17$ and $M = 1.68, SE = .17$, respectively, $p = .309$) and post-occlusion ($M = 1.12, SE = .12$ and $M = 1.11, SE = .10$, respectively, $p = .790$);
- (3) Stimulus and Distortion significantly interacted during occlusion ($F_{(1, 24)} = 9.23, p = .006, \eta_p^2 = .27$) but not during pre-occlusion ($F_{(1, 24)} = 3.23, p = .085, \eta_p^2 = .12$) and post-occlusion ($F_{(1, 24)} = .03, p = .867, \eta_p^2 = .00$). However, here, in six separate paired-sample t -tests, no Bonferroni-corrected significant effects emerged (all $t \leq 2.59$). As Bonferroni-corrected t -tests may over-correct for the family-wise error, we would like to mention that human continuous movement resulted in slightly higher occipital alpha power as compared to human non-continuous movement during the occlusion phase ($p = .016$; all other p -values $\geq .076$).

In summary, results for occipital alpha activity were consistent with the hypothesis that attentional demands are higher for object movement than for human movement, and higher for non-continuous movement than for continuous movement when visual information is available.

3.4. Frontal theta activity

The three-way repeated-measures ANOVA revealed main effects of Phase ($F_{(1.47, 35.17)} = 7.72, p = .004, \eta_p^2 = .24$) and Distortion ($F_{(1, 24)} = 7.49, p = .011, \eta_p^2 = .24$). In addition, there was an interaction effect of (a) Phase and Distortion ($F_{(1.6, 38.5)} = 4.9, p = .02, \eta_p^2 = .17$) and (b) Phase and Stimulus ($F_{(2, 48)} = 3.23, p = .048, \eta_p^2 = .12$). Follow-up repeated measures ANOVAs separately per level of Phase indicated that:

- (1) mean frontal theta power was higher for non-continuous than for continuous movement during pre-occlusion ($M = 2.23, SE = .18$ and $M = 2.10, SE = .16$, respectively, $p = .024$) and post-occlusion ($M = 2.09, SE = .14$ and $M = 1.90, SE = .13$, respectively, $p = .000$); there was no such difference during occlusion ($M = 1.91, SE = .13$ and $M = 1.9, SE = .11$, respectively, $p = .824$),
- (2) mean frontal theta power was higher for object than for human movement during occlusion ($M = 1.96, SE = .11$ and $M = 1.85, SE = .12$, respectively, $p = .017$) but not during pre-occlusion ($M = 2.19, SE = .16$ and $M = 2.15, SE = .18$, respectively, $p = .403$) and post-occlusion ($M = 1.97, SE = .14$ and $M = 2.02, SE = .13$, respectively, $p = .304$). The main effect of Stimulus and the three-way interaction did not reach significance (all $F \geq 1.16$; all $p \geq .293$).

In sum, frontal theta activity increased when processing of movement was cognitively more demanding. This was reflected in larger theta power in response to distorted movements during pre- and post-occlusion, and to object movement during occlusion. These findings are in line with previous reports on adult participants (Urgen et al., 2013).

3.5. Central alpha activity

Using repeated-measures ANOVA, we found no significant effects for mean central alpha power (all $F \leq 2.64$; all $p \geq .104$). Fig. 3 illustrates the results of all three EEG measures.

Thus, the analyses provided no evidence for differential involvement of sensorimotor simulation, as reflected in central alpha activity, neither when the infants observed human movement nor when they observed non-human movement in a continuous or non-continuous fashion.

4. Discussion

This study investigated the contribution of infants' neural mechanisms related to attention, memory, and sensorimotor simulation to the tracking and internal representation of occluded movements. Ten-month-old infants, capable of crawling, watched videos showing crawling and abstract object movement that were transiently occluded. Prior to occlusion, the movement was presented in a continuous or distorted fashion. Coding of gazing away from the monitor indicated that human targets captured more attention than objects and that occlusions challenged continued orientation towards the movement. Using EEG, occipital alpha, frontal theta, and central alpha oscillations were examined as indicators of attentional, mnemonic, and sensorimotor activity, respectively, captured before, during, and after occlusion. The results support three main interpretations. First, attention-related processes contribute to the tracking of movements. Second, memory-related processes support tracking as well as internally representing observed movement during occlusion. Third, the various movement conditions did not differentially activate sensorimotor simulation.

In sum, our results show that the processing of occluded movement recruits broadly distributed and functionally diverse neural mechanisms. Natural human movement is a rich source of information, both internally via available memory content and externally via available

motion cues based on perceptual analysis; and 10-month-old infants' neural system seems well prepared to account for this information.

4.1. Differential attentional processing of visual input is reflected in occipital alpha activity

Occipital alpha activity is regarded as a neural correlate of controlled information processing in visual areas of the brain (e.g., Klimesch, 2012; Orekhova et al., 2001). Here, we observed occipital alpha modulations reflecting more than just variations in the perceptual input across conditions: First, the oscillatory activity distinguished between human and object movement during pre- and post-occlusion – activity was reduced during the tracking of a crawling companion as compared to the abstract object movement. Second, oscillations at occipital electrodes differentiated between continuous and distorted movement during pre-occlusion, in that alpha activity was lower during the observation of continuous compared to non-continuous movement. This pattern of results cannot be explained by the visual complexity of the stimuli as human and non-continuous movements were certainly more complex than object and continuous movements. In fact, these findings rather suggest that infants were more attentively engaged when watching movement that was within their motor repertoire (i.e., human vs. object) and within their perceptual experience (i.e., continuous vs. non-continuous). This view is supported by complementary behavioral results showing that infants also gazed away less during the observation of continuous crawling movement as opposed to the other conditions. Therefore, our findings are in line with evidence indicating that infants prefer actions that are similar to their own actions (e.g., Sanefuji et al., 2008) and demonstrate remarkable capacities to discriminate social from non-social or distorted stimuli (Grossmann and Johnson, 2007). As human and object targets in the present study differed in important visual aspects such as dimensionality and morphology, future studies may design stimuli that have the ability to contrast target properties in the presence of higher perceptual comparability. This would allow further differentiation of infants' ability to categorize human and non-human stimuli.

Both increases (i.e., active inhibition, Klimesch et al., 2007) and decreases (i.e., active excitation, Hanslmayr et al., 2012) in occipital alpha activity have been associated with active attentional processing, but assigned varying functional implications. Interestingly, here, the overall oscillatory activity during occlusion was elevated for all movement types. Such an active inhibition of perceptual processing might be necessary when internally driven cognitive operations, such as visual input maintenance during occlusion, are executed elsewhere in the brain (Klimesch et al., 2007; Orekhova et al., 2001). Accordingly, the release from inhibition during pre- and post-occlusion (i.e., decreased activity) might be interpreted as effort to perceptually extract information from the ongoing movement (Hanslmayr et al., 2012; Werkle-Bergner et al., 2014). Thus, the present finding indicates that attentional demands decreased during a brief occlusion of observed movement, which is also implied by the increased level of gazing away when the monitor briefly turned black. Vice versa, the differences in occipital alpha activity during pre- and post-occlusion most likely reflect differences in the level of controlled perceptual processing of the movement types presented in this study.

During post-occlusion the movement was always presented in a continuous fashion. Results did not provide evidence that the movement information during post-occlusion was processed depending on the presentation mode during pre-occlusion (i.e., continuous vs. non-continuous). Moreover, during occlusion the occipital alpha oscillations did not differ reliably between the four experimental conditions. This finding suggests that controlled perceptual processing neither supported internal representation during transient occlusion nor integration of pre- and post-occlusion input into a coherent movement perception.

It has been argued that processing of social information interacts with attentional processing (Fiske, 1993); nevertheless, the relevance

of occipital alpha oscillations during movement observation in infants has rarely been acknowledged. In a recent study on action perception in toddlers, Warreyn et al. (2013) included occipital alpha activity as a control variable to examine whether occipital oscillations differed from central alpha ones associated with sensorimotor simulation. They found a similar decrease in alpha activity at central and occipital sites when toddlers watched an action that they were asked to imitate subsequently, but not during action execution and observation of intransitive movement. The authors concluded that the imitation task might have enhanced the personal relevance of the action observation. The present findings extend previous research showing that, first, attentional mechanisms are recruited during movement observation even in infants as young as 10 months old, and, second, attentional processes are elicited even when infants passively watch ongoing movements. Therefore, in sum, our study underlines the role of occipital alpha activity in attentive processing of socially relevant stimuli.

4.2. Modulations of frontal theta activity suggest differential demands for controlled information integration during processing of occluded movement

Frontal theta activity has been linked to demanding processing in spatial, working, and long-term memory tasks (e.g., Lisman and Jensen, 2013; Orekhova et al., 1999). Here, in both pre- and post-occlusion phases, we observed increased frontal theta activity when jumping non-continuous movement was presented, as compared to when the same movement was presented in a natural continuous fashion. During post-occlusion, movement was always presented in a continuous fashion. Thus, this finding indicates that the presentation mode prior to occlusion influenced the processing of the movement following the occlusion.

For non-continuous movements, the pre-occlusion trajectory did not match the newly incoming input during the post-occlusion. Assuming that cognitive demands result from extracting, maintaining, recalling, and integrating relevant information, binding pre- and post-occlusion input into a unitary percept may have thus been more demanding compared to continuous movement. In this way, the present task resembles working memory paradigms that are known to tap into frontal theta mechanisms (Gevins and Smith, 2000; Jensen and Tesche, 2002). Based on the notion that fronto-central theta activity implements a neural accumulator (Bland and Oddie, 2001; van Vugt et al., 2012), increased theta activity observed here likely reflects increased demands to extract and integrate information during non-continuous pre-occlusion movements, as well as serving to bind information of pre- and post-occlusion input into a coherent movement representation. In addition, conflict processing based on competing memory representations (Bunting and Cowan, 2005; Hsieh and Ranganath, 2014; Nigbur et al., 2012) may have contributed to the observed effects as the movement styles during pre- and post-occlusion did not match.

During occlusion, there was no difference in frontal theta activity between continuous and non-continuous movement. This suggests that maintaining information on both natural and distorted movement was equally demanding for the infants. Nevertheless, activity was more pronounced for object as compared to human targets. This finding suggests that more cognitive effort was required to maintain information extracted from object than from human movement. This appears surprising as human crawling seems to be more complex than abstract object motion. However, daily experience with natural crawling might offer detailed and easily accessible information on the observed target, for instance concerning movement direction. Correspondingly, in adults, Urgen et al. (2013) found pronounced frontal theta activity for less biological motor acts (i.e., android and robotic motion) as compared to human action. Consequently, frontal theta oscillation might assist the processing of movement that does not comply with familiar rules of biological motion.

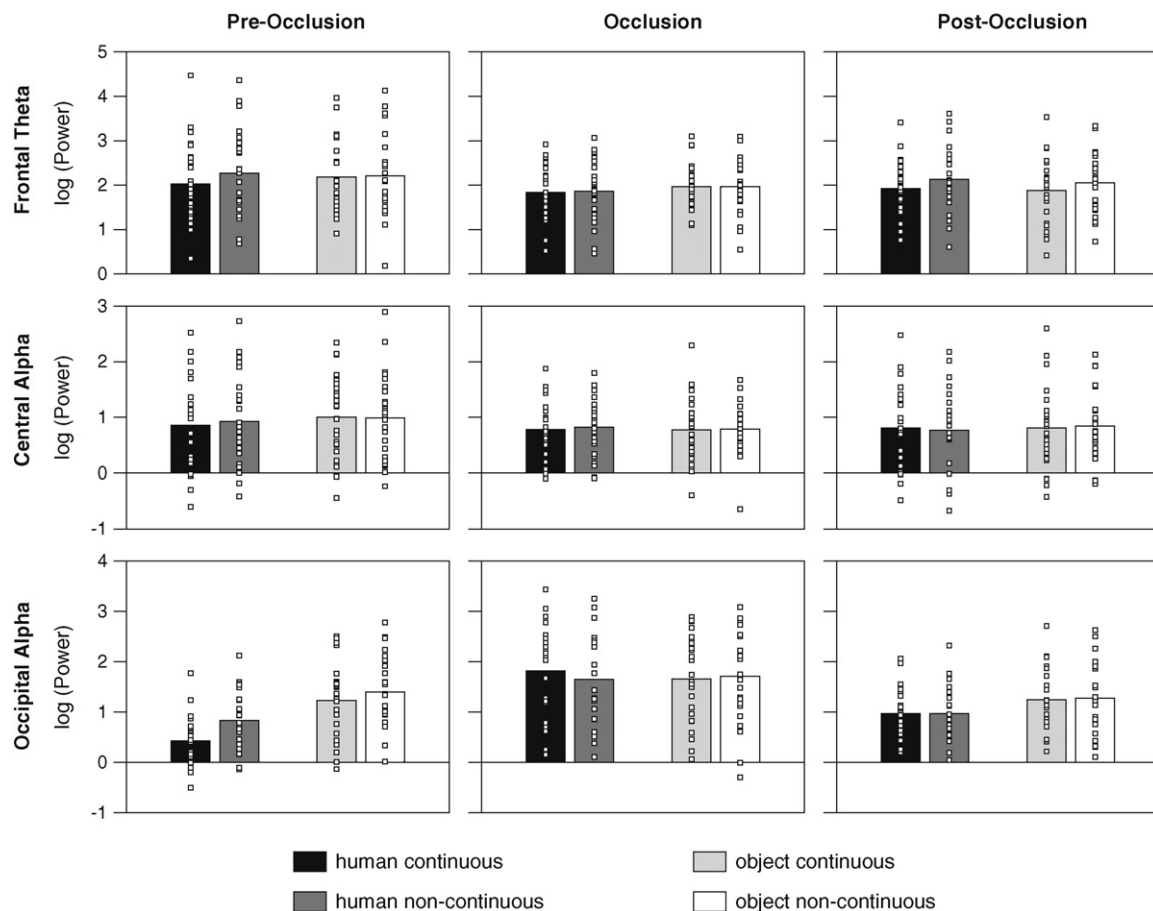


Fig. 3. Mean power differences between experimental conditions (i.e., human continuous, human non-continuous, object continuous, and object non-continuous) and phases (i.e., pre-occlusion, occlusion, and post-occlusion) for frontal theta, central alpha, and occipital alpha activity. Squares indicate single cases demonstrating the distribution within the sample.

Overall, our findings indicate that observing occluded movement induced the cognitively demanding integration of movement information assisted by mnemonic functions. This corresponds to previous studies that found increased theta activity during conditions requiring a high level of information integration and sustained attention, for instance, during dynamic social interaction (Orekhova et al., 1999; Orekhova et al., 2006) or when an observed action suddenly stops (Reid et al., 2009). Moreover, the present study is the first to show the involvement of infants' frontal theta activity in the processing of biological information inherent in observed movement.

4.3. No evidence for differential involvement of sensorimotor simulation

Reductions in central alpha activity are often assumed to index processing in cortical sensorimotor areas during the observation of other persons' actions (e.g., Marshall et al., 2011; Muthukumaraswamy and Johnson, 2004; Nyström et al., 2011). There is evidence that, at least during the last third of the first year of life, infants readily recruit motor brain regions during the observation of movements that are within their own motor repertoire (Nyström et al., 2011; Stapel et al., 2010; van Elk et al., 2008). Nevertheless, testing 10-month-old crawling infants, we did not observe evidence for differential responses in central alpha activity in relation to the observation of crawling and three other forms of movement that were transiently occluded.

The involvement of mechanisms related to attention, memory, and sensorimotor simulation during movement observation may vary with age and stimulus characteristics. Correspondingly, a central role of frontal theta activity in the integration of perceptual, sensory, and sensorimotor information (Bland and Oddie, 2001; Cruikshank et al., 2012) as

well as in the development of a cognitive system enabling this integration (Del Giudice et al., 2009) has been proposed. Furthermore, a recent fMRI study in adults suggests that the differential contribution of sensorimotor and attentional processes might depend on the task-specific context (Thioux and Keysers, 2014). Therefore, in the present study, it seems possible that a brief full-screen occlusion of ongoing movement might have triggered attentional and mnemonic mechanisms in young crawlers.

The role of familiarity of observed movement in the involvement of sensorimotor simulation is subject to inconclusive empirical findings. On the one hand, there is accumulating evidence that the motor system is involved whenever humans are observing movement, independent of the (current) motor abilities of the observer or even motor practicability (e.g., Grossmann et al., 2012; Zago and Lacquaniti, 2005), suggesting that the sensorimotor system is sensitive to a broad range of movement cues (e.g., Cross et al., 2012). Schubotz (2007) argued that humans internally simulate any external event within their premotor cortex to predict its ongoing progression, irrespective of whether the event can actually be mapped onto the observer's motor experience or not. From this perspective, it seems possible that the motor system of 10-month-old infants responded equally to human and object movement presented in both continuous and distorted fashions, as indicated by the present study. This interpretation also corresponds to recent findings in young adults showing that central alpha activity decreased equally during the observation of human, android, and robotic movement (Urgen et al., 2013). Similar relations between human and non-human agents were also shown using functional magnetic resonance imaging in frontal areas of the sensorimotor system (Cross et al., 2012).

On the other hand, there is substantial evidence that rich motor and perceptual experience drives the recruitment of sensorimotor

simulation during action observation (e.g., Casile and Giese, 2006), even in infants (Stapel et al., 2010; van Elk et al., 2008), suggesting that motor brain regions are selectively recruited for familiar movement cues. Heyes (2010) argued that bidirectional links are formed during the concurrent perception and production of actions. The resulting sensorimotor representation is strengthened due to repeated associative learning and can ultimately be elicited by observation alone (see also Del Giudice et al., 2009). Accordingly, the representation of an intransitive crawling movement might not be built rapidly because the opportunity to observe one's own and others' crawling are limited in everyday life as compared to, for instance, object-directed grasping actions. In line with this, one may assume that sensorimotor involvement was not captured here because the motor system of 10-month-old crawlers could not yet be recruited strongly enough. Correspondingly, in 14–16-month-old crawlers, van Elk et al. (2008) reported more sensorimotor simulation during crawling than during walking within the alpha frequency range at fronto-central electrodes.

Overall, the present finding suggests that sensorimotor simulation is invariant with regard to target characteristics (i.e., human vs. object) and movement properties (i.e., continuous vs. non-continuous) during a short full-screen occlusion. Furthermore, it seems reasonable to assume that intransitive crawling requires extensive experience before significant differences appear in central alpha activity. Considering the discrepancies in the literature, we suggest that future studies should disentangle the influences of age, motor, and visual experience as well as measurement methods on sensorimotor simulation during the observation of occluded movement in infancy.

5. Conclusions

The present findings show that 10-month-old infants recruit attention- and memory-related processes while observing briefly occluded movements. In particular, the findings suggest that early internal representations serving maintenance and integration draw on neural mechanisms related to memory. Furthermore, neural activity associated with attention particularly assists the processing of socially relevant stimuli. Concluding, at the end of the first year of life infants are capable of tracking and internally representing moving targets.

In sum, we argue that research on the development of action perception in infancy may profit from combining and thereby complementing the longstanding focus on sensorimotor representations by paying more attention to domain-general neural mechanisms that are crucially involved in the encoding, retention, and prediction of movement patterns perceived in a constantly changing social world.

Acknowledgments

This research was part of the Max Planck Research Network for the Cognitive and Neurosciences (Maxnet *Cognition*) and funded by the strategic innovation fund of the Max Planck Society. The study was conducted in partial fulfillment of the doctoral dissertation of CB. CB received training and financial support from the International Max Planck Research School on the Life Course (*LIFE*, <http://www.life-imprs.mpg.de>). WS received funding from the Deutsche Forschungsgemeinschaft, DFG (Project: STA 1076/1-1). We cordially thank the infants and their parents for participating in this study and our student assistants for their support in data collection, coding, and preprocessing. We further wish to thank Berndt Wischniewski for technical assistance and Amy Michèle for improving the English of this article.

References

Aglioti, S.M., Cesari, P., Romani, M., Urgesi, C., 2008. Action anticipation and motor resonance in elite basketball players. *Nat. Neurosci.* 11 (9), 1109–1116. <http://dx.doi.org/10.1038/nn.2182>.

- Aru, J., Aru, J., Priesemann, V., Wibral, M., Lana, L., Pipa, G., ... Vicente, R., 2015. Untangling cross-frequency coupling in neuroscience. *Curr. Opin. Neurobiol.* 31, 51–61. <http://dx.doi.org/10.1016/j.conb.2014.08.002>.
- Babiloni, C., Babiloni, F., Carducci, F., Cincotti, F., Coccozza, G., Del Percio, C., ... Rossini, P.M., 2002. Human cortical electroencephalography (EEG) rhythms during the observation of simple aimless movements: a high-resolution EEG study. *Neuroimage* 17 (2), 559–572. <http://dx.doi.org/10.1006/nimg.2002.1192>.
- Bell, A.J., Sejnowski, T.J., 1995. An information-maximization approach to blind separation and blind deconvolution. *Neural Comput.* 7 (6), 1129–1159. <http://dx.doi.org/10.1162/neco.1995.7.6.1129>.
- Bell, M.A., 2001. Brain electrical activity associated with cognitive processing during a looking version of the A-not-B task. *Infancy* 2 (3), 311–330. http://dx.doi.org/10.1207/s15327078IN0203_2.
- Bell, M.A., 2012. A psychobiological perspective on working memory performance at 8 months of age. *Child Dev.* 83 (1), 251–265. <http://dx.doi.org/10.1111/j.1467-8624.2011.01684.x>.
- Bertenthal, B.I., Longo, M.R., Kenny, S., 2007. Phenomenal permanence and the development of predictive tracking in infancy. *Child Dev.* 78 (1), 350–363. <http://dx.doi.org/10.1111/j.1467-8624.2007.01002.x>.
- Blake, R., Shiffrar, M., 2007. Perception of human motion. *Annu. Rev. Psychol.* 58, 47–73. <http://dx.doi.org/10.1146/annurev.psych.57.102904.190152>.
- Bland, B.H., Oddie, S.D., 2001. Theta band oscillation and synchrony in the hippocampal formation and associated structures: the case for its role in sensorimotor integration. *Behav. Brain Res.* 127 (1), 119–136. [http://dx.doi.org/10.1016/S0166-4328\(01\)00358-8](http://dx.doi.org/10.1016/S0166-4328(01)00358-8).
- Brass, M., Heyes, C., 2005. Imitation: is cognitive neuroscience solving the correspondence problem? *Trends Cogn. Sci.* 9 (10), 489–495. <http://dx.doi.org/10.1016/j.tics.2005.08.007>.
- Bremner, J.G., Johnson, S.P., Slater, A., Mason, U., Foster, K., Cheshire, A., Spring, J., 2005. Conditions for young infants' perception of object trajectories. *Child Dev.* 76 (5), 1029–1043. <http://dx.doi.org/10.1111/j.1467-8624.2005.00895.x>.
- Bunting, M.F., Cowan, N., 2005. Working memory and flexibility in awareness and attention. *Psychol. Res.* 69 (5–6), 412–419. <http://dx.doi.org/10.1007/s00426-004-0204-7>.
- Casile, A., Giese, M.A., 2006. Nonvisual motor training influences biological motion perception. *Curr. Biol.* 16 (1), 69–74. <http://dx.doi.org/10.1016/j.cub.2005.10.071>.
- Cochin, S., Barthelemy, C., Roux, S., Martineau, J., 1999. Observation and execution of movement: similarities demonstrated by quantified electroencephalography. *Eur. J. Neurosci.* 11 (5), 1839–1842. <http://dx.doi.org/10.1046/j.1460-9568.1999.00598.x>.
- Cohen, M.X., 2011. Hippocampal–prefrontal connectivity predicts midfrontal oscillations and long-term memory performance. *Curr. Biol.* 21 (22), 1900–1905. <http://dx.doi.org/10.1016/j.cub.2011.09.036>.
- Cross, E.S., Liepelt, R., Hamilton, A.F., Parkinson, J., Ramsey, R., Stadler, W., Prinz, W., 2012. Robotic movement preferentially engages the action observation network. *Hum. Brain Mapp.* 33 (9), 2238–2254. <http://dx.doi.org/10.1002/hbm.21361>.
- Cruikshank, L.C., Singhal, A., Huepelsheuser, M., Caplan, J.B., 2012. Theta oscillations reflect a putative neural mechanism for human sensorimotor integration. *J. Neurophysiol.* 107, 65–77. <http://dx.doi.org/10.1152/jn.00893.2010>.
- Danziger, K., 1990. *Constructing the Subject: Historical Origins of Psychological Research*. Cambridge University Press, Cambridge.
- de Haan, M., 2007. Visual attention and recognition memory in infancy. In: de Haan, M. (Ed.), *Infant EEG and Event-related Potentials*. Psychology Press, New York, pp. 101–138.
- Del Giudice, M., Manera, V., Keyesers, C., 2009. Programmed to learn? The ontogeny of mirror neurons. *Dev. Sci.* 12 (2), 350–363. <http://dx.doi.org/10.1111/j.1467-7687.2008.00783.x>.
- Demanuele, C., James, C.J., Sonuga-Barke, E.J., 2007. Distinguishing low frequency oscillations within the 1/f spectral behaviour of electromagnetic brain signals. *Behav. Brain Funct.* 3, 62. <http://dx.doi.org/10.1186/1744-9081-3-62>.
- Diersch, N., Mueller, K., Cross, E.S., Stadler, W., Rieger, M., Schütz-Bosbach, S., 2013. Action prediction in younger versus older adults: neural correlates of motor familiarity. *PLoS One* 8 (5), e64195. <http://dx.doi.org/10.1371/journal.pone.0064195>.
- Doppelmayr, M., Klimesch, W., Pachinger, T., Ripper, B., 1998. Individual differences in brain dynamics: important implications for the calculation of event-related band power. *Biol. Cybern.* 79 (1), 49–57. <http://dx.doi.org/10.1007/s004220050457>.
- Falck-Ytter, T., Gredebäck, G., von Hofsten, C., 2006. Infants predict other people's action goals. *Nat. Neurosci.* 9 (7), 878–879. <http://dx.doi.org/10.1038/nn1729>.
- Fiske, S.T., 1993. Social cognition and social perception. *Annu. Rev. Psychol.* 44, 155–194. <http://dx.doi.org/10.1146/annurev.ps.44.020193.001103>.
- Freunberger, R., Klimesch, W., Griesmayr, B., Sauseng, P., Gruber, W., 2008. Alpha phase coupling reflects object recognition. *Neuroimage* 42 (2), 928–935. <http://dx.doi.org/10.1016/j.neuroimage.2008.05.020>.
- Freunberger, R., Werkle-Bergner, M., Griesmayr, B., Lindenberger, U., Klimesch, W., 2011. Brain oscillatory correlates of working memory constraints. *Brain Res.* 1375, 93–102. <http://dx.doi.org/10.1016/j.brainres.2010.12.048>.
- Gevins, A., Smith, M.E., 2000. Neurophysiological measures of working memory and individual differences in cognitive ability and cognitive style. *Cereb. Cortex* 10 (9), 829–839. <http://dx.doi.org/10.1093/cercor/10.9.829>.
- Graf, M., Reitzner, B., Corves, C., Casile, A., Giese, M., Prinz, W., 2007. Predicting point-light actions in real-time. *Neuroimage* 36, T22–T32. <http://dx.doi.org/10.1016/j.neuroimage.2007.03.017>.
- Grandy, T.H., Werkle-Bergner, M., Chicherio, C., Lövdén, M., Schmiedek, F., Lindenberger, U., 2013. Individual alpha peak frequency is related to latent factors of general cognitive abilities. *Neuroimage* 79, 10–18. <http://dx.doi.org/10.1016/j.neuroimage.2013.04.059>.
- Grandy, T.H., Werkle-Bergner, M., Chicherio, C., Schmiedek, F., Lövdén, M., Lindenberger, U., 2013. Peak individual alpha frequency qualifies as a stable neurophysiological

- trait marker in healthy younger and older adults. *Psychophysiology* 50 (6), 570–582. <http://dx.doi.org/10.1111/psyp.12043>.
- Gredebäck, G., von Hofsten, C., 2004. Infants' evolving representations of object motion during occlusion: a longitudinal study of 6- to 12-month-old infants. *Infancy* 6 (2), 165–184. http://dx.doi.org/10.1207/s15327078in0602_2.
- Grönqvist, H., Gredebäck, G., von Hofsten, C., 2006. Developmental asymmetries between horizontal and vertical tracking. *Vision Res.* 46 (11), 1754–1761. <http://dx.doi.org/10.1016/j.visres.2005.11.007>.
- Grossmann, T., Cross, E.S., Ticini, L.F., Daum, M.M., 2012. Action observation in the infant brain: the role of body form and motion. *Soc. Neurosci.* 8 (1), 22–30. <http://dx.doi.org/10.1080/17470919.2012.696077>.
- Grossmann, T., Johnson, M.H., 2007. The development of the social brain in human infancy. *Eur. J. Neurosci.* 25 (4), 909–919. <http://dx.doi.org/10.1111/j.1460-9568.2007.05379.x>.
- Guitart-Masip, M., Barnes, G.R., Horner, A., Bauer, M., Dolan, R.J., Duzel, E., 2013. Synchronization of medial temporal lobe and prefrontal rhythms in human decision making. *J. Neurosci.* 33 (2), 442–451. <http://dx.doi.org/10.1523/JNEUROSCI.2573-12.2013>.
- Hanslmayr, S., Staudigl, T., Fellner, M.C., 2012. Oscillatory power decreases and long-term memory: the information via desynchronization hypothesis. *Front. Hum. Neurosci.* 6, 74. <http://dx.doi.org/10.3389/fnhum.2012.00074>.
- Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., Rizzolatti, G., 1998. Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proc. Natl. Acad. Sci. U. S. A.* 95 (25), 15061–15065.
- He, B.J., Zempel, J.M., Snyder, A.Z., Raichle, M.E., 2010. The temporal structures and functional significance of scale-free brain activity. *Neuron* 66 (3), 353–369. <http://dx.doi.org/10.1016/j.neuron.2010.04.020>.
- Hespos, S., Rochat, P., 1997. Dynamic mental representation in infancy. *Cognition* 64 (2), 153–188. [http://dx.doi.org/10.1016/S0010-0277\(97\)00029-2](http://dx.doi.org/10.1016/S0010-0277(97)00029-2).
- Heyes, C., 2010. Mesmerising mirror neurons. *Neuroimage* 51 (2), 789–791. <http://dx.doi.org/10.1016/j.neuroimage.2010.02.034>.
- Heyes, C., 2014. False belief in infancy: a fresh look. *Dev. Sci.* 17 (5), 647–659. <http://dx.doi.org/10.1111/desc.12148>.
- Hommel, B., Musseler, J., Aschersleben, G., Prinz, W., 2001. The theory of event coding (TEC): a framework for perception and action planning. *Behav. Brain Sci.* 24 (5), 849–937. <http://dx.doi.org/10.1017/S0140525X01000103>.
- Hsieh, L.T., Ranganath, C., 2014. Frontal midline theta oscillations during working memory maintenance and episodic encoding and retrieval. *Neuroimage* 85 (Pt 2), 721–729. <http://dx.doi.org/10.1016/j.neuroimage.2013.08.003>.
- Hunnius, S., Bekkering, H., 2010. The early development of object knowledge: a study of infants' visual anticipations during action observation. *Dev. Psychol.* 46 (2), 446–454. <http://dx.doi.org/10.1037/a0016543>.
- Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J.C., Rizzolatti, G., 2005. Grasping the intentions of others with one's own mirror neuron system. *PLoS Biol.* 3 (3), e79. <http://dx.doi.org/10.1371/journal.pbio.0030079>.
- Jacobs, J., Kahana, M.J., 2010. Direct brain recordings fuel advances in cognitive electrophysiology. *Trends Cogn. Sci.* 14 (4), 162–171. <http://dx.doi.org/10.1016/j.tics.2010.01.005>.
- Jensen, O., Tesche, C.D., 2002. Frontal theta activity in humans increases with memory load in a working memory task. *Eur. J. Neurosci* 15 (8), 1395–1399. <http://dx.doi.org/10.1046/j.1460-9568.2002.01975.x>.
- Johnson, J.S., Olshausen, B.A., 2005. The recognition of partially visible natural objects in the presence and absence of their occluders. *Vision Res.* 45 (25), 3262–3276. <http://dx.doi.org/10.1016/j.visres.2005.06.007>.
- Johnson, J.S., Sutterer, D.W., Acheson, D.J., Lewis-Peacock, J.A., Postle, B.R., 2011. Increased alpha-band power during the retention of shapes and shape–location associations in visual short-term memory. *Front. Psychol.* 2, 128. <http://dx.doi.org/10.3389/fpsyg.2011.00128>.
- Johnson, S.P., Amsco, D., Slemmer, J.A., 2003. Development of object concepts in infancy: evidence for early learning in an eye-tracking paradigm. *Proc. Natl. Acad. Sci. U. S. A.* 100 (18), 10568–10573. <http://dx.doi.org/10.1073/pnas.1630655100>.
- Johnson, S.P., Bremner, J.G., Slater, A.M., Mason, U.C., Foster, K., 2002. Young infants' perception of unity and form in occlusion displays. *J. Exp. Child Psychol.* 81 (3), 358–374. <http://dx.doi.org/10.1006/jecp.2002.2657>.
- Jung, T.P., Makeig, S., Humphries, C., Lee, T.W., Mckeown, M.J., Iragui, V., Sejnowski, T.J., 2000. Removing electroencephalographic artifacts by blind source separation. *Psychophysiology* 37 (2), 163–178. <http://dx.doi.org/10.1111/1469-8986.3720163>.
- Kaduk, K., Elsner, B., Reid, V.M., 2013. Discrimination of animate and inanimate motion in 9-month-old infants: an ERP study. *Developmental Cognitive Neuroscience* 6, 14–22. <http://dx.doi.org/10.1016/j.dcn.2013.05.003>.
- Kaufman, J., Csibra, G., Johnson, M.H., 2003. Representing occluded objects in the human infant brain. *P. Roy. Soc. B-Biol. Sci.* 270 (Suppl 2), S140–S143. <http://dx.doi.org/10.1098/rsbl.2003.0067>.
- Klimesch, W., 1999. EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Res. Rev.* 29 (2), 169–195. [http://dx.doi.org/10.1016/S0165-0173\(98\)00056-3](http://dx.doi.org/10.1016/S0165-0173(98)00056-3).
- Klimesch, W., 2012. Alpha-band oscillations, attention, and controlled access to stored information. *Trends Cogn. Sci.* 16 (12), 606–617. <http://dx.doi.org/10.1016/j.tics.2012.10.007>.
- Klimesch, W., Sauseng, P., Hanslmayr, S., 2007. EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res. Rev.* 53 (1), 63–88. <http://dx.doi.org/10.1016/j.brainresrev.2006.06.003>.
- Knoblich, G., Sebanz, N., 2008. Evolving intentions for social interaction: from entrainment to joint action. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 363 (1499), 2021–2031. <http://dx.doi.org/10.1098/rstb.2008.0066>.
- Kuhlmeier, V.A., Bloom, P., Wynn, K., 2004. Do 5-month-old infants see humans as material objects? *Cognition* 94 (1), 95–103. <http://dx.doi.org/10.1016/j.cognition.2004.02.007>.
- Legerstee, M., 1994. Patterns of 4-month-old infant responses to hidden silent and sounding people and objects. *Early Dev. Parenting* 3 (2), 71–80. <http://dx.doi.org/10.1002/edp.2430030204>.
- Lisman, J.E., Jensen, O., 2013. The theta-gamma neural code. *Neuron* 77 (6), 1002–1016. <http://dx.doi.org/10.1016/j.neuron.2013.03.007>.
- Marshall, P.J., Bar-Haim, Y., Fox, N.A., 2002. Development of the EEG from 5 months to 4 years of age. *Clin. Neurophysiol.* 113 (8), 1199–1208. [http://dx.doi.org/10.1016/S1388-2457\(02\)00163-3](http://dx.doi.org/10.1016/S1388-2457(02)00163-3).
- Marshall, P.J., Meltzoff, A.N., 2011. Neural mirroring systems: exploring the EEG mu rhythm in human infancy. *Developmental Cognitive Neuroscience* 1 (2), 110–123. <http://dx.doi.org/10.1016/j.dcn.2010.09.001>.
- Marshall, P.J., Young, T., Meltzoff, A.N., 2011. Neural correlates of action observation and execution in 14-month-old infants: an event-related EEG desynchronization study. *Dev. Sci.* 14 (3), 474–480. <http://dx.doi.org/10.1111/j.1467-7687.2010.00991.x>.
- Meltzoff, A.N., 2007. 'Like me': a foundation for social cognition. *Dev. Sci.* 10 (1), 126–134. <http://dx.doi.org/10.1111/j.1467-7687.2007.00574.x>.
- Michel, C.M., Murray, M.M., Lantz, G., Gonzalez, S., Spinelli, L., Grave de Peralta, R., 2004. EEG source imaging. *Clin. Neurophysiol.* 115 (10), 2195–2222. <http://dx.doi.org/10.1016/j.clinph.2004.06.001>.
- Miller, E.K., Cohen, J.D., 2001. An integrative theory of prefrontal cortex function. *Annu. Rev. Neurosci.* 24, 167–202. <http://dx.doi.org/10.1146/annurev.neuro.24.1.167>.
- Muthukumaraswamy, S.D., Johnson, B.W., 2004. Primary motor cortex activation during action observation revealed by wavelet analysis of the EEG. *Clin. Neurophysiol.* 115 (8), 1760–1766. <http://dx.doi.org/10.1016/j.clinph.2004.03.004>.
- Nesselroade, J.R., Gerstorff, D., Hardy, S.A., Ram, N., 2007. Idiographic filters for psychological constructs. *Measurement: Interdisciplinary Research and Perspectives* 5, 217–235. <http://dx.doi.org/10.1080/15366360701741807>.
- Nesselroade, J.R., Molenaar, P.C.M., 2010. Emphasizing intraindividual variability in the study of development over the lifespan. In: Overton, W.F. (Ed.), *Handbook of Life-span Development. Volume 1: Cognition, Biology, and Methods*. Wiley, New York, pp. 30–54.
- Neuper, C., Pfurtscheller, G., 2001. Event-related dynamics of cortical rhythms: frequency-specific features and functional correlates. *Int. J. Psychophysiol.* 43 (1), 41–58. [http://dx.doi.org/10.1016/S0167-8760\(01\)00178-7](http://dx.doi.org/10.1016/S0167-8760(01)00178-7).
- Niedermeyer, E., 1999. The normal EEG of the waking adult. In: Niedermeyer, E., Lopes da Silva, F.H. (Eds.), *Electroencephalography: Basic Principles, Clinical Applications and Related Fields*. Williams & Wilkins, Baltimore, pp. 149–173.
- Nigbur, R., Cohen, M.X., Ridderinkhof, K.R., Sturmer, B., 2012. Theta dynamics reveal domain-specific control over stimulus and response conflict. *J. Cogn. Neurosci.* 24 (5), 1264–1274. http://dx.doi.org/10.1162/jocn_a_00128.
- Nyhus, E., Curran, T., 2010. Functional role of gamma and theta oscillations in episodic memory. *Neurosci. Biobehav. Rev.* 34 (7), 1023–1035. <http://dx.doi.org/10.1016/j.neubiorev.2009.12.014>.
- Nyström, P., 2008. The infant mirror neuron system studied with high density EEG. *Soc. Neurosci.* 3 (3–4), 334–347. <http://dx.doi.org/10.1080/17470910701563665>.
- Nyström, P., Ljunghammar, T., Rosander, K., von Hofsten, C., 2011. Using mu rhythm desynchronization to measure mirror neuron activity in infants. *Dev. Sci.* 14 (2), 327–335. <http://dx.doi.org/10.1111/j.1467-7687.2010.00979.x>.
- Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.-M., 2011. FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput. Intell. Neurosci.* 2011, 156869. <http://dx.doi.org/10.1155/2011/156869>.
- Orekhova, E.V., Stroganova, T.A., Posikera, I.N., 1999. Theta synchronization during sustained anticipatory attention in infants over the second half of the first year of life. *Int. J. Psychophysiol.* 32 (2), 151–172. [http://dx.doi.org/10.1016/S0167-8760\(99\)00011-2](http://dx.doi.org/10.1016/S0167-8760(99)00011-2).
- Orekhova, E.V., Stroganova, T.A., Posikera, I.N., 2001. Alpha activity as an index of cortical inhibition during sustained internally controlled attention in infants. *Clin. Neurophysiol.* 112 (5), 740–749. [http://dx.doi.org/10.1016/S1388-2457\(01\)00502-8](http://dx.doi.org/10.1016/S1388-2457(01)00502-8).
- Orekhova, E.V., Stroganova, T.A., Posikera, I.N., Elam, M., 2006. EEG theta rhythm in infants and preschool children. *Clin. Neurophysiol.* 117 (5), 1047–1062. <http://dx.doi.org/10.1016/j.clinph.2005.12.027>.
- Paulus, M., Hunnius, S., van Elk, M., Bekkering, H., 2012. 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. *Developmental Cognitive Neuroscience* 2 (1), 90–96. <http://dx.doi.org/10.1016/j.dcn.2011.05.006>.
- Perry, A., Stein, L., Bentin, S., 2011. Motor and attentional mechanisms involved in social interaction: evidence from mu and alpha EEG suppression. *Neuroimage* 58 (3), 895–904. <http://dx.doi.org/10.1016/j.neuroimage.2011.06.060>.
- Pfurtscheller, G., Lopes da Silva, F.H., 1999. Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clin. Neurophysiol.* 110 (11), 1824–1857. [http://dx.doi.org/10.1016/S1388-2457\(99\)00141-8](http://dx.doi.org/10.1016/S1388-2457(99)00141-8).
- Piaget, J., 1937/1959. *The Construction of Reality in the Child*. Basic Books, New York.
- Pineda, J.A., 2005. The functional significance of mu rhythms: translating "seeing" and "hearing" into "doing". *Brain Res. Rev.* 50 (1), 57–68. <http://dx.doi.org/10.1016/j.brainresrev.2005.04.005>.
- Press, C., Gillmeister, H., Heyes, C., 2006. Bottom-up, not top-down, modulation of imitation by human and robotic models. *Eur. J. Neurosci.* 24 (8), 2415–2419. <http://dx.doi.org/10.1111/j.1460-9568.2006.05115.x>.
- Reid, V.M., Hoehl, S., Grigutsch, M., Groendahl, A., Parise, E., Striano, T., 2009. The neural correlates of infant and adult goal prediction: evidence for semantic processing systems. *Dev. Psychol.* 45 (3), 620–629. <http://dx.doi.org/10.1037/a0015209>.
- Reid, V.M., Hoehl, S., Landt, J., Striano, T., 2008. Human infants dissociate structural and dynamic information in biological motion: evidence from neural systems. *Soc. Cogn. Affect. Neurosci.* 3 (2), 161–167. <http://dx.doi.org/10.1093/scan/nsn008>.
- Reid, V.M., Hoehl, S., Striano, T., 2006. The perception of biological motion by infants: an event-related potential study. *Neurosci. Lett.* 395 (3), 211–214. <http://dx.doi.org/10.1016/j.neulet.2005.10.080>.

- Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. *Annu. Rev. Neurosci.* 27, 169–192. <http://dx.doi.org/10.1146/annurev.neuro.27.070203.144230>.
- Rohenkohl, G., Nobre, A.C., 2011. Alpha oscillations related to anticipatory attention follow temporal expectations. *J. Neurosci.* 31 (40), 14076–14084. <http://dx.doi.org/10.1523/JNEUROSCI.3387-11.2011>.
- Rosander, K., von Hofsten, C., 2004. Infants' emerging ability to represent object motion. *Cognition* 91 (1), 1–22. [http://dx.doi.org/10.1016/S0010-0277\(03\)00166-5](http://dx.doi.org/10.1016/S0010-0277(03)00166-5).
- Saby, J.N., Marshall, P.J., 2012. The utility of EEG band power analysis in the study of infancy and early childhood. *Dev. Neuropsychol.* 37 (3), 253–273. <http://dx.doi.org/10.1080/87565641.2011.614663>.
- Sanefuji, W., Ohgami, H., Hashiya, K., 2008. Detection of the relevant type of locomotion in infancy: crawlers versus walkers. *Infant Behav. Dev.* 31 (4), 624–628. <http://dx.doi.org/10.1016/j.infbeh.2008.07.003>.
- Santiesteban, I., Catmur, C., Hopkins, S.C., Bird, G., Heyes, C., 2014. Avatars and arrows: implicit mentalizing or domain-general processing? *J. Exp. Psychol. Hum. Percept. Perform.* 40 (3), 929–937. <http://dx.doi.org/10.1037/a0035175>.
- Saunier, G., Martins, E.F., Dias, E.C., De Oliveira, J.M., Pozzo, T., Vargas, C.D., 2012. Electrophysiological correlates of biological motion permanence in humans. *Behav. Brain Res.* <http://dx.doi.org/10.1016/j.bbr.2012.08.038>.
- Saxe, R., Tzelnic, T., Carey, S., 2006. Five-month-old infants know humans are solid, like inanimate objects. *Cognition* 101 (1), B1–B8. <http://dx.doi.org/10.1016/j.cognition.2005.10.005>.
- Schubotz, R.I., 2007. Prediction of external events with our motor system: towards a new framework. *Trends Cogn. Sci.* 11 (5), 211–218. <http://dx.doi.org/10.1016/j.tics.2007.02.006>.
- Simons, J.S., Spiers, H.J., 2003. Prefrontal and medial temporal lobe interactions in long-term memory. *Nat. Rev. Neurosci.* 4 (8), 637–648. <http://dx.doi.org/10.1038/nrn1178>.
- Southgate, V., Johnson, M.H., Karoui, I.E., Csibra, G., 2010. Motor system activation reveals infants' on-line prediction of others' goals. *Psychol. Sci.* 21 (3), 355–359. <http://dx.doi.org/10.1177/0956797610362058>.
- Southgate, V., Johnson, M.H., Osborne, T., Csibra, G., 2009. Predictive motor activation during action observation in human infants. *Biol. Lett.* 5 (6), 769–772. <http://dx.doi.org/10.1098/rsbl.2009.0474>.
- Spelke, E.S., Katz, G., Purcell, S.E., Ehrlich, S.M., Breinlinger, K., 1994. Early knowledge of object motion: continuity and inertia. *Cognition* 51 (2), 131–176. [http://dx.doi.org/10.1016/0010-0277\(94\)90013-2](http://dx.doi.org/10.1016/0010-0277(94)90013-2).
- Spelke, E.S., Phillips, A., Woodward, A.L., 1995. Infants' knowledge of object motion and human action. In: Premack, A.J., Premack, D., Sperber, D. (Eds.), *Causal Cognition: A Multidisciplinary Debate*. Clarendon Press, Oxford, pp. 44–77.
- Springer, A., Parkinson, J., Prinz, W., 2013. Action simulation: time course and representational mechanisms. *Front. Psychol.* 4, 387. <http://dx.doi.org/10.3389/fpsyg.2013.00387>.
- Stadler, W., Schubotz, R.I., von Cramon, D.Y., Springer, A., Graf, M., Prinz, W., 2011. Predicting and memorizing observed action: differential premotor cortex involvement. *Hum. Brain Mapp.* 32 (5), 677–687. <http://dx.doi.org/10.1002/hbm.20949>.
- Stadler, W., Springer, A., Parkinson, J., Prinz, W., 2012. Movement kinematics affect action prediction: comparing human to non-human point-light actions. *Psychol. Res.* 76 (4), 395–406. <http://dx.doi.org/10.1007/s00426-012-0431-2>.
- Stapel, J.C., Hunnius, S., van Elk, M., Bekkering, H., 2010. Motor activation during observation of unusual versus ordinary actions in infancy. *Soc. Neurosci.* 5 (5–6), 451–460. <http://dx.doi.org/10.1080/17470919.2010.490667>.
- Stroganova, T.A., Orekhova, E.V., Posikera, I.N., 1998. Externally and internally controlled attention in infants: an EEG study. *Int. J. Psychophysiol.* 30 (3), 339–351. [http://dx.doi.org/10.1016/S0167-8760\(98\)00026-9](http://dx.doi.org/10.1016/S0167-8760(98)00026-9).
- Stroganova, T.A., Orekhova, E.V., Posikera, I.N., 1999. EEG alpha rhythm in infants. *Clin. Neurophysiol.* 110 (6), 997–1012. [http://dx.doi.org/10.1016/S1388-2457\(98\)00009-1](http://dx.doi.org/10.1016/S1388-2457(98)00009-1).
- Tan, H.R., Leuthold, H., Gross, J., 2013. Gearing up for action: attentive tracking dynamically tunes sensory and motor oscillations in the alpha and beta band. *Neuroimage* 82, 634–644. <http://dx.doi.org/10.1016/j.neuroimage.2013.04.120>.
- Thiou, M., Keyser, C., 2014. Object visibility alters the relative contribution of ventral visual stream and mirror neuron system to goal anticipation during action observation. *Neuroimage* 105, 380–394. <http://dx.doi.org/10.1016/j.neuroimage.2014.10.035>.
- Thompson, J., Parasuraman, R., 2011. Attention, biological motion, and action recognition. *Neuroimage* 59 (1), 4–13. <http://dx.doi.org/10.1016/j.neuroimage.2011.05.044>.
- Urgen, B.A., Plank, M., Ishiguro, H., Poizner, H., Saygin, A.P., 2013. EEG theta and Mu oscillations during perception of human and robot actions. *Frontiers in Neurorobotics* 7, 19. <http://dx.doi.org/10.3389/fnbot.2013.00019>.
- Urgesi, C., Savonitto, M.M., Fabbro, F., Aglioti, S.M., 2012. Long- and short-term plastic modeling of action prediction abilities in volleyball. *Psychol. Res.* 76 (4), 542–560. <http://dx.doi.org/10.1007/s00426-011-0383-y>.
- van Elk, M., van Schie, H.T., Hunnius, S., Vesper, C., Bekkering, H., 2008. You'll never crawl alone: neurophysiological evidence for experience-dependent motor resonance in infancy. *Neuroimage* 43 (4), 808–814. <http://dx.doi.org/10.1016/j.neuroimage.2008.07.057>.
- van Vugt, M.K., Simen, P., Nystrom, L.E., Holmes, P., Cohen, J.D., 2012. EEG oscillations reveal neural correlates of evidence accumulation. *Front. Neurosci.* 6, 106. <http://dx.doi.org/10.3389/fnins.2012.00106>.
- Virji-Babul, N., Cheung, T., Weeks, D., Kerns, K., Shiffar, M., 2007. Neural activity involved in the perception of human and meaningful object motion. *Neuroreport* 18 (11), 1125–1128. <http://dx.doi.org/10.1097/WNR.0b013e32821c5470>.
- Virji-Babul, N., Rose, A., Moiseeva, N., Makan, N., 2012. Neural correlates of action understanding in infants: influence of motor experience. *Brain and Behavior* 2 (3), 237–242. <http://dx.doi.org/10.1002/brb3.50>.
- von Hofsten, C., 2004. An action perspective on motor development. *Trends Cogn. Sci.* 8 (6), 266–272. <http://dx.doi.org/10.1016/j.tics.2004.04.002>.
- von Hofsten, C., Feng, Q., Spelke, E.S., 2000. Object representation and predictive action in infancy. *Dev. Sci.* 3 (2), 193–205. <http://dx.doi.org/10.1111/1467-7687.00113>.
- von Hofsten, C., Kochukhova, O., Rosander, K., 2007. Predictive tracking over occlusions by 4-month-old infants. *Dev. Sci.* 10 (5), 625–640. <http://dx.doi.org/10.1111/j.1467-7687.2007.00604.x>.
- Warreyn, P., Ruysschaert, L., Wiersema, J.R., Handl, A., Pattyn, G., Roeyers, H., 2013. Infants' mu suppression during the observation of real and mimicked goal-directed actions. *Dev. Sci.* 16 (2), 173–185. <http://dx.doi.org/10.1111/desc.12014>.
- Werkle-Bergner, M., Grandy, T.H., Chicherio, C., Schmiechel, F., Lövdén, M., Lindenberger, U., 2014. Coordinated within-trial dynamics of low-frequency neural rhythms controls evidence accumulation. *J. Neurosci.* 34 (25), 8519–8528. <http://dx.doi.org/10.1523/jneurosci.3801-13.2014>.
- Werkle-Bergner, M., Shing, Y.L., Müller, V., Li, S.C., Lindenberger, U., 2009. EEG gamma-band synchronization in visual coding from childhood to old age: evidence from evoked power and inter-trial phase locking. *Clin. Neurophysiol.* 120 (7), 1291–1302. <http://dx.doi.org/10.1016/j.clinph.2009.04.012>.
- Zago, M., Lacquaniti, F., 2005. Cognitive, perceptual and action-oriented representations of falling objects. *Neuropsychologia* 43 (2), 178–188. <http://dx.doi.org/10.1016/j.neuropsychologia.2004.11.005>.