Predictive occluder tracking in infancy: Combining analysis of high density EEG with eye tracking movements

by

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Trondheim, January 2013

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Acknowledgements

The work presented in this Master's thesis has been carried out at the Developmental Neuroscience Laboratory at the Norwegian University of Science and Technology.

Firstly I would like to thank Audrey van der Meer for her supervision, support and advice throughout the process of finishing the present thesis. Special thanks also to Magnus Holth and Seth Agyei for their invaluable assistance during the course of this work. Also thanks to my fellow students Kenneth Vilhelmsen and Belde Mutaf for many fruitful discussions on data analysis and interpretation.

Finally, I would like to thank my family and André for all their support and patience while finishing this project.

Trondheim, January 2013
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Abstract

An essential function of the human visual system is to perceive natural scenes as coherent even if objects are temporarily out of sight due to eye saccades or object occlusion. While a great deal of behavioural studies investigated the emerging ability of object permanence during infancy, little is known about the development of mediating neural structures. In the present study responses to a moving stimulus over a brief occlusion are investigated in 4/5-month-old-infants and 11/12-month-old infants by combining measurements of eye movements with analysis of neuronal gamma oscillations, commonly known as correlates of object processing and perception. Recordings of gamma activity were obtained via high-density electroencephalogram (EEG). With age, infants showed more instances of shifting gaze predictively over the occluder, which was accompanied with a shift of neuronal gamma oscillations from occipital areas in the dorsal stream to anterior temporal areas in the ventral stream. This shift in activity in neuronal regions suggests different strategies of occluder tracking between the two age groups, where the younger infants appear to let themselves mainly be guided by spatio-temporal information processed in the dorsal pathway, whereas ventral pathway activation observed in the older infants suggests that 11/12-month-old infants take object identity into account for individuation processes.

1. Introduction

Visual scenes we encounter in daily life consist of multiple objects hiding behind and overlapping each other. Yet we are able to perceive single items as enduring entities and meaningful units. This seemingly effortless ability of object perception in humans is the result of complex neuronal processes by the human visual system, refining and differentiating in interaction with the environment throughout infancy into childhood, eventually resulting in the highly specialized adult brain (Johnson, 2001). Object perception includes both object recognition, the ability of matching a current object to one that was previously experienced, and object identification or categorization (Gerhardstein, Shroff, Dickerson & Adler, 2009). How human object perception evolves and develops in the course of time is a fundamental issue in developmental psychology (Johnson, 2001). In this regards, Piaget (1954) was one of the first researchers reflecting upon infants' understanding of objects. He introduced the concept of "object permanence", the ability to represent an object mentally even if it is out of sight. For Piaget active search for formerly fully hidden objects was the critical feature, implying that object permanence is present in the child. In his theory of object concepts he claimed that infants until the age of 8 months (stage 4 of the 6-stage theory of sensorimotor-development) cannot represent objects mentally unless they are presently perceived, thus occlusion of an object annihilates the object itself. In the following 40 years substantial knowledge about cognitive and perceptual abilities of infants has accumulated as a result of behavioural testing (Johnson, 2001), and various studies contradict Piaget's results, suggesting that infants at a much earlier age believe in the continuing existence of occluded objects. In this respect, studies using the violation-of-expectancy paradigm revealed that infants show increased looking times to displays where the spatio-temporal continuity during occlusion periods of objects has been violated suggesting that infants from the age of 2.5 months detect some discrepancy between the actual and expected event (Aguiar & Baillargeon, 1999; Baillargeon & DeVos, 1991). Sensitivity to spatio-temporal violations is suggested to be fairly stabilized in 5- to 6-month-old infants (Baillargeon, 1986; Baillargeon, Spelke & Wasserman, 1985). The dissonance in age between Piaget's findings and more recent behavioural studies was generally explained by the lack of young infants to coordinate two actions to perform one goal (means-end actions) (Baillargeon, 1987; Baillargeon, Spelke, & Wasserman, 1985; Willats, 1997). That implies that even though young infants can reason about occlusion events they might not be able to perform the specific action operators of lifting the cover and setting it aside to retrieve the object until a few months later. This assumption is consistent with findings by Van der Meer, van der Weel, & Lee (1994), who reported that whereas 11-month-old infants showed anticipatory reaching and tracking of moving objects that were temporarily hidden (0.3-0.6 s) behind an occluder on a horizontal track, infants at the age of 5 months anticipated the reappearance of the object by shifting their gaze but predictive reaching did not occur until about 7/8 months of age. Visual tracking studies are also revealing about infants' ability to represent occluded object motion since they investigate one of the first goal-oriented actions available in humans, eye movements. Several studies operationalized predictive gaze shifts to the reappearing side of the occluder as behavioural indicator of the infants' ability to represent object motion during the temporarily occlusion of moving objects. In accordance with Van der Meer, Van der Weel, & Lee (1994) the age of 2.5-5 months is repeatedly referred to as a time in development were the ability to preserve the spatio-temporal continuity of occluded objects in visual tracking tasks is already observable, depending on the target velocity, the occlusion duration, and occluder width (Johnson, Slemmer & Amso, 2004; Rosander & von Hofsten, 2004; von Hofsten, Kochukhova & Rosander, 2007; Wilcox & Schweinle, 2003).

However, infants` ability to maintain the spatio-temporal continuity of objects over occlusion events is not necessarily a sign of sophisticated object knowledge at this age. Studies investigating the basis of object representation showed that object individuation over occlusion periods based on surface features of physical objects (e.g. size, shape, pattern, colour) occurs only in late infancy (Leslie, Xu, Tremoulet & Scholl, 1998; Southgate, Csibra, Kaufman & Johnson, 2008; Xu, 1999; Xu & Carey, 1996). In this respect 4-month-old infants have been shown to use spatio-temporal information to infer that two parts, separated by an occcluder that undergo common motion are in fact one single unitary object, but fail to bind to the two parts based on featural information to a coherent percept (i.e. colour and shape) (Kellman & Spelke, 1983). In a similar vein, Xu & Carey (1996) revealed that 10-month-old infants who had to use either spatio-temporal information or featural information to individuate objects over an occlusion event. The infants succeeded in the former condition whereas they did not successfully individuate objects based on featural information such as shape, pattern, texture and object category. In contrast, 12-month-old infants in the same study used both type of information for object individuation, like adults. Results from different studies are not conclusive though, e.g. Wilcox (1999) suggests that infants are able to use shape already at 7 months, texture at 11 months, and colour only at 12 months to individuate objects. Taken together findings suggest that from an early age on infants are able to perceive and track objects through space even though a representation of the object based on its featural properties might not persist over occlusion periods at the same age and presumably only occurs fully by the end of the first year of life.

Not only predictive gaze shifts over an occluder in anticipation of the reappearance of an object in visual tracking tasks demand some kind of prospective knowledge, but also the successful smooth tracking of object motion itself. The visual system has to combine head and eye movements in order to visually track a moving object successfully. Two different types of eye movements are involved in this type of task in primates, smooth pursuit and eye saccades (Leigh & Zee, 2006). Whereas smooth pursuit represents smooth tracking movements by the eye of an object moving against a stationary patterned background stimulated by an image moving across the retina (Jacobs, Harris, Shawkat & Taylor, 1997), eye saccades include a range of behaviours (e.g., voluntary or involuntary shifts of fixation, quick phases of vestibular and optokinetic nystagmus) and are generally defined as rapid eye movements which shift the line of sight between successive points of fixation (Leigh & Zee, 2006). Smooth pursuit eye movements only appear in response to visual motion in order to stabilize gaze on the moving target, and in healthy adults smooth pursuit is performed very accurately, resulting in eye velocities invariably less than the target motion (Philipps, Finocchio, Ong & Fuchs, 1997). In order to keep the projection of the moving target on the fovea irrespective of changes in velocity and direction the control of eye movements has to compensate for delays in the sensorimotor system (Rosander, 2007). Hence successful visual tracking requires anticipating future events, which implies that both eye and head movements and visual and vestibular information have to be controlled prospectively (Guitton, 1992; Rosander & von Hofsten, 2004, Leigh & Zee, 2006). Whereas some authors suggested smooth pursuit eye movements are absent in neonates (e.g. Aslin, 1981; Dayton & Jones, 1964), whose immature ocular systems rely on separate re-foveations ("catch-up" saccades) to keep up with target motion of moving objects, others proposed that even in infants as young as 4 weeks smooth pursuit eye movements are observable dependent on the target velocity (Philipps et al., 1997). A gradual increase of smooth pursuit eye movements until 6 months is well documented (Richards & Holley, 1999; von Hofsten & Rosander, 1997), especially between 2 and 3 month the gain of smooth pursuit is suggested to be high (Hosten & Rosander, 1996, 1997; Jacobs et al., 1997; Johnson, Davidow, Hall-Haro, & Frank, 2008). In principle the younger the infant the more the infant seems to profit from the display of large target objects travelling at rather slow constant speeds for the performance of smooth pursuit. For a review of oculomotor development in infants see also Rosander (2007).

Development of motion sensitivity and smooth pursuit in infants show a concurrent developmental course (Johnson et al., 2008). A key function in visual motion processing is attributed to the V5 area, or medial temporal (MT) area of the occipito-temporal cortex, which is a functionally specialized region for the processing of visual motion, as initially suggested by studies on macaque monkeys (Zeki, 1974; Zeki, 2004). Several studies point to a human homologue of the V5/ MT area, a region that receives information of primary visual cortex (V1) and further projects to the adjacent medial superior temporal cortex (MST) and other associated areas of higher cortical functions. Both the MT area and the MST area (referred to as MT+ complex) are not only critical for motion perception, but also for the control of smooth pursuit as initially demonstrated in monkeys (Komatsu & Wurtz, 1988; Lisberger & Movshon, 1999; Rudolph & Pasternak, 1999) and as recently revealed by functional magnetic resonance imaging (fMRI) studies are also involved in human smooth pursuit (Petit & Haxby, 1999) and catch-up saccades (Newsome, Wurtz, Dürsteler & Mikami, 1985; May, Keller & Suzuki, 1988; Orban de Xivry & Lefevre, 2007). Higher order saccades (including voluntary, memory-guided and anticipatory saccades) on the other hand, involve some kind of cognitive judgement when and where to move gaze (Leigh & Zee, 2006; Walker, Walker, Husain & Kennard, 2000) and are to a higher extent connected to neurophysiological pathways incorporating anterior areas of the cerebral cortex (Gaymard, Ploner, Rivaud, Vermersch & Pierrot-Deseilligny, 1998; Leigh & Zee, 2006; Mort et al., 2003). In adults, the signal input to the MT+ complex follows two main pathways, the primary pathway and a phylogenetically older, subcortical pathway (Callaway, 2005; Schoenfeld, Heinze & Woldorff, 2002). The primary pathway projects incoming information through the lateral geniculate nucleus (LGN) to the primary visual cortex (V1) and further to the MT/MST area. The subcortical stream projects to the MT/MST area via the superior colliculus (SC) and pulvinar area (PU) of the thalamus. The latter stream is supposed to be the dominant one in immature visual motion processing in neonates (Atkinson, 2000) at least up until the age of two months (Dubowitz, Mushin, DeVries & Arden (1986). 1986), and is thought to develop gradually during the first months of life into a functioning cortical pathway by the age of 5 months (Wattam-Bell, 1991). The maturation of the MT+ area at around 5 months corresponds well with the development of smooth eye pursuit around the same age (Rosander, Nyström, Gredebäck & von Hofsten, 2007).

The MT+ complex is part of the dorsal (or parietal) visual pathway, one of two visual pathways arising from the early visual areas. The dorsal pathway is proposed to hold an executive function in processing spatial and temporal object information (e.g., speed and path of motion) involved in guiding action, such as visuo-motor control, as well as online control during the course of an action, whereas the ventral (or temporal) pathway is suggested to be involved in the identification of possible and actual goal objects (Milner & Goodale, 2008) (see Figure 1). The streams work in a segregated, yet interactional way with several cross talks between the streams (Blatt, Andersen & Stoner, 1990; Johnson, Mareschal & Csibra, 2001; Maunsell & van Essen, 1983) and project both to the frontal lobe (Goodale, 1993).

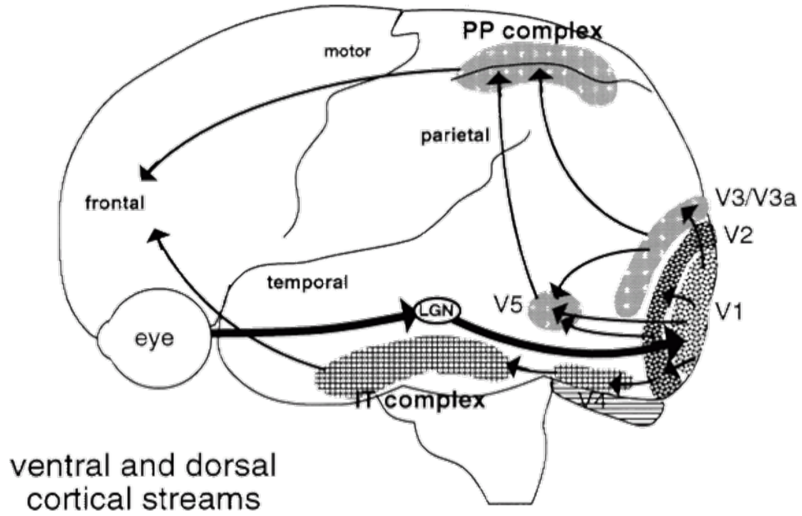


Figure 1: Connections of cortical modules of the ventral and dorsal stream, including lateral geniculate nucleus (LGN), inferior temporal (IT) complex and psterior parietal (PP) complex (map from Atkinson, 2000).

A method to uncover the underlying neural basis of perceptual and cognitive processes is to analyse event-related (de-) synchronizations (ERD/ERS) by neuronal populations with electroencephalography (EEG). These event-related phenomena are reflected by changes in power in given frequency bands of the ongoing EEG activity and are due to a decrease or increase in synchrony of the underlying neuronal populations (Pfurtscheller & Lopes da Silva, 1999). Analysis of changes in frequency bands over time encompasses both phase-locked (evoked) and non-phase-locked (induced) electrical responses to stimulus presentation with good resolution in both the time and frequency domain (Hoechstetter et al., 2004). In this regard, synchronized induced gamma band oscillations (> 20 Hz) within and between neural assemblies with a latency of about 200-400 ms after stimulus presentation were repeatedly referred to as correlates of object recognition in human adults (Bertrand & Tallon-Baudry, 2000; Lachaux et al, 2005; Martinovic, Gruber, Hantsch & Müller, 2008; Martinovic, Gruber & Müller, 2007; Supp, Schlögl, Trujillo-Barreto, Müller & Gruber, 2007). Gamma oscillations are not unique to isolated, single processes but observed in connection to various perceptual and cognitive functions including feature binding and attentional processes (Müller, Gruber & Keil, 2000). For a review of the functional role of human gamma oscillations in the human adult brain, see also Başar- Eroglu, Strueber, Schuermann, Stadler & Başar (1996) or Tallon-Baudry & Bertrand (1999). Recently the functional role of gamma band oscillations related to object representation over occlusion periods in infants was investigated, where gamma-band oscillatory activity was found during maintenance of object representations after gradual occlusion of objects in 6-month-old infants in the right posterior temporal cortex (Kaufman, Csibra & Johnson, 2003,2005). For infants at this age it is suggested that the increase in gamma power over posterior sites reflects the maintenance of spatio-temporal information during the brief occlusion of graspable objects (Southgate et al., 2008). Whereas these infant studies mainly concentrated on the investigation of oscillatory gamma activity as a correlate of mental object maintenance during the occlusion of an object, the present study intends to study neuronal gamma oscillations as elicited by the recognition of an object as previously already detected in the human adult brain. Two different age groups were chosen for comparison, infants at 4/5 months of age, whose object presentations over occlusion periods is presumably mainly based on the maintenance of spatio-temporal object information, and infants at the age of 11/12 months, who are able to perceive an object as a stable entity during object occlusion based on a holistic, sophisticated object representation comprising featural and spatio-temporal properties. Two epochs of stimulus presentation were chosen for comparison, which only differed by their perceptual history, i.e. occlusion of the object. By doing so it was possible to study the plain effect of object reappearance on neuronal gamma oscillation without interference of gamma band activity elicited by the coherent moving stimulus display itself (Singer & Gray, 1995). Additionally, in order to shed light on the relationship between neuronal processes and behavioural development, the matureness and effectiveness of the visual system was assessed by analysing predictive eye movements over the occluder as well as the ratio of smooth pursuit in eye movements during visual tracking of the moving object. As opposed to traditional paradigms in which EEG epoch onset for analysis is time-locked to stimulus onset, EEG analysis onset was time-locked to a behavioural onset in the present study. This behavioural onset was defined as the “catch-up-event”, the point in time when the infant was able to track the target for the first time during a trial. Thus developmental improvements in predictive visual tracking accompanied with changes in neuronal oscillations in the gamma range as elicited by object reappearance are going to be investigated.

2. Methods

2.1 Participants

A total number of 18 infants were included in the study. EEG recordings were collected on 19 4/5-month-old and 23 11/12-month-old infants in the Developmental Neuroscience Laboratory at the Norwegian University of Science at Technology (NTNU). Nine 4/5-month-old infants (2 girls/ 7 boys) at a mean age of 19 weeks (SD=2.07) and nine 11/12-month-old infants (3 girls/6 boys), mean age 50 weeks (SD=2.4), provided sufficient artefact-free trials in the EEG recordings together with adequate eye data for subsequent data analysis. Such high drop-out rate is common in infant EEG studies (Jeschonek, Marinovic, Hoehl, Elsner & Pauen, 2010; Striano, Reid & Hoehl, 2006) and necessary to ensure the quality of EEG data. In the present study, especially the absence of good quality eye data due to difficulties in calibrating prelinguistic participants restricted the amount of EEG data available for analysis.

All infants were born at term apart from one boy who was born slightly preterm (5 weeks), but tested corrected for prematurity. Four infants (3 boys/ 1girl) provided longitudinal data. All infants were recruited from birth announcements in the newspaper. According to parental report all infants were born without birth complications and showed a typical, age-related development. Two of the 11/12-month-old infants mastered independent walking, while seven could comfortably crawl on hands and knees. None of the 4/5-month-old infants had any crawling experience yet, but most of them could roll over from back to stomach.

EEG recording as a psychophysical procedure does not cause any physical harm to the participants. The Norwegian Regional Ethics Committees and The Norwegian Data Services for Social Science approved the study. Parents gave their informed written consent and were aware that they could withdraw from participation in the study at any time during or after the testing.

2.2 Occlusion stimulus

The stimulus consisted of a red car, moving along a rectangular path during which it disappeared twice behind a green occluder (Figure 2). The stimulus was mirror-reversed projected onto a large screen (108 x 67 cm). The start position of the car was set in the lower left hand side corner. The horizontal movement of the car from the lower left to lower right corner was counted as one trial, while the horizontal movement from upper right hand side to upper left corner was considered as the next trial. The car drove a distance of 100 cm within one trial on the screen, which constituted a visual angle of 64°. The car had a length of 40 pixels (px) equivalent to 6.75 cm on the screen, while the occluder had a length of 60 px, which constituted a length of 10.12 cm on the screen.

Two different start speeds of the car dependent on the respective age group (for details, see Figure 2) were chosen in order to keep the experiment equally challenging for infants at both ages, whereas three different deceleration conditions were included to vary the spatiotemporal information available in each trial so that the infants could not rely on an automated gaze shifting response which should increase their interest in the task and the stimulus.

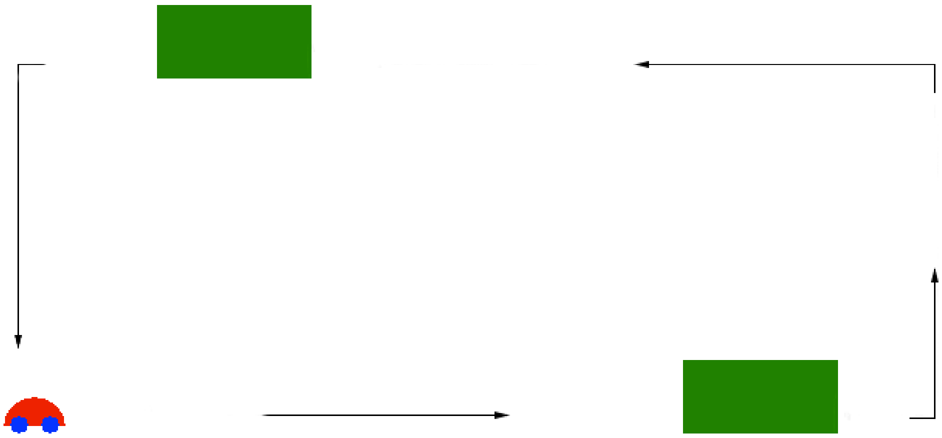


Figure 2: Stimulus set-up: The car moved along a rectangular path on the screen, and was occluded twice on its way. 4/5-month-old infants were presented with a start speed of 42.3 cm/s and 11/12-month-old infants were presented with a start speed of 67.4 cm/s. Related to the start speed the car moved under three different constant decelerations, i.e. “fast” (10% deceleration), “medium” (50% deceleration) and “slow” (90% deceleration). Deceleration started after 400 ms of stimulus start for the younger group of infants and after 250 ms for the older group of infants. The car drove the distance from the start position to the occluder in 1810 ms (“fast”), 2040 ms (“medium”) and 2210 ms (“slow”) for a start speed of 42.3 cm/s, and in 1130 ms (“fast”), 1270 ms (“medium”) and 1380 ms (“slow”) for a start speed of 67.4 cm/s. Occlusion duration was 261 ms (“fast”), 388 ms (“medium”) and 566ms (“slow”) for a start speed of 42.3 cm/s, and 164 ms (“fast”), 242 ms (“medium”) and 354 ms (“slow”) for a start speed of 67.4 cm/s. After the car had fully reappeared from behind the occluder deceleration stopped and the car continued driving under i constant end speed, i.e. 37.9 cm/s (“fast”), 21.1 cm/s (“medium”), 4.2 cm/s (“slow”) for a start speed of 42.3 cm/s, and 60.7 cm/s (“fast”), 33.7 cm/s (“medium”), 6.7 cm/s (“slow”) for a start speed of 67.4 cm/s. Inter-stimulus intervals were set to 2000 ms. Attention pictures presented with sounds attracted infants’ interest to the start position of the car. Different speed conditions were presented in a random order. Stimuli were generated with E-prime (Psychology Software Tools, Inc.).

2.3 Apparatus

EEG activity was recorded by a Geodesic Sensor Net 200 (GSN) 200 (Tucker, 1993). An array of 128 electrodes was evenly distributed over the infants’ head surface. Amplified EEG signals were recorded with Net Station software on a Macintosh computer at a sampling rate of 500 Hz. Impedances of all electrodes were kept under 50 kΩ as recommended for an optimal signal-to-noise ratio (Ferree, Luu, Russell & Tucker, 2001; Picton et al., 2000). Triggers about the onset and offset of stimuli were communicated by E-Prime (Psychology Software Tools, Inc) onto the EEG recordings of infant brain electrical activity.

Infants’ gaze was recorded using Tobii X50 infrared eye camera and further processed with ClearView software on a PC. Additionally, recordings from two digital video cameras mounted in two different angles in front of the participants secured monitoring of infants’ looking behaviour during the experiment and made off-line analyses of behaviour possible. All collected data were stored on a hard disk for off-line analyses.

2.4 Procedure

Parents were informed about the purpose and procedure of the experiment and signed a consent form. After the infant got acquainted and was comfortable with the laboratory environment, the head circumference was measured and the appropriate net was immersed in a saline electrolyte solution in order to optimize electrical conductivity. The net was partially dried before mounting it on the infant's head. The infant was sitting on the parent's lap during this procedure. Immediately afterwards the infant was brought to the experimental room, accompanied by one parent and an experimental assistant. The infant was positioned in front of the screen at about 80 cm from the screen. At 4/5 months infants sat on the parent's lap, whereas infants at 11/12 months were seated in a baby car seat. The net was connected to the amplifier and the impedance of the electrodes was measured. Electrodes with insufficient scalp contact were additionally moisturized with saline electrolyte solution and their position adjusted.

The whole experiment was operated from an adjacent room, separated by a window from the experimental room. Before the experiment started, lights were switched off and calibration of the infant's eye movement in virtual space to the Tobii X50 camera took place. Subsequently presentation of the stimulus material started. The number of trials performed during one session varied between infants. Typically, between 50 and 100 trials were recorded. The experiment was paused in case the infant lost interest or became fussy and the experimental assistant tried to reengage the infant´s interest to the screen. The experiment was aborted when the infant showed fussiness, or when a considerable level of tiredness or disinterest was observed.

The occlusion experiment was presented as the last out of three different experiments, all investigating visual motion perception in infants. It was preceded by experiments on looming (van der Weel & van der Meer, 2009) and optic flow (van der Meer, Fallet & van der Weel, 2008). Each experiment lasted for approximately five minutes.

2.5 Eye data analysis

The initiation of tracking eye movements typically starts with a catch-up saccade to the moving object. The latency of a catch-up saccade to a horizontally moving target lies around 600 ms for infants as young as 4 months (Gredebäck, Ornkloo & von Hofsten, 2006) dependent on the speed of the object, and gradually decreases with age.

The catch-up saccade was operationalized in the present study as the point in time where the horizontal eye movement equalled the horizontal velocity of the car for the first time. This event was determined in each trial and used as a behaviourally defined onset for further EEG analysis.

Trials were only included if a catch-up saccade occurred in a time interval of [0; 1410] ms after stimulus onset for the 4/5-month-old infants, and an interval of [0; 730] ms for the

11/12-month-old infants. This time restriction was necessary in order to ensure a sufficiently long epoch after the catch-up event for EEG analysis before subsequent occlusion of the car. If no catch-up event occurred in the above time intervals, the trial was discarded. Furthermore, trials were only included in the EEG analysis if infants attentively tracked the car after the catch-up event, shifted gaze over the occluder to the reappearing side, and subsequently continued to track the car. Gaze shifts initiated before the car had fully reappeared behind the occluder were counted as predictive. The catch-up event was time locked to EEG data in further analysis and compared to EEG data of the time epoch of car reappearance after occlusion. Eye data were analysed by a custom written program in Python software.

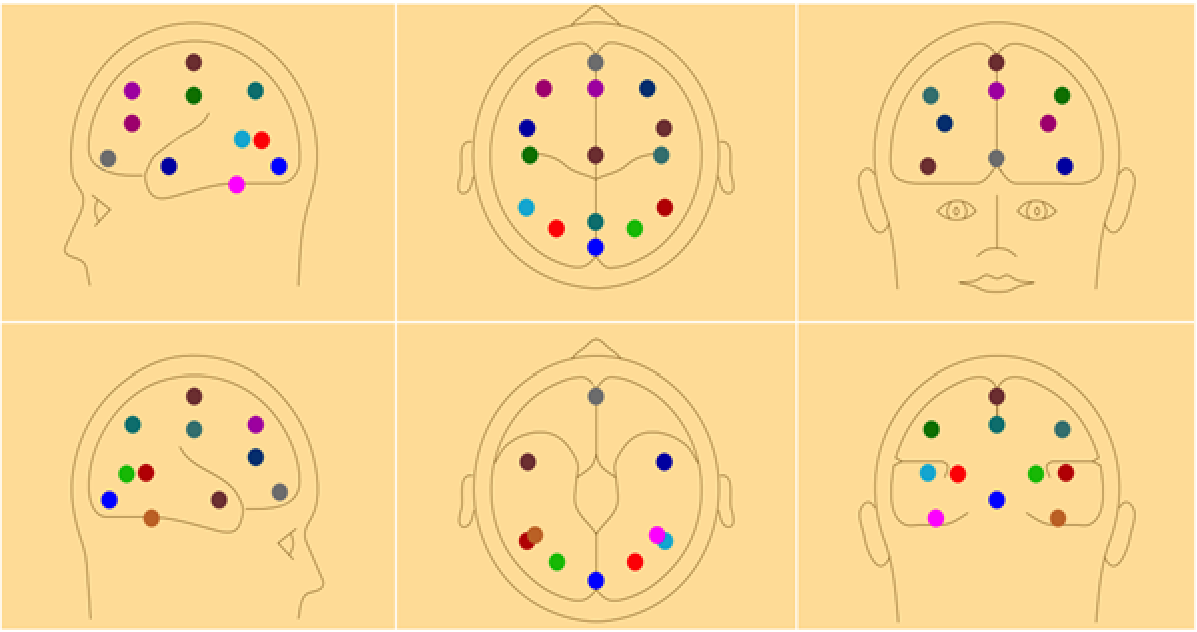
2.6 EEG data analysis

EEG recordings were segmented by Net Station software and exported as raw files. Raw data were analysed with Brain Electrical Source Analysis (BESA) research software version 5.3. Notch filter was set to 50.0 Hz. Low cut-off (high band pass) filter was set to 1.6 Hz to remove slow drift in the data and high cut-off (low band pass) filter was set to 60.0 Hz.

Two different epochs of interest were defined to be compared in further analysis, one set around the catch-up event [-100, 400] ms and one time locked to the reappearance of the car [-100, 400] ms.

EEG channels and epochs contaminated by body/head movements were discarded by visual inspection or interpolated if possible. Data with more than 10% bad channels were not used in further analysis. Furthermore, threshold values were set, gradients higher than 75 μV and signals below 0.1 μV were excluded from analysis as well as channels and epochs in which the difference between maximum and minimum amplitude exceeded 200 μV (220 μV in a few cases). Additionally, a manual form of artefact correction, designed to separate artefacts and brain activity based on spatial filtering, was employed in order to remove physiological artefacts such as blinking from the raw EEG data (Berg & Scherg, 1994a; Ille, Berg & Scherg, 2002). Horizontal eye movements that were naturally present in our visual tracking task were also manually removed.

EEG raw data were transformed by spatial filters into brain space using regional sources to estimate contributions of a set of brain regions (see Figure 3). This virtual source montage (a predefined BESA montage) contained sources distributed in brain space, with an increased number of sources in the visual cortex in the occipital lobe. Thus, particular attention was paid to regions believed to be active during the processing of visual motion (Probst, Plendl, Paulus, Wist & Scherg, 1993; Tootell et al., 1995; Zeki, 1995). The transformation of data from sensor level to brain source space disentangles possibly overlapping activity at the scalp surface (Hoechstetter et al., 2004). Regional sources were chosen over dipoles so as to analyse absolute power in sources instead of their orientations and because they are more robust to spread neuronal activity and EEG data contaminated with artefacts (Scherg, 2002)



Fp-M: x=0.0, y=54.6, z=4.9; F-M: x=0.0, y=28.9, z= 47.1; F-R: x= 33.8, y=31.8, z=25.8; F-L: x= 33.8, y=31.8, z=25.8; C-M : x= 0.0, y=24.2, z= 60.5 ; C-R: x= 42.9, y=21.3, z= 38.9; C-L: x=-42.9, y=-21.3, z= 38.9; TA-R: x=44.7, y=-1.1, z=-14.1; TA-L: x=-44.7, y=-1.1, z=-14.1; P-M: x= 0.0, y=-72.3, z= 37.0 ; VCl-L: x=-45.2, Y=-57.2, z= 6.5; VCl-R: x= 45.2, y=-57.2, z= 6.5; VCr-L: x=-25.6, y=-73.0, z= 4.2; VCr-R: x= 25.6, y=-73.0, z= 4.2; VCb-L: x=-40.0, y=-48.6, z=-22.7; VCb-R: x= 40.0, y=-48.6, z=-22.7; Op-M: x= 0.0, y=-84.9, z=-14.3

Figure 3: Head model depicting virtual brain sources including respective Talairach coordinates (Talairach & Tournoux, 1988) underneath (colour matched).

The acquired source waveforms were inserted into a 4-shell ellipsoidal head model (Berg & Scherg, 1994b), bone thickness was adjusted as recommended for infants from 7.0 mm to 3.0 mm (Grieve, Emerson, Fifer, Isler & Stark, 2003), and conductivity was adjusted from 0.0042 σ to 0.02 σ (BESA info).

Source waveform analysis revealed that the virtual source montage explained all on-going brain activity within the two epochs of interest efficiently. Thus, for 4/5-month-old infants the mean residual variance of unexplained brain activity was 12% (SD= 2.49) in the epoch of the catch-up event and 12% (SD=3.54%) in the epoch of car reappearance. In the group of 11/12-month-old infants the unexplained mean variance was 11% (SD=3.85%) in the epoch of the catch-up event and 12.5 % (SD=3.78%) in the epoch of car reappearance

2.6.1 Time spectral evolution (TSE) of time-frequency activity

The acquired source waveforms were transformed into the time-frequency domain to analyse the power spectrum as a function of time. The change of power (=squared envelope amplitude) was calculated for each source for the epochs of interest and displayed as a function of frequency and latency in (de-) synchronization plots (ERD/ERS) (Pfurtscheller & Lopes da Silva, 1999). In BESA 5.3, complex demodulation (Papp & Ktonas, 1977) is implemented as a method to transform the time-domain signal into the time-frequency-domain (Hoechstetter, 2004). Data were sampled between 4-60 Hz in steps of 2 Hz and a finite impulse response (FIR) filter was applied in sampling steps of 25 ms at [-100, 400] ms around epoch onset. The main analysis concentrated on the analysis of activity in the gamma band range (approximately over 20 Hz). Nevertheless, the possibility of investigating potential time-coupled activation in other frequency bands, which could be functionally related to the gamma band activity, should not be excluded (e.g., von Stein & Sarnthein (2000) found gamma and theta band activity co-occurring in adults during working memory tasks, and Schack, Vath, Petsche, Geissler & Möller (2001) observed the same phenomenon during short-term memory processing).

It was intended to remove evoked activity (time- and phase locked to stimulus onset) from time-frequency plots by using regression analysis so that only effects of induced activity remained. However no visually apparent difference in the plots before and after removal of averaged data ascertained, indicating that no perfectly time-locked neuronal activity could be determined in the time-frequency plots. Considering that gamma activity in adults has been reported to be subject to high temporal inter-individual differences (Hoogenboom, Schoffelen, Oostenfeld, Parkes & Fries, 2006) it seems plausible that infants show, as a consequence of neurodevelopment, even higher differences in neuronal activity patterns.

BESA Statistics 1.0 was used for statistical comparison of TSE source data. In a first step, data clusters were defined (Bullmore et al., 1999) in order to investigate significant effects of the different conditions within the group by means of preliminary Student's t-tests. In the present study two paired, two-tailed t-tests were employed to investigate differences in brain oscillatory activity between the epoch of car reappearance and the epoch time-locked to the catch-up event for each age group. In a second step, parameter-free permutation testing (Ernst, 2004; Maris & Oostenveld, 2007) was implemented to test whether the initial data clusters survive systematic interchange. Thus, nine subjects compared for two conditions using a paired t-test leads to 512 permutations (2^n; n=9). A new t-test is calculated for every permutation and a new cluster value is derived for each of the initial clusters. Based on this new distribution the significance of the initial cluster value can be evaluated.

3. Results

On average, infants contributed to the analyses with 25 trials (SD= 12) at 4/5 months and with 31 trials (SD=9) at 11/12 months. Table 1 gives an overview of the number of trials provided by each infant consisting of sufficient eye data together with adequate EEG data for data analysis.

Table 1

Number of trials consisting of both good quality eye and EEG data each infant contributed to the data analysis in the group of nine 4/5-month-old and nine 11/12-month-old infants

Infant	A	B	C	D	E	F	G	H	I
4/5 months	**16**	**23**	**22**	**33**	**49**	**36**	**13**	**15**	**14**
Infant	A	B	C	D	J	K	L	M	N
11/12 months	**41**	**30**	**31**	**34**	**17**	**21**	**45**	**35**	**26**

Note: The same letter is assigned to infants tested at both ages.

3.1 Eye data analysis

Both 4/5-month-old infants and 11/12-month-old infants started their eye tracking with a saccade to catch up with the target motion. 4/5-month-old infants performed the catch-up event to the moving car on average 1028 ms (SD= 124) after stimulus start, whereas 11/12-month-old infants performed the catch-up event significantly faster, on average 682 ms (SD= 64) after stimulus onset, t (16) = 7.43, p < .01.

Further differences between the age groups occurred in terms of eye tracking movement. For typical eye movements in one trial for a 4-month-old and a 12-month-old infant, see Figure 4. After the initial catch-up saccade, 4/5-month-old infants tracked the car with saccadic eye movements in 87% of all trials, and used the more mature eye movements of smooth pursuit in only 13% of the trials. The 11/12-month-olds, on the other hand, used smooth pursuit to follow the target motion in 67% of all trials. Still, most infants used both smooth pursuit and saccadic tracking in different trials, but 11/12-month-old infants employed more often smooth pursuit and 4/5-month-old infants used predominantly saccades to follow the car's movement. Only three infants from the group of 4/5-month-olds, amongst them the preterm infant, performed exclusively saccadic tracking.

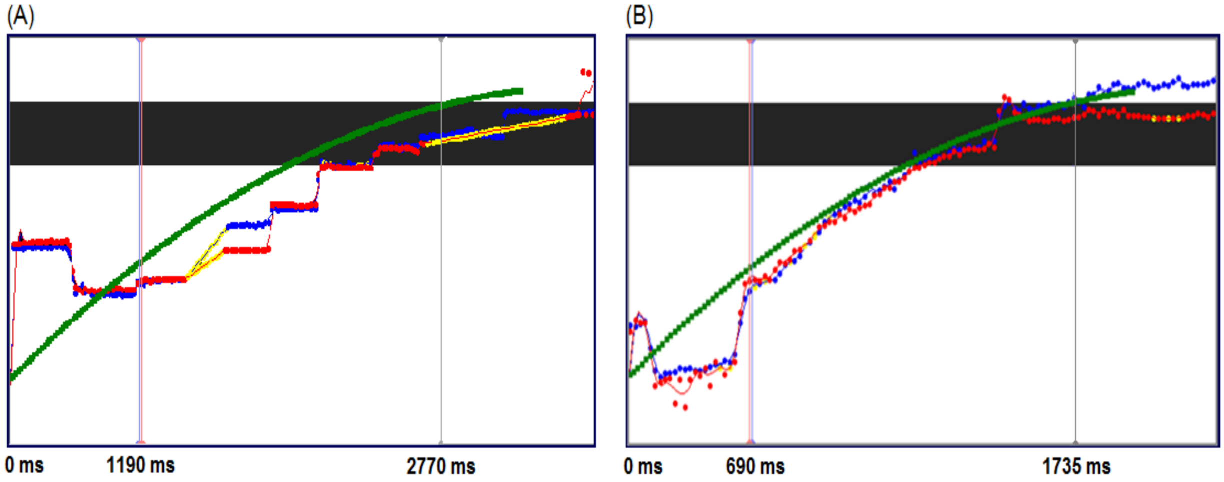


Figure 4: Eye data (↑ position and → time) of a typical trial with the car travelling at slow speed ("high deceleration") for a 4-month-old infant (**A**) and a 12-month-old infant (**B**). The black bar represents the occluder and the green squares represent the car motion, while the red and blue dots represent the right and the left eye, respectively. Yellow dots stand for missing data. The markers on the left in **(A)** and **(B)** represent the catch-up event, defined as the first point in time where the horizontal eye velocity equals the velocity of the car and the acceleration of the eye velocity is negative. The markers on the right represent the point in time at which the car starts to reappear from behind the occluder. These markers indicate the two events used as starting points for the analysis of EEG epochs. The 4-month-old infant shows typical saccadic tracking to keep up with the target motion **(A)**, whereas the 12-month-old infant follows the car with smooth pursuit **(B)**. The 12-month-old infant shows an anticipatory saccade to the end of the occluder before car reappearance, whereas the 4-month-old infant shows no such prospective eye movement. Visual tracking of the car was disrupted by an anticipatory saccade, occurring typically when the car was already hidden behind the occluder, to the reappearing side in 47.5% of all trials for the 11/12-month-old infants, while the 4/5-month-old infants showed anticipation of car reappearance only in 28.6% of the trials. Again prediction of object reappearance was not an all or none response, all infants in both age groups showed predictive eye movements but less infants in the younger age group.

A repeated measures ANOVA with the within subjects factors eye movements (smooth pursuit, saccadic tracking), gaze shift (predictive, non-predictive) and the between subjects factor age group (4/5-month-old infants, 11/12-month-old infants) was conducted on the number of performed trials. No significant main effects were found. As expected, a significant interaction effect between eye movements*age group (F (1, 16) = 18. 318, p < .01) was revealed, indicating that the 4/5-month-olds performed significantly more saccades than smooth pursuit, whereas the opposite was true for the 11/12-month-olds (see Figure 5).

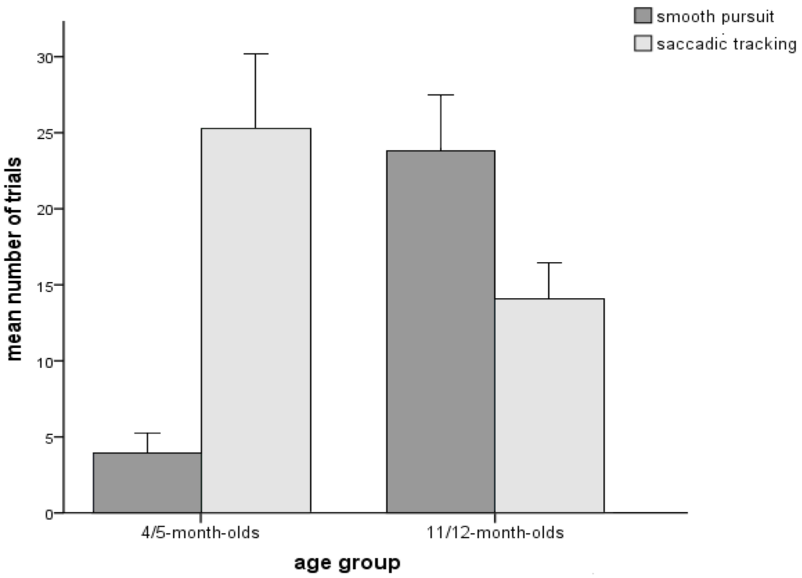


Figure 5: Mean number of trials (and standard errors) performed with smooth pursuit and saccadic tracking in nine 4/5-month-old and nine 11/12-month-old infants.

A second interaction effect between gaze shift*age group was found (F (1, 16) = 8.007, p < .05). 4/5-month-old infants carried out significantly more trials in which they did not show a predictive gaze shift to the reappearing side of the occluder than trials where they anticipated car reappearance. 11/12-month-old infants, in contrast, performed significantly more trials in which they showed a predictive gaze shift to the reappearing side of the occluder (see Figure 6).

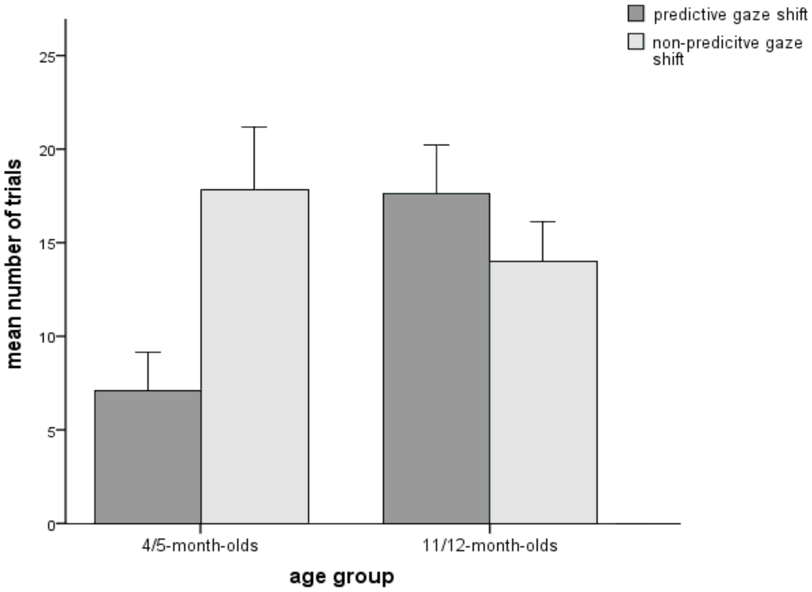


Figure 6: Mean number of trials (and standard errors) of trials performed with predictive gaze shift and non-predictive gaze shift to the reappearing side of the occluder for nine 4/5-month-old and nine 11/12-month-old infants.

A last interaction effect between eye movements* gaze shift was detected (F (1, 16)= 18. 296, p<.01), implying that significantly more saccadic tracking was performed in trials where the car was not anticipated, whereas smooth pursuit was observed more often in trials where a predictive gaze shift to the reappearing side of the occluder was performed.

3.2 EEG data analysis

Instead of time locking EEG epochs to stimulus start, as it is traditional in EEG/VEP research, in the present study onset of EEG epochs was precisely time locked to the catch-up event, i.e. a behaviourally determined onset was used. Furthermore, eye data recordings served to monitor infants' visual tracking behaviour so that only trials were included in the EEG analysis in which infants followed the car with their gaze over the whole trial over the whole trial. EEG data analysis intended to investigate two basically identical epochs of stimulus presentation, which only differed by their perceptual history, i.e. is occlusion of the car. In this regard possible effects of perceptual recognition reflected by gamma oscillatory activity elicited by the brain were studied with TSE analysis.

TSE analysis concentrated on frequencies in the 20-70 Hz range since no apparent oscillatory activity in other frequency bands coupled to the occurrence of gamma band activity could be observed by visual analysis. This band includes frequency ranges commonly used to study gamma band oscillations in infants (e.g. Csibra, Davis, Spratling & Johnson, 2000; Kaufman, Csibra & Johnson, 2003, Kaufman, Csibra & Johnson, 2005).

3.2.1 Brain source activity in the time-frequency domain of single subjects

ERD/ERS plots are shown in Figure 7 representing time-frequency plots in the range of 20-70 Hz in time windows of [0, 450] ms with a baseline of [-100, 0] ms for a typical 4-month-old infant (A) and an 11-month-old infant (B). In 4/5-month-old infants induced synchronized oscillations in the 40 Hz range were observed by visual analysis in two or more visual cortical sources in response to the epoch of car reappearance with a latency onset between 100 - 200 ms after epoch onset and lasting until approximately 400 ms after epoch onset. The epoch of the catch-up event did not lead to any distinct pattern in (de-) synchronization of oscillatory brain activity in these sources. As typical example for the group of 4/5-month-old infants, Figure 7A depicts the VCr-L and VCl-R brain sources of the visual cortex of a single infant (infant "D"). In the group of 11/12-month-old infants the epoch of car reappearance elicited in 7 out of 9 infants an increase in induced synchronized activity in the range of 40 Hz in two or more visual cortical sources as response to car reappearance, whereas no similar oscillatory activity could be observed in the epoch of the catch-up event in the same sources. Additionally, sustained synchronizations in the 40 Hz band were observed in the 11/12-month-olds in all but one infant in response to car reappearance in the brain sources of the left and right anterior temporal lobe, whereas in the epoch after catch-up event desynchronization in the 40 Hz band could be observed in these sources. See Figure 7B for a depiction of gamma activity in the TA-L and TA-R sources of the temporal lobes in a typical infant (infant “K”) of the group of 11/12-month-olds.

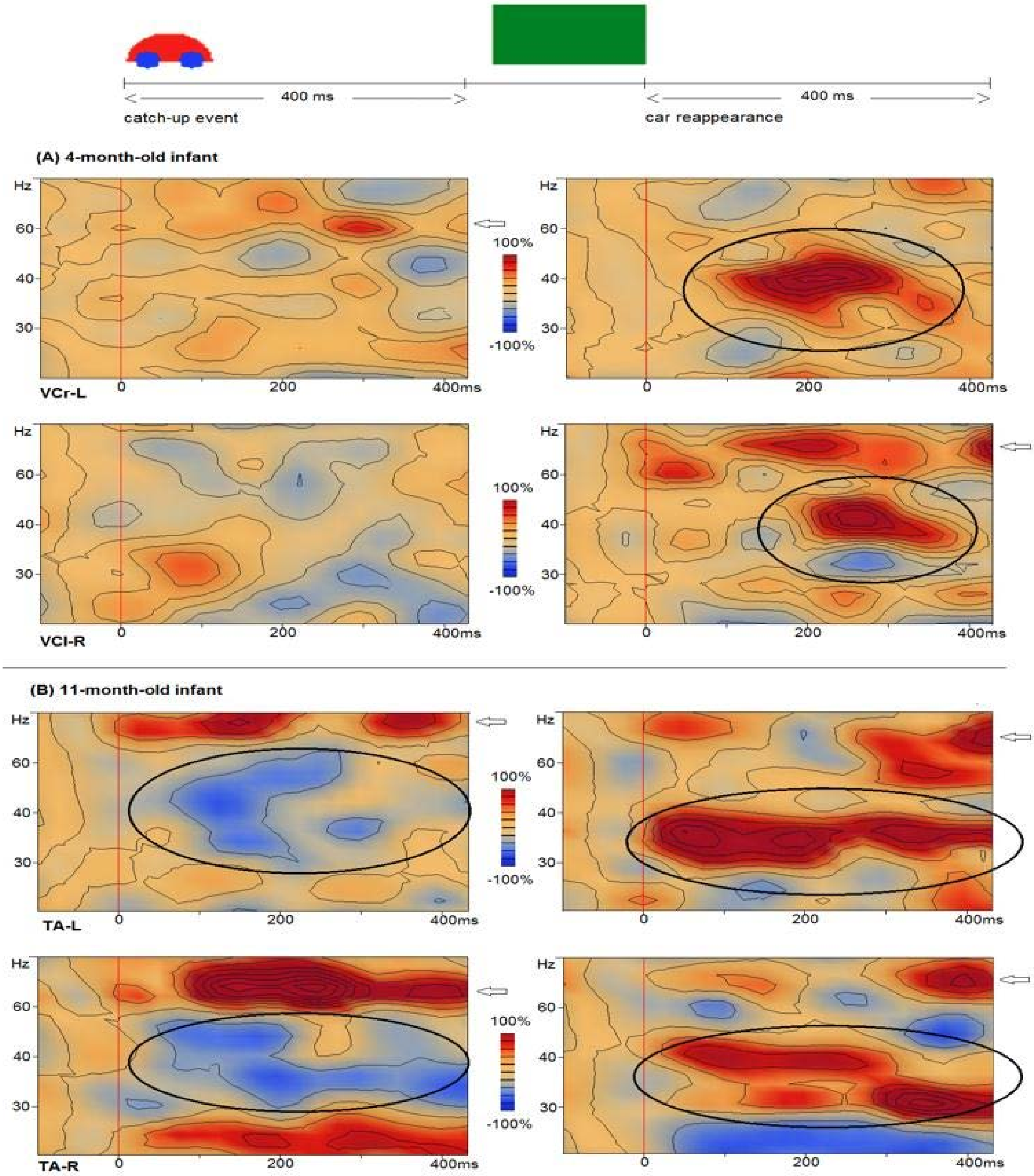
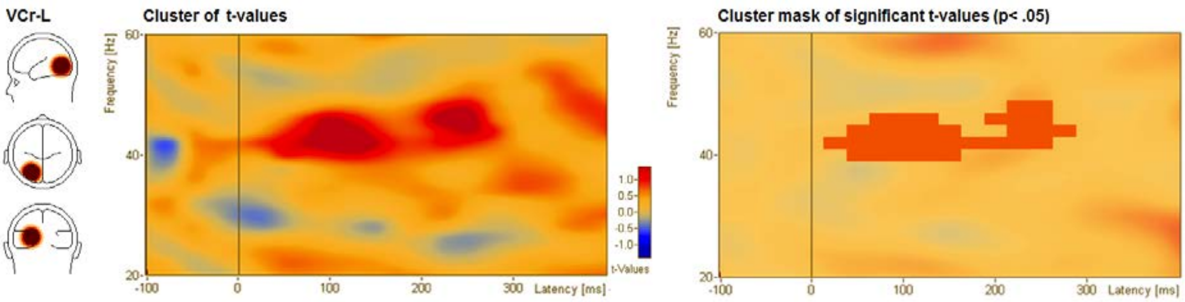


Figure 7: Brain source activity as a change of frequency (in Hz) over time (in ms) measured in absolute power (squared envelope amplitude) in the range of 20-70 Hz in a time window of [0, 400] ms as elicited by the presentation of the epoch of the catch-up event and car reappearance (corresponding epochs depicted above), in (**A**) a typical 4-month-old infant, “infant D”, and (**B**) a typical 11-month-old infant, “infant K”. The vertical line at time 0 indicates epoch onset. Red-coloured patterns indicate induced synchronized activity, whereas blue patterns indicate desynchronization in oscillatory activity. In (**A**) TSE plots display oscillatory brain activity of the VCr-L (left visual cortex) and VCl-R brain source (right visual cortex) in a 4-month-old infant. As can be readily seen, the reappearance of the car provoked bursts of neuronal synchronization in the gamma band (~40 Hz), whereas no similar neuronal activity was observed in response to the catch-up event. In the 11-month-old infant (**B**) the reappearance of the car led to two bands of sustained gamma oscillations around 40 Hz in the TA-L (anterior temporal left) and TA-R (anterior temporal right) brain source, starting right after epoch onset. In the epoch of the catch-up event, on the other hand, desynchronization was observed in the range between 20-60 Hz. Note: The synchronized neuronal activity at approximately 60 Hz in (**B**) (indicated by arrows) is apparent in both epochs of interest and is therefore not specifically connected changes in gamma activity connected to reappearance of the object but rather to stimulus properties of the moving object itself.

3.2.2 Brain source activity in the time-frequency domain of averaged group data

The epoch of car reappearance was statistically compared to the epoch of the moving car with the defined onset at catch-up event in time windows of [0, 450] ms after epoch start with a baseline of [-100, 0]. Group analysis of the 4/5-month-old infants revealed a significant positive cluster ($p < 0.05$) in a frequency band of 39-48 Hz with a latency of [20, 290] ms in the brain source of the left visual cortex (VCr-L), indicating the epoch of car reappearance had significantly larger cluster values (M= 0.15) than the epoch of the catch-up event (M= -0.20). This suggests the epoch of car reappearance elicited significantly stronger synchronized oscillations in the left visual cortex in the above time and frequency intervals compared to the epoch of catch-up event (see Figure 8A). No other brain sources measured significantly different cluster activity in gamma oscillations between the two epochs of interest.

A 4/5-month-old infants



B 11/12-month-old infants

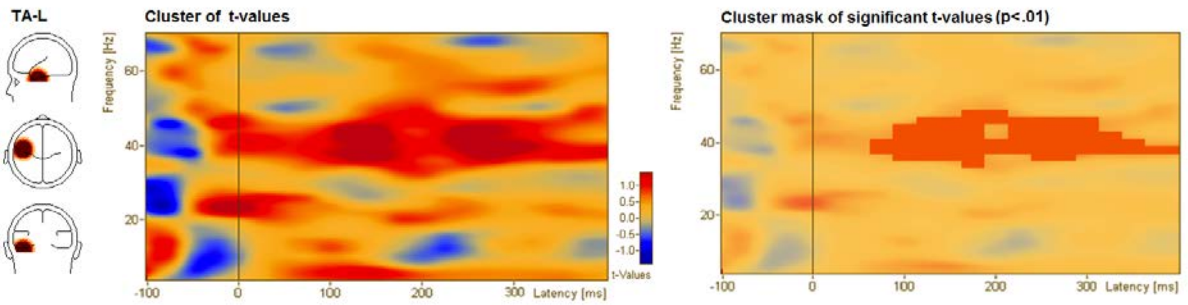


Figure 8: Clusters of t-values displayed as a function of time (in ms) and frequency (in Hz) as obtained by TSE statistical analysis (on the left) where statistically significant areas are overlaid by a cluster mask (on the right) for 4/5-month-old infants (**A**) and 11/12-month-old infants (**B**). Whereas the plots on the left show the distribution of t-values, the cluster masks on the right side display the area of significant differences. In the group of 4/5-month-olds (**A**), comparison of brain oscillatory activity of the epoch of car reappearance to the epoch time locked to catch-up event led to two observable peaks of largest t-values, i.e. a first peak at a latency of 100 ms and a second peak at a latency of 250 ms in the VCr-L brain source. The cluster mask shows an area of significance ($p< .05$) at a frequency of 39-48 Hz and a latency of [20, 290]. The cluster is significantly positive (indicated by red colour) which implies significantly increased synchronized oscillations as response to car reappearance compared to catch-up event. Statistical analysis of 11/12-month-old infants (**B**) revealed two peaks of highest t-values, the first one around 120 ms and the second one around 250 ms in the TA-L brain source. A significant positive cluster ($p< .01$) was detected at a frequency of 35-45 Hz at latency of [60, 400] ms, indicating significantly increased oscillatory activity in response to car reappearance compared to the catch-up event.

Comparing the epoch of car reappearance to the epoch of the catch-up event in time windows of [0, 400] ms after epoch onset with a baseline of [-100, 0] ms in the group of 11/12-month-old infants revealed a significant positive cluster in a frequency band of 35-45 Hz, in a time period of [60, 400] ms in the left anterior temporal brain source (TA-L) (see Figure 8B). The cluster is significantly positive ($p < .01$), indicating larger cluster values for the epoch of car reappearance (M= 0.19) than for the epoch of the catch-up event (M= -0.23), implying significantly increased neuronal synchronized oscillations as response to car reappearance compared to the epoch time locked to catch-up event in the TA-L source.

No other significant cluster could be detected in the data indicating neuronal oscillatory activity was not significantly different between the epochs of interest. Nevertheless second highest absolute t-values were found in the hemispherical equivalent source to TA-L in the right anterior temporal cortex (TA-R). The positive cluster was observable at a frequency range of 32-38 Hz in a time window [100, 350] ms, indicating that the increased synchronized oscillations as response to car reappearance were not solely left lateralized as already suggested by visual analysis of single subjects.

4. Discussion

Results of the present thesis provided insights into visual object processing over occlusion in 4/5-month-old and 11/12-month-old infants. Analysis of predictive visual tracking was complemented by analysis of neuronal gamma oscillations via EEG as elicited by object reappearance. Results of eye-movement analysis are in accordance with previous studies demonstrating that the ability of anticipatory eye movements improves considerably in the course of the first year of life (Gredebäck & von Hofsten, 2004). The match of sensory stimulus information after object reappearance with the perceptual template of the object over the invisible period elicited neuronal gamma activity in a posterior occipital brain source (dorsal pathway) in 4/5-month-old infants and an anterior temporal source (ventral pathway) in 11/12-month-old infants. It is suggested that 4/5-month-old infants generated anticipatory eye movements to spatio-temporal stimulus information whereas in 11/12-month-olds′ gaze was primarily guided by properties of object identity.

4.1 Visual tracking and predictive saccades

The ability to perform smooth pursuit as well as predictive eye movements increased considerably between the ages of 4/5 months and 11/12 months. The ratio of smooth pursuit eye movements on overall performed trials increased from 14% to 63% with age and the ratio of predictive gaze shifts from 29% to 56%. Both smooth pursuit and predictive occluder tracking are suggested to rely on the ability to anticipate future motion based on the representation and prediction of a continuous motion trajectory of a moving object (Rosander & von Hofsten, 2004). Smooth pursuit systems have to overcome visuo-motor delays of about 100-200 ms (Schlag & Schlag- Rey, 2002), a time in which a visual target might move significantly, thus smooth pursuit eye movements have to be adjusted predictively. Three different deceleration conditions were presented in the present study so as to prevent trial-to-trial learning of spatio-temporal contingencies as reported earlier (Bertenthal, Longo & Kenny, 2007; Jonsson & von Hofsten, 2002; von Hofsten, Feng & Spelke, 2000). Brief time spans of stimulus presentation before occlusion of 1-2 sec have been proven to be sufficient to elicit predictive occluder tracking in very young infants previously (von Hofsten et al., 2007). The proportion of predictive gaze shifts in the present report corroborates previous studies of anticipatory eye movements in infancy which revealed that young infants anticipate repetitive, predictable events on 15–30% of trials (Canfield, Smith, Brezsnyak & Snow, 1997; Johnson, Amso & Slemmer, 2003), depending on the specific paradigm, with few improvements in anticipation frequency in simple event sequences from 3 to 12 months of age (Canfield et al., 1997).

Higher proportions of predictive gaze shifts already in very young infants have been reported (von Hofsten et al., 2007; Rosander & von Hofsten, 2004) by using a white rectangular in the same colour as the background in order to minimize visual salience of the occluder instead of an opaque occluder, which, if salient, might compete for attention with the moving stimulus so that the predictive gaze shift is disrupted. Despite this finding, an opaque occluder was used in the present report since it resembles far better the natural environment where objects get effectively hidden behind other objects instead of gradually disappearing into thin air, even though the rate of predictive gaze shifts might have been slightly reduced attributed to competing attentional processes. Especially the younger infants might have had difficulties to disengage selective attention from the occluder, which competes with the moving object for attention and representational resources (Gredebäck & von Hofsten, 2004; Jonsson & von Hofsten, 2003).

All infants showed predictive eye movements and smooth pursuit to a certain extent (apart from 2 infants in the younger age group who only carried out saccadic tracking), indicating that object prediction, as well as smooth pursuit, is not an all or none response that infant either lack or possess but rather a gradual developing ability depending on parameters of the current occlusion event (Gredebäck & von Hofsten, 2007). In trials in which infants followed the car with saccadic tracking significantly less predictive eye movements were performed, which is plausible since only if the spatio-temporal characteristics of the car can be anticipated before occlusion as indicated by smooth pursuit, it is possible to disengage attention from tracking the apparent moving object to re-orient gaze in a predictive manner over an obstacle. In accordance, a trend of performing smooth pursuit in combination with predictive occluder tracking in trials was revealed in both age groups. Munakata (2001) argued that object representations degrade with time and that behavioural failures of object interaction over occlusions are due to weak object representations. In this regard the overall smaller number of predictive eye movements in 4/5-month-old infants compared to 11/12-month-old infants suggests that perceptual object representations in the younger age group were too fragile to be acted upon in a consistent predictive manner. Thus the greater proportion of predictive eye movements in the older age group may be taken as evidence for the influence of functional object representations on eye movements (Hollingworth, Richard & Luck, 2008).

4.2 Changes in brain oscillatory activity in the gamma range

EEG data revealed significantly greater gamma activity in response to the moving car after a transient stimulus occlusion compared to the presentation of the identical moving stimulus before occlusion. In both age groups a very reliable gamma activity could be revealed induced by car reappearance resulting in high t-values. Irrespective of the age group, obtained gamma bands were of a limited bandwidth (centred around 40 Hz), with a clear observable upper and lower bound. This is in accordance with visually induced spectral patterns of gamma band activity recently observed by Hoogenboom et al. (2006) and also by Kaufman, Csibra & Johnson (2003), but differs from several studies reporting a transient broadband gamma frequency response in response to cognitive functions connected to object perception (e.g. Tallon-Baudry, Bertrand, Delpuech, & Permier, 1997; Gruber, Trujillo-Barreto, Giabbiconi, Valdés-Sosa, & Müller, 2006); Martinovic et al., 2007, 2008; Supp et al., 2007). Indeed, Yuval- Greenberg & Deoull (2009) suggested that findings of broadband gamma activity need to be treated cautiously, since the saccadic spike potential (SP), a strong electrical potential produced by extra-ocular muscles during the execution of saccades, equals in time and frequency spectrum the transient broadband gamma response classically referred to as induced gamma band activity of neural populations. Furthermore, the SP seems to be susceptible to the same cognitive manipulation as broadband induced gamma, where effect of familiarity is thought to enhance both (Yuval-Greenberg, Tomer, Keren, Nelken & Deouell, 2008). Hence, the different spectral patterns might be due to confounding activity by the SP potential.

The spectro-temporal pattern of enhanced gamma activity coincided on a group level in 4/5- and 11/12-month-olds. Two enhanced peaks of gamma band activity could be observed, the first one around 100 ms in 4/5-month-old infants and slightly later in 11/12-month-old infants, and a second peak after 200 ms in both groups. Interestingly, even though the spectro-temporal pattern of observed gamma activity coincided in both groups, localisation in brain source space differed and sources of increased gamma activation could be assigned to regions along the dorsal pathway for 4/5-month-old infants and along the ventral pathway for 11/12-month-old infants, both localized in the left hemisphere. The divergence in gamma band topography between the age groups is interpreted to reflect developmental changes in neuronal mechanisms serving object tracking over transient occlusion periods in the course of the first year of life. In order to successfully track an object over an occlusion period a perceptual representation of the object must be formed before the occlusion period, enduring the retention period, which subsequently allows for comparison with sensory object information after object reappearance that can lead to visuo-motor integration, in this case a continued eye tracking. In adults, the visual short-term memory (VSTM) has been shown to successfully fill perceptual gaps and visually guide behaviour over transient occlusions periods in the visual array by retaining visual online presentations between successive visual inputs as acquired every time we blink, make a saccadic eye movement so as to compare two objects which cannot be simultaneously fixated, or observe objects that are momentarily occluded (Hollingworth, 2004; Johnson, Hollingworth & Luck, 2008). Traditionally, a differentiation is made between an early evoked gamma response that is suggested to be the neuronal correlate of the comparison between a perceptual template of an object in VSTM and the perceived stimulus occurring in the cortical region computing the process, and a late induced gamma response, which is associated which large scale coherence “broadcasting” the synchronized message to other brain areas relevant for task performance (Herrmann, Munk & Engel, 2004; Herrmann & Mecklinger, 2010). The early onset of the augmented gamma activity in regional sources as found in the present study, suggests that it is based on comparative processes of templates maintained in VSTM with the perceived stimulus after object reappearance. Oakes, Ross-Sheehy and Luck (2006) found evidence that the ability to bind colour and location in VSTM, prototypical ventral and dorsal pathway features, respectively, over occlusion periods as brief as 300 ms develops rapidly between 6 and 8 months of age. It is suggested that the comparison between memory processes and perceived stimulus after object reappearance in the present study was reflected by the enhanced gamma activation shifting from occipital to anterior temporal areas with age. Considering that VSTM is coded by temporary activation of an ensemble of neurons in the region of associated cortex also responsible for processing visual information (Mishkin, 1982; Miyashita & Chang, 1988), together with the fact that it is suggested to be responsible for object correspondence between separate fixations (Hollingworth, Richards & Luck, 2008), it is a plausible assumption that the difference in regional gamma activity points out a motion-based account of object individuation over occlusion in the younger infants, whereas the older infants took properties of object identity for individuation processes into account. In this regard, the gamma activation is interpreted as a top-down process, or “highspeed memory comparison” (Herrman & Mecklinger, 2010) of the object template maintained over the perceptual gap with the perceived stimulus. In addition, it is suggested that the capacity of VSTM comprises integrated objects, rather than individual object features (Lee & Chun, 2001; Luck & Vogel, 1997). Differences in spatial distribution of gamma activity functionally connected to respective cortical areas have been found before, with gamma activity connected to complex object processing in regions distributed along the ventral pathway (Lachaux et al., 2005), whereas motion specific gamma was reported to be restricted to occipital visual areas in the dorsal pathway (Hoogenboom et al., 2006; Müller, Junghöfer, Elbert & Rochstroh, 1997). Even though 7 out of 9 infants in the older age group showed some increased gamma activity in sources of the visual cortex, this activity did not reach significance. Van Wermeskerken et al. (2011) implied that vision for perception (a typical ventral stream task) could replace vision for action (typically connected to the dorsal stream) to successfully guide 11-month-old infants´ arm movements in an anticipatory reaching task in an occlusion situation. Empirical evidence for this was provided by the present findings, with observed neuronal gamma activation in temporal sources in 11/12-month-old infants suggesting that the guidance of eye movements over the occluder was primarily processed in the ventral stream.

Findings of Kaufman, Csibra and Johnson (2003, 2005), who suggested gamma activity in the 40 Hz range reflects the actual neuronal maintenance of visual representations over occlusion periods, are in no contrast to the present findings considering that a memory match reinforces feedback of the frequency at which the process operates anyway (Herrmann & Mecklinger, 2010).

Present findings fit into theoretical accounts of object correspondence over occlusion periods. Leslie et al. (1998) formulated a conceptual framework, following on “object files” (Kahneman & Treisman & Gibbs, 1992) and Pylyshyn’s ‘FINST’ (‘Fingers of INSTantiation’) theory of visual indexing (Pylyshyn, 1989). The authors suggested an object index, a selective attentional mechanism that points to a single object and keeps track of it through space and time. According to the model, young infants individuate objects by assigning location and motion information to objects ("where" system), and only towards the end of the first year infants are able to integrate object property or object kind information, which refers to specific categories of objects ("what" system), in order to individuate and identify objects.

Until now, evidence of the functional development of the ventral and dorsal pathway in humans on a neurophysiological level is sparse. It has been proposed that the dorsal and ventral pathways undergo different developmental trajectories, thus the dorsal stream arising from early visual areas extending to the parietal cortex is a supposedly earlier developed structure as compared to the ventral stream maturing at a slower rate (Kovács, 2000), a hypothesis supported by studies in monkeys (Distler, Bachevalier, Kennedy, Mishkin & Ungerleider, 1996). Wilcox, Haslup & Boas (2010) provided the first direct evidence for a dissociation of object processing according to the ventral and dorsal stream by showing that posterior temporal areas in 5/7-month-old infants mediate spatio-temporal but not featural properties of objects over occlusion. In contrast, the anterior temporal areas were connected to object individuation, indicating a hierarchically organization of functional units (Wilcox et al., 2010). Earlier, a close correlation between hemodynamic responses and synchronized gamma activity has also been reported (Koch, Werner, Steinbrink, Fries & Obrig, 2009; Niessing et al., 2005).

A clear functional dissociation between an early evoked and late induced gamma activity was difficult to make because no perfectly time-locked signal to car reappearance was found. If the gamma activity occurring after 200 ms is related to the broadcast of the synchronized message to distributed neuronal regions would need to be investigated further by source coherence measures of oscillatory activity.

4.3 Summary and Conclusion

In order to predict successfully and accurately the reappearance of a moving object, the object and its motion need to be represented over the invisible period (Jonsson & von Hofsten, 2003). Over the first month of life, infants rely on motion as the primary source of information about object properties. The presence of motion affords young infants the opportunity to develop rudimentary representations of object persistence, spatial depth, object boundaries, and three-dimensional form before they can master the use of other types of cues in the scene (Gerhardstein et al., 2009). Investigating how the infant visual system responds to object motion by linking neuronal processes to what we observe behaviourally, advances our understanding of how the human visual system evolves. Based on the present results it is suggested that infants during the first months of life primarily rely on spatio-temporal object information to fill perceptual gaps over transient occlusions. In this regard, even though infants perceived and tracked the moving stimulus, the car itself might have remained unidentified (Kahneman, Treisman & Gibbs, 1992). Even though this strategy appears inferior to mature object tracking, infants are capable to generate anticipatory eye movements to this type of information to a certain extent. Infants at the end of their first year, on the other hand, possess advanced object knowledge reflected by the incorporation of object features into perceptual representations, leading to stronger representations, which in turn can be acted upon. On a behavioural level this is expressed by a more consistent pattern of anticipatory eye movements.

Even though the body of literature of neuronal oscillations in human adults is steadily growing, the nature of neuronal oscillations in infants has only recently begun to be investigated. Especially the study of gamma activity is a valuable supplement to traditional ERP research investigating perceptual and cognitive processes. In this regard, the combination of behavioural measures with EEG becomes a powerful tool to validate results. Because of high inter-individual variability in spectro-temporal patterns of high frequency gamma oscillations in infants, a longitudinal design might be the method of choice, since intra-individual differences in gamma activity over different points in time have been shown to be fairly stable (Hoogenboom et al., 2006).

5. References

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