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

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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.

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

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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 commonsense 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 desynchronization) 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