Perception of looming visual motion from infancy to school age: A high-density EEG study of full-term and preterm children

by

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Abstract

By using high-density electroencephalogram (EEG), the present study investigated developmental trends in brain activity in response to looming visual motion from infancy to school-age in preterm children and their age- and gender-matched full-term peers. The children were tested at 4-5 months, 11-12 months, and at 6 years, where their looming-related brain responses were measured on a trials-by-trial basis. Analyses of looming-related visual evoked potentials (VEPs) revealed that the full-term children gradually decreased their VEP duration and time-to-collision with increasing age. The preterm children only decreased their VEP duration and time-to-collision from 11-12 months to 6 years, and showed significantly longer duration and time-to-collision at both 11-12 months and at 6 years compared to the full-term children. In addition, three preterm children were not able to switch to a more efficient timing-strategy based on the loom’s time-to-collision when timing their looming-related brain responses to the upcoming collision. Time-frequency analyses (TSEs) revealed that the full-term children showed shorter brain responses in higher frequency-bands with increasing age, while the preterm children showed their brain activity in the same duration and frequency-band during all three test sessions. In addition, the Movement Assessment Battery for Children (M-ABC) was included to investigate the children's motor function at 6 years. However, no differences between the full-term and preterm children could be observed in the motor domain. In sum, a clear developmental trend was observed in the full-term children's perception of looming visual motion, probably due to brain maturation and experience with self-produced locomotion. As the same developmental trend was not found in the preterm children, in addition to their worse performance compared to their full-term peers at both 11-12 months and 6 years, the developmental delay has been attributed to dorsal visual stream vulnerability related to preterm birth. Follow-up studies are therefore necessary to investigate if the preterm children will catch up with their full-term peers at a later age, or if they continue to show impaired perception of visual motion.

1.0 Introduction

According to the World Health Organization (WHO), on average 9% of babies born in higher income countries are born premature. Preterm birth is defined as delivery before 37 weeks of completed pregnancy and is divided into subcategories based on gestational age; late to moderate preterm (32-37 weeks), very preterm (28-32 weeks) and extremely preterm (less than 28 weeks) (WHO, 2017). In Norway 2016, the number of preterm births was approximately 5.2% of all registered child births (3368 babies), with preterm birth being connected to 50% of brain damage found in children, and cause 65% of infant death in connection with childbirth (Norsk helseinformatikk, 2018). Despite dramatically reductions in mortality and complications the last decades (Saugstad, 2010), preterm children are still at greater risk for developmental problems that can affect cognitive function and learning abilities, even in absence of evident brain damage (Saigal, Hoult, Streiner, Stroskopf & Rosenbaum, 2000). Among the most common neurosensory deficits related to premature birth are problems with vision observed in as many as 64% of individuals born with very low birth weight. Some of the causes to these deficits can either be attributed to retinal conditions (retinopathy of prematurity), visual functions (strabismus, myopia, hypermetropia), or perception (stereopsis, acuity) (Darlow, Clemett, Horwood, Mogridge, 1997).

The overall processing of visual information has been associated with the structural and functional organization of the dorsal and ventral streams (e.g., see review by Creem & Proffitt, 2001). Preterm birth has also been found to disrupt the development of visual pathways in the brain, and in particular the dorsal visual processing stream as it is considered to be more vulnerable during early development compared to the ventral stream (Birtles, Braddick, Wattam-Bell, Wilkinson & Atkinson, 2007; Hammarrenger et al. 2003; Hammarrenger et al. 2007). As impaired dorsal-stream related functions in preterm children have been found in general, and ventral stream impairments have only been observed in line with brain damage, a comprehensive dorsal stream vulnerability has been suggested as a result of being born preterm (Guzzetta et al., 2009). The dorsal stream, also referred to as the magnocellular visual pathway or “where” stream, is involved in perception of spatial aspects of stimuli such as the direction and speed of motion, and is therefore essential for the ability to perceive and plan movements. The dorsal stream leads from the occipital lobe, through the medial temporal (MT) and the medial superior temporal (MST) area, further on to the parietal lobe (Creem & Proffitt, 2001). The ventral stream, also referred to as the parvocellular visual pathway or “what” stream, leads from the occipital lobe to the temporal lobe, and is essential for object recognition (Creem & Proffitt, 2001). Accordingly, the information perceived in an individual's surroundings, as well as how the individual moves and responds to sudden changes in the environment, depends on these two separated, but integrated cortical streams (Zotcheva & Van der Meer, 2016).

In Gibson's ecological theory of visual perception, patterns of visual information caused by an observer's own movements are termed optic flow (Gibson, 2015). In his theory, Gibson (2015) proposed that perception and action are interdependent and cannot be treated separately as our behavior is being directed by our perception, and vice versa. Consequently, optic flow patterns are essential for our ability to plan and perform precisely calculated movements adapted to our changing surroundings, referred to as prospective control (Adolph, Eppler, Marin, Weise & Clearfield, 2000; Lee, 1993). Prospective control is essential for fundamental and automatic movements such as adjusting posture (Vaina & Rushton, 2000), avoiding obstacles (Turano, Yu, Hao & Hicks, 2005; Wilkie & Wann, 2003), reaching a target efficiently (Lappe, Bremmer & Van der Berg, 1999), and to estimate when objects are about to hit (Kayed & Van der Meer, 2009). As dorsal-stream vulnerability has been found in preterm children, this may indicate that individuals born premature have problems with prospective control, and accordingly with all these fundamental skills.

Prospective control becomes more and more important as an infant grows older, and development of smooth visual pursuit of moving objects is one of the earliest indications that an infant develops prospective control (Von Hofsten & Rosander, 1996). This implies that an infant is able to predict forthcoming motion of a moving object, which has been found to be developed during the first three months of life (Von Hofsten, 2007; Von Hofsten & Rosander, 1996). Accordingly, one way to measure development of prospective control in infancy is by simulating a object approaching on direct collision course and measuring the children's estimation of when the looming object is about to hit (Agyei, Van der Weel & Van der Meer, 2016a). A looming object on a direct collision course creates an expanding image with a rapid symmetrical growth on the retina, providing information about the approaching object and how imminent the collision is (Schiff, Caviness & Gibson, 1962). The term “looming” refers to the last part of the optical event where an object is accelerating toward the individual (Kayed & Van der Meer, 2007).

Perception of looming has been investigated in a variety of different species such as locusts (Rind & Simmons, 1997), pigeons (Sun & Frost, 1998), monkeys (King & Cowey, 1992), and humans (Kayed & Van der Meer, 2000, 2007; Van der Meer, Svantesson, Van der

Weel, 2012; Yonas, Pettersen & Lockman, 1997). Wang and Frost (1992) found that a subpopulation of neurons in the nucleus rotundus in pigeons responds selectively to looming objects on a direct collision course. This subpopulation of neurons can be divided into three smaller groups based on their responses to optical variables; tau neurons firing at a relative rate of expansion resulting in responses at a fixed time-to-collision, rho neurons firing at an absolute rate of expansion, and eta neurons firing in response to angular size (Sun & Frost, 1998). In humans as well, the visual system has been found to be more sensitive to expanding or looming motion, creating an impression of motion towards the observer, compared to motion that do not (Holliday & Meese, 2005; Shirai & Yamaguchi, 2004).

Research on infant perception was at its peak in the 1960s and 1970s, where looming stimuli played a central role when examining how early infants could respond to visual motion (Bower, Broughton & Moore, 1971; Schiff, Caviness & Gibson, 1962; Yonas, Pettersen & Lockman, 1997). Today, is it well established that blinking is the most reliable indicator of awareness to stimuli on a collision course in early infancy. In order to protect the eyes, a blink has to be perfectly timed based on the looming object's upcoming collision. Kayed and Van der Meer (2000, 2007) investigated infants' defensive blinks in response to looming by looking at different timing strategies based on the loom's visual angle, velocity, and time away from the virtual collision. The results showed that the infants at first applied a strategy based on the loom's visual angle or velocity, while they at around 6/7 months switched to a strategy based on the loom's time away from collision. The infants using a strategy based on angle or velocity showed a significantly higher number of late defensive blinks compared to the infants using a strategy based on time. This made the researchers suggest a developmental trend entailing a shift from a not so useful to a more sophisticated timing strategy less prone to miscalculations around 6/7 months of age (Kayed & Van der Meer, 2000, 2007).

When investigating defensive blinking responses as an indication of prospective control in both preterm and full-term infants, Kayed, Farstad and Van der Meer (2008) found that the preterms showed the same developmental pattern as full-terms, but only when corrected for prematurity. Out of eight infants at 26 weeks corrected for prematurity, three of them based their defensive blink on the loom's visual angle, one on the loom's velocity, and four infants based their blink on the loom's time away from collision. The infants using a visual angle or velocity strategy had problems timing their blinks to faster approaching looms, while the infants using a time-strategy correctly timed their blink irrespective of loom speed. Longitudinal data were available for three of the infants, where one preterm infant stood out as he used a timing strategy based on velocity at all test sessions, leading him to blink too late on a high number of trials even at 30 weeks. In addition, the same infant had severe timing problems when reaching for moving toys in a later longitudinal study of prospective control in catching (Kayed & Van der Meer, 2009). An inability to switch from a less efficient timing strategy to a more efficient one could indicate a small degree of flexibility, important for successful interaction with the environment (Agyei, Van der Weel & Van der Meer, 2016a).

In a longitudinal study conducted by Van der Meer, Svantesson and Van der Weel (2012), looming-related visual evoked potential (VEP) responses and timing strategies were investigated in full-term infants using high-density EEG. The results revealed different responses with age, where the younger infants showed VEPs earlier in the looming-sequence and VEP responses with longer duration than the older infants. The timing-strategy analysis showed that 4 infants shifted from a less efficient strategy based on velocity to a more sophisticated strategy based on the loom's time away from collision. At 5-6 months, activity was observed in occipital areas, while at 12-13 months the activity was observed higher up the dorsal stream in the parietal area. Thus, this study indicated a developmental trend in visual motion perception during the first year of life due to propagated VEP activation towards higher information processing areas in the visual pathway and a shift to a more efficient timing strategy with age (Van der Meer, Svantesson & Van der Weel, 2012).

Benefits of using high-density EEG are due to the technique's direct measure of brain activity with high temporal resolution, allowing for investigation of brain responses as they happen in real-time. Event-related potentials (ERP) are transient brain electrical activity generated by the summation of dendritic postsynaptic activity of neurons firing synchronously in response to a stimulus (Luck, 2005). Visual evoked potentials (VEP) are ERPs in the visual cortex, where neurons are firing in a postsynaptic pattern at a particular time to a specific stimulus (Webb, Long & Nelson, 2005). For instance, simulating a looming object could evoke looming-related VEP peaks at a certain time during the loom sequence as investigated in Van der Meer, Svantesson & Van der Weel (2012).

In order to completely understand the complex brain responses following visual motion, analysis of induced activity in addition to evoked activity like VEPs could be useful in EEG studies. Time-frequency analysis (TSE - temporal spectral evolution) is considered an appropriate method as it detects event-related time-frequency responses (Pfurtscheller & Lopes da Silva, 1999). These responses are assumed to represent local cortical neuronal interactions in the ongoing EEG activity as a result of changes in communication between neurons and interneurons that can be seen by an increase or decrease in amplitude

(Pfurtscheller & Lopes da Silva, 1999). Increased synchrony between the neurons is called event-related synchronization (ERS) (Pfurtscheller, 1992), indicating that neuronal networks are in a resting state (Pfurtscheller & Lopes da Silva, 1999). In contrast, when the synchrony between the neurons decreases, referred to as event-related desynchronization (ERD) (Pfurtscheller & Aranibar, 1977), it is considered a sign of neuronal networks preparing to process sensory information (Pfurtscheller, 1992), as well as an indication of task complexity (Boiten, Sergeant & Geuze, 1992).

In a cross-sectional study, Van der Weel and Van der Meer (2009) looked at how the infant nervous system extracts and processes information about an imminent collision by investigating induced brain activity with TSE in response to looming stimuli. The results indicated that looming-related brain activity between 5 and 11 months of age is dominated by theta oscillations taking place in the visual cortex. The youngest infants at 5-7 months used approximately twice as long time to process the looming information compared to the oldest infants at 10-11 months. As the oldest infants in addition showed very neat, short and separated brain waves, these findings could indicate a developmental trend in visual motion perception in the latter half of the first year of life (Van der Weel & Van der Meer, 2009). Based on synchrony of neural oscillations, brain activity can be divided into five different frequency bands shown to reflect neurophysiological processes with functionally different roles (Buzsáki & Draguhn, 2004; Saby, & Marshall, 2012). Low-frequency rhythms have been especially observed in infants, and accordingly been interpreted as a sign of immaturity (Orekhova, Stroganova, Posikera & Elam, 2006; Stroganova & Orekhova, 2007). Furthermore, in line with increased age and development, shifts from lower to higher frequencies have been considered as a sign of maturation in a variety of developmental studies (Hudspeth & Pribram, 1992; Stroganova, Orekhova & Posikera, 1999; Agyei, Holt, Van der Weel & Van der Meer, 2016b).

During the first year of life, the infant brain undergoes rapid changes and as much as doubles in weight (Johnson, 2000). These changes are essential for the infant's ability to more correctly and effectively perceive visual motion in the environment. A study investigating perception of optic flow has found full-term infants to discriminate between radial motion patterns with increased age (Agyei, Holt, Van der Weel & Van der Meer, 2015). Rapid cortical synapse formation and overproduction in most cortical areas are important for the plasticity of the brain and adaptation during maturation. This occurs in the first two postnatal years (Casey, Giedd & Thomas, 2000), particularly in the primary visual cortex between 4 and 6 months where peak synaptogenesis occurs (Huttenlocher, 1990). In the same period, glucose metabolic rates become more efficient which are thought to improve processing of motion (Chugani, Muller & Chugani, 1996). As a result, this process, along with the increased myelination of connecting fibers (Grieve, Emerson, Fifer, Isler & Start, 2003), contribute to make functional processes in cortex more efficient.

Another study investigating perception of optic flow has found full-term infants to discriminate between radial motion patterns with increased age during the first year of life with no such developmental differences found in preterm infants (Agyei, Van der Weel & Van der Meer, 2016b). Furthermore, studies of young children have found similar results. For example, Feng, Xu, Wang, Guo & Yang (2011) investigated perception of pattern reversal visual evoked potentials with different spatial frequencies in 4- to 6-year-old preterm children. The results revealed that preschoolers born premature are at risk of deficits in visual-spatial perception, especially when they are presented with more complex information, despite average cognitive abilities. In another study (Sayeur et al., 2015), investigating visual perception of varying spatial frequencies in 7- to 8-year-old preterm children, significantly higher amplitudes in the visual evoked potentials were observed in the preterm children compared to full-term controls. Taken together, these studies indicate that perceptual difficulties observed in individuals born preterm could be a persistent problem with increasing age.

Perceptual difficulties in preterm children without CP are assumed to be caused by the dorsal visual stream vulnerability related to preterm birth (Birtles, Braddick, Wattam-Bell, Wilkinson & Atkinson, 2007; Braddick, Atkinson & Wattam-Bell, 2003; Van Braeckel et al., 2008). While the fiber volume of white matter normally increases during early infancy until adulthood due to ongoing axial myelination (Dubois, Hertz-Pannier, Dehaene-Lambertz, Cointepas & Le Bihan, 2006), preterm infants at 2 weeks corrected for prematurity are found to have less cortical white matter compared to their full-term controls (Hüppi et al., 1998; Mewes et al., 2006). Other magnetic resonance imaging (MRI) and diffusion tensor imaging (DTI) studies have found that preterm infants, compared with full-term controls, have significantly reduced absolute cerebral volumes of cortical grey matter, deep nuclear grey matter, and myelinated white matter, and increased volume of cerebrospinal fluid (Counsell & Boardman, 2005; Inder, Warfield, Wang, Hüppi & Volpe, 2005). Cerebral damage, and in particular abnormalities in white matter essential for neural connectivity between brain areas, have been connected to deficits in visual and visuocognitive development graded according to the severity of damage, and have been found to predict later neurocognitive status (Atkinson & Braddick, 2012).

In addition, perceptual-motor difficulties in preterm children have been found using the Movement Assessment Battery for Children (M-ABC). Preterm children compared to their age-matched term-born peers at 3 years of age show more difficulties performing the M-ABC test (De Rose et al., 2013). The performance at 4 years has further shown to be a good predictor of motor functioning at 8 years of age (Jary, 2017; Griffiths et al., 2017). In addition, significant differences between full-term and preterm children when performing the M-ABC at early school-age have been found (Foulder-Hughes & Cooke, 2003a). Despite intelligence within the normal range, minor motor impairments found in very low birthweight children appear to have an impact on overall school performance (Foulder-Hughes & Cooke, 2003b). Through a meta-analysis of cognitive and behavioral outcomes in school-aged children born premature, it becomes clear that they are at risk for reduced cognitive test scores, and that their immaturity at birth directly corresponds to their mean cognitive scores at school-age. It was also found that preterm children have increased incidence of ADHD and other externalizing and internalizing behaviors compared to children born at term (Bhutta, Cleves, Casey, Cradock & Anand, 2002).

As infants born preterm are not fully mature at birth, it is crucial to map difficulties related to preterm birth as well as to facilitate optimal development after birth. High-density EEG can be a valuable tool to investigate brain development trends in young infants and children as the method is non-invasive and presents brain activity in real-time with high temporal resolution. Early investigation and close monitoring will hopefully help them reach their true social and cognitive capabilities comparable with their term-born peers (Atkinson & Braddick, 2012). As perception of visual motion is essential for prospective control (Gibson, 2015), and preterm birth is characterized by dorsal-stream vulnerability (Guzzetta et al., 2009), further research on visual motion perception and everyday functioning in preterm children is necessary.

The aim of the present study was therefore to investigate the development of visual motion perception from early infancy to school-age by presenting a looming virtual object approaching on a direct collision course. The study was carried out using a longitudinal design to further assess normal development of visual motion perception in full-term children, as well as to investigate impairments associated with preterm birth in moderate to very preterm children. By investigating a combination of looming-related VEPs and time-frequency analyses using high-density EEG, the children were tested at 4-5 months, 11-12 months, and at 6 years of age. Our main hypothesis was that preterm children would show impaired development of visual motion perception, in the form of longer time-to-collision, longer VEP duration and lower brain frequencies when perceiving looming visual motion compared to full-term children. A secondary hypothesis was that preterm children would show a reduced ability to shift to a more efficient timing-strategy. Finally, as dorsal visual stream vulnerability has also been linked to perceptual motor difficulties, reduced performance on the M-ABC in the preterm children was expected as well.

2.0 Method

2.1 Participants

A total of 20 healthy infants, 10 full-term and 10 preterm (5 girls in each group), were recruited for this study through birth announcements, contact with parents and / or with help of the pediatrician in charge of the Neonatal Intensive Care Unit at St. Olav's University Hospital in Trondheim, Norway. The full-term infants had a mean gestational age of 40 weeks (SD = 1.4, range = 38-42) and mean birthweight of 3621 gram (SD = 595, range = 3085-5120). The preterm infants (moderate to very preterm) were born at mean gestational age of 31 weeks (SD = 1.7, range = 28-33) with a mean birth weight of 1591 gram (SD = 453, range = 1000-2670). With exception of one preterm boy diagnosed with CP at two years of age, the preterm children did not have any major neurological deficits including severe brain damage, retinopathy of prematurity (ROP), or other perinatal issues requiring serious medical interventions that may lead to abnormal development.

The study followed a longitudinal design where the same children were tested at three different test sessions. Full-term and preterm children were matched according to age and sex, and in order to ensure valid matching the preterm children's age was corrected for prematurity. For the first testing, the mean age of the full-term children was 4 months and 4 days (SD = 18, range = 100-164 days), and the mean age of the preterm children was 5 months (SD = 11.2, range = 141-177 days). At this time point, the children had no experience with self-produced locomotion. For the second testing, mean age was 11 months and 17 days (SD = 13.1, range = 330-372 days) for the full-terms, and 1 year and 5 days (SD = 19.5, range = 341-415 days) for the preterm children. At the second test session, all children could crawl and independently pull to stand or walk with help. Three of the preterm children were not possible to test at third test session as two of the girls had not yet reached six years, while the boy with CP refused to wear the EEG net. Hence, three matching full-term children were then excluded from the last test session as well to ensure equal group sizes. In the third and last testing session, the mean age of the 7 remaining children (3 girls in each group) was then 6 years and 7 months (SD = 6, range = 73-88 months) for the full-terms, and 6 years and 9 months (SD = 1, range = 81-85 months) for the preterm children. All the children had started primary school at this time.

Electroencephalogram (EEG) is a physiological procedure that causes no harm or pain to the participants. The parents gave their informed consent prior to the experiment and were made aware that they were free to withdraw from the study at any time. The study has been approved by the Norwegian Data Services for the Social Sciences and The Norwegian Regional Ethics Committee.

2.2 Stimuli

The looming stimulus comprised a black 2D circle rotating with a constant angular velocity of 300 degrees per second on a cream white background. Within the black circle were four smaller rotating circles with a radius of 1/3 of the black circle in blue, red, green, and yellow. The stimulus loomed towards the children with different speeds and accelerations before it came up to the children’s face with the purpose of creating an experience of a virtual collision (see Figure 1a).

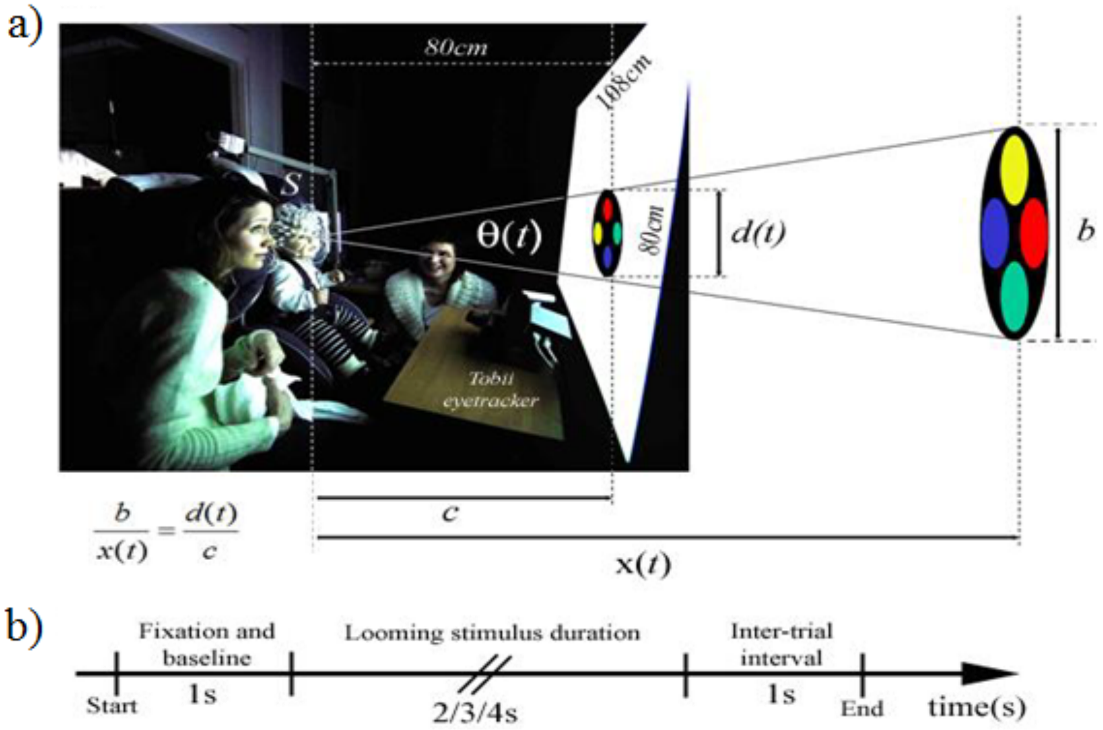

Figure 1. *Experimental set-up with a diagram of stimulus configuration (a) and a time-line of stimulus sequence (b). The figure is adapted, with permission, from Van der Meer, Svantesson & Van der Weel (2012).*

The rotating circle approached the children under three different conditions with durations of 2, 3, and 4 seconds, and with constant accelerations of -21.1 m/s^2, -9.4 m/s^2, and -5.3 m/s^2, respectively. Irrespective of the virtual loom's approach speed, the visual angle and size of the circle was the same at the beginning (visual angle 5° and diameter 6.5 cm) and the end (visual angle 131° and diameter 350 cm) of the approach. As illustrated in Figure 1b, the circle first appeared and stayed at its minimum size on the screen before it expanded over one of the three durations, finally disappearing and leaving the screen blank for 1 s before the next trial. In the first two test sessions, a reversed looming condition simulating the loom moving away from the infants was used in order to maintain the infant's interest. In order to keep the children's interest during the third session, the reversed looming condition was omitted, and the six-year-olds were told to time the loom's virtual collision by pressing a button every time the loom virtually collided with their face.

2.3 Apparatus

All visual stimuli were presented using E-prime (Psychological Software Tools) and displayed using an Ask M2 projector onto a wide screen (80 cm x 108 cm) 80 cm in front of the child. A Geodesic Sensor Net (GSN) 200 was used to record EEG activity (Tucker, 1993; Tucker, Liotti, Potts, Russell & Posner, 1994) with 128/256 (4-5 and 11-12 months / 6 years) sensors evenly distributed on the children's head. To ensure amplification of signals at maximum impedance of 50 kΩ, a high-input EGI amplifier was connected to the net, as recommended for an optimal signal-to-noise ratio (Budai, Contento, Locatelli & Comi, 1995; Ferree, Luu, Russell & Tucker, 2001; Picton et al., 2000). Amplified EEG signals with a sampling rate of 500 Hz were recorded with Net Station software on a Macintosh computer. To control for whether the children were looking at the screen or not, eye tracking was included by using an infrared Tobii X50 camera, with the visual feed processed with Clear View software on an HP computer. Additionally, digital videos were recorded with two cameras positioned at different angles in front to track the children's behavior while looking at the screen. All the recorded data were subsequently stored for off-line analyses.

2.4 Procedure

All the data were collected at the Developmental Neuroscience lab at NTNU in Trondheim. In good time before the test session started, the child arrived at the lab together with his/her parent(s). They were met by the experimenter who carefully informed the parents about everything they needed to know for signing an informed written consent, while the child got used to the laboratory surroundings. In this process, an assistant measured the child's head and soaked an EEG net in a saline electrolyte to optimize electrical conductivity. The net was then gently put on the child's head while the assistant distracted the infant with noise producing toys and soap bubbles in the two first testing sessions. Next, the child was placed in a chair in front of the large screen in the experimental room with a parent on the one side to avoid any stress, and with the experimenter on the other side of the chair to ensure that the child focused sufficiently on the screen. The net was connected to the amplifier, and if the impedance was not satisfying enough, the electrodes were adjusted, or saline electrolyte was added to improve contact. A control room was separated from the experimental room with a transparent glass window where two assistants were responsible for the computers necessary for data acquisition.

The data acquisition was carried out in one block, right after the child's eye movements were calibrated in virtual space. The children were presented with an average of 46 (SD = 6, range = 34-58) looming trials at the first test session, 47 (SD = 9, range = 29-68) at the second test session, and 60 (SD = 14, range = 44-97) at the third test session, not including the reversed looming control condition. The number of trials was equally distributed among the three looming conditions and was presented in random sequential order. The looming experiment, lasting for 4-6 minutes on average, was the second of three visual motion experiments performed by each child during all the three testing sessions. If the child at some point lost interest, the stimulus presentation was paused, and toys were presented to retain the infant's attention in the first and second test session. Whenever the child expressed tiredness or fussiness in any of the three test sessions, the experiment was aborted.

In the third and last test session, after EEG data were collected, the children performed the Movement ABC test (see paragraph 2.5.5) consisting of eight standardized tasks in order to test their motor function. One assistant explained and showed the children how to perform the tasks, while another assistant recorded the performance with a video camera and wrote down the children's test score for the different tasks as well as remarks on their performance.

2.5 Data analysis

For all the three test sessions, analysis of EEG raw data was carried out in the software program BESA (Brain Electrical Source Analysis) version 6.0. As an initial pre-processing step, recordings were segmented with the Net Station software and exported as raw files, followed by a standard channel configuration and digitized head surface points that were added to the raw data for each child. Bad channels and artefact-contaminated trials as a result of head/body movements were removed or interpolated by visual inspection. A maximum limit of channels defined as bad was set to 10%. To remove mainline noise interference in the EEG data, notch filter was set at 50 Hz, the low cut-off filter (high band pass) was set at 1.6 Hz to remove slow drift in data, and high cut-off filter (low band pass) was set at 80 Hz. During the VEP peak selection, the high cut-off filter was changed to 8 Hz, and a reference-free montage showing the EEG data at 27 standard electrodes was used.

2.5.1 VEP responses. To find looming-related peaks, a trial-by-trial investigation was performed on each child's raw EEG recordings. By looking at the reference-free channel distribution, highly prominent VEP peaks were marked at the main occipital and parietal electrodes (Oz and Pz) based on earlier studies investigating VEPs (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; Van der Meer, Svantesson & Van der Weel, 2012). The marked VEP peaks provided information about the looming-related activity at the selected brain regions. Additionally, this could also be visualized by a 3D-mapping of a build-up and decline of voltage activity in the visual cortex. The criteria for selecting looming-related VEP peaks were based on visual inspection of the peaks as well as the 3D-mapping procedure (see Figure 2). Occasionally, when consecutive peaks were observed in one trial, the peak closest to stimulus end and/or showing the best cortical activity in the 3D-mapping was marked and assumed to be more functionally related to the looming stimulus. At the time each VEP peak occurred, the time remaining to stimulus end, or the loom's time-to-collision, was recorded.

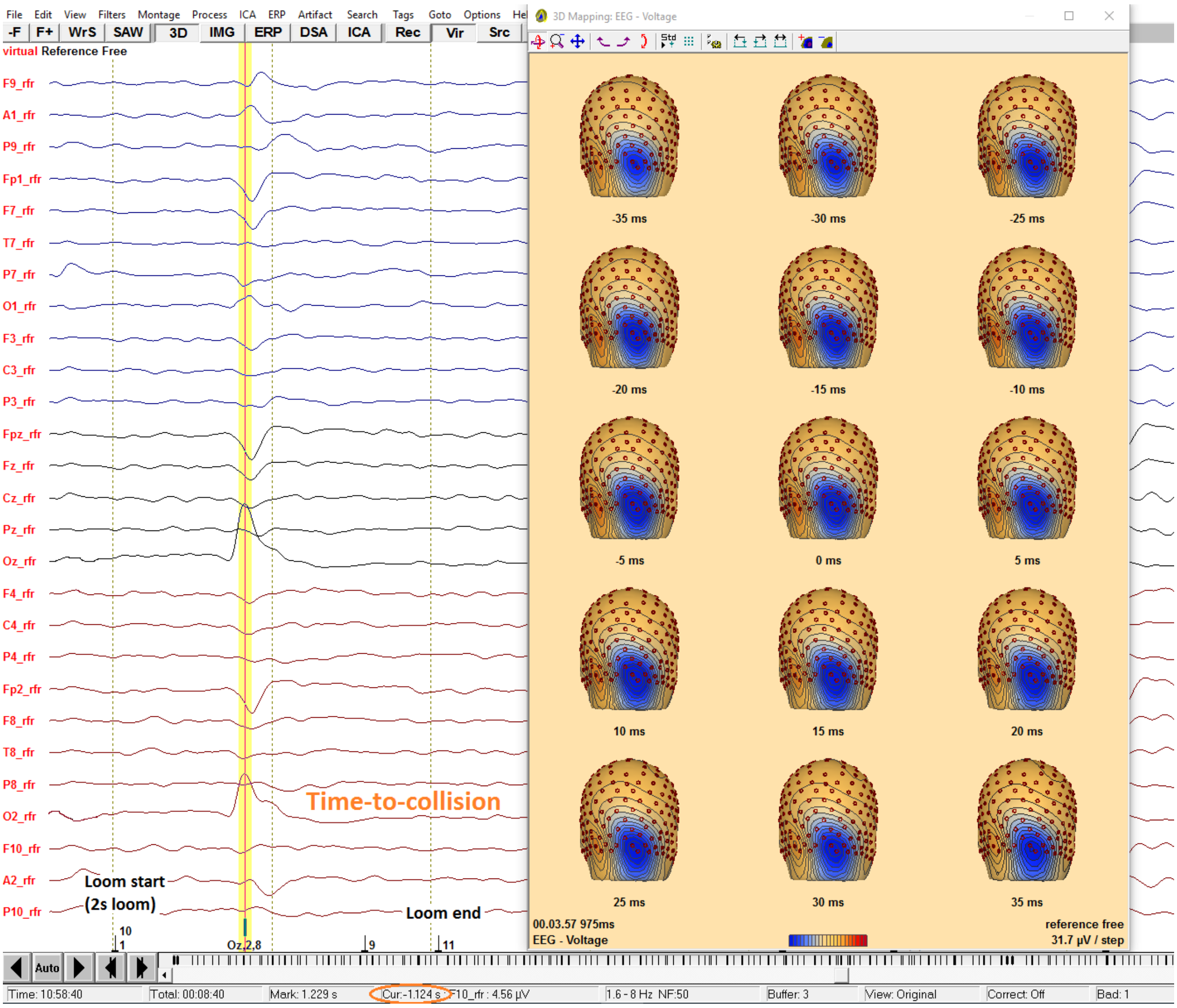

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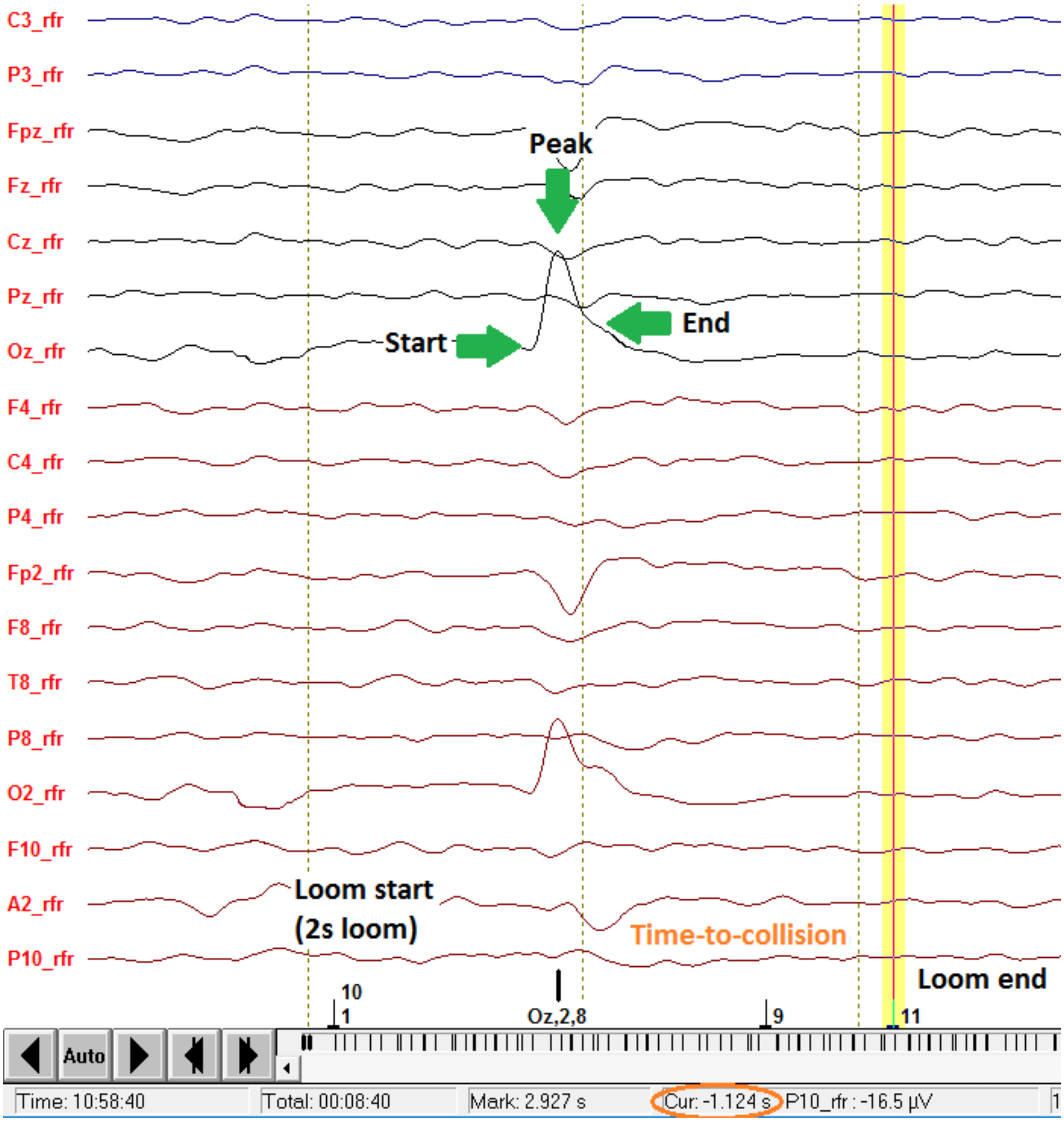
Figure 2. *Raw EEG data illustrating a typical looming-related VEP peak using a standard reference free montage of 27 electrodes. The VEP peak can be seen in electrode Oz (and O2) marked by a vertical yellow line while a 3D voltage map shows high activity in visual cortex. The looming trial lasts for 2 s and the VEP peak is viewed as a direct response to the looming stimulus. Time-to-collision (in this example -1.124 s on the horizontal axis) is measured as the remaining time from top of the VEP peak to loom end.*

2.5.2 VEP duration. In addition to the timing of the VEP peak with respect to the virtual collision, the duration of the looming-related VEP peak response was also measured. The VEP duration was defined by Van der Meer, Svantesson & Van der Weel (2012) as the difference in time between the start and the end of the looming related VEP response: VEP duration = VEPstart – VEPend (see Figure 3).



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Mark: 2.927 s
Cur: -1.124 s
P10_rfr : -16.5 µV

Figure 3. *An example of how the start, peak, and end of the looming-related VEP response in single trials was marked manually in the Oz electrode. The yellow vertical line is aligned with the end of the looming trial, and the time from peak start to peak end (in this example 0.23 s) is measured as VEP duration.*

2.5.3 Timing strategies. How accurate the children are able to time the loom's virtual collision depends on which timing strategy they use. Which strategy they apply depends on which information variable of the looming object they are holding constant across trials. Possible information variables are the loom's velocity, visual angle and time before collision (Kayed & Van der Meer, 2000, 2007). The timing strategies based on the loom's visual angle and time before collision were investigated in the present study.

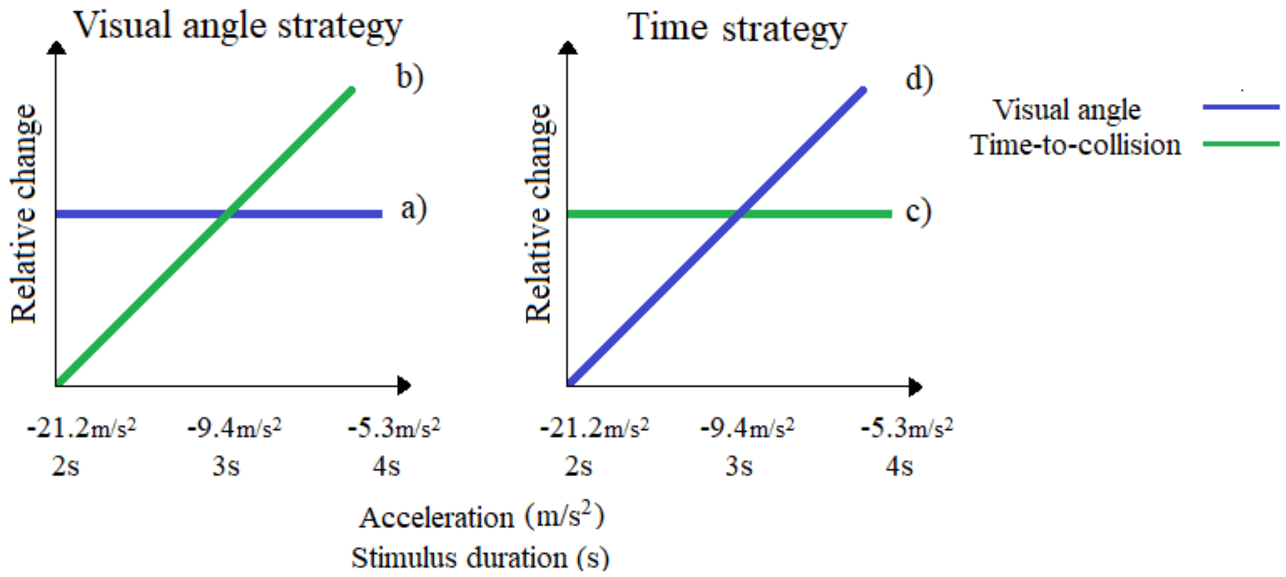

Figure 4. *A theoretical graph of the loom's visual angle and time before collision as a function of the duration and acceleration of the looming sequences. As the acceleration of the loom decreases, the strategies based on different information variables have different implications for the looming-related neuronal responses. A visual angle strategy implies that if the loom's visual angle is held relatively constant (a) and the loom's acceleration decreases, the time before collision will increase (b). A time strategy implies that if the loom's time before collision is held relatively constant (c) and the loom's acceleration decreases, the visual angle will increase (d). For convenience, the lines are drawn as straight lines. The figure is adapted, with permission, from Van der Meer, Svantesson & Van der Weel (2012).*

Children using a strategy based on the loom's visual angle will depend on changes occurring in the angle subtended by the edge of the visual loom. If the loom's visual angle is held relatively constant (Figure 4a) and the loom's acceleration decreases, the time before collision will increase (Figure 4b). If the children use this strategy, they are at risk of under- or overestimating the loom's time-to-collision as the looming object reaches a certain visual angle at different times depending on loom speed. If the children show looming-related VEP responses at different times before collision depending on the three different loom speeds, this would then indicate that they are using the less efficient timing strategy based on the loom's visual angle.

In contrast, children using a time strategy will rely on the loom's time before the virtual collision. If the loom's time before collision is held relatively constant (Figure 4c) and the loom's acceleration decreases, the visual angle at which the looming-related VEP is shown will increase (Figure 4d). This strategy has shown to be more efficient to time the loom's virtual collision (Kayed, Farstad & Van der Meer, 2008; Kayed & Van der Meer, 2000, 2007; Van der Meer, Svantesson & Van der Weel, 2012). If the children show their looming-related VEP responses at a constant time before the virtual collision, irrespective of loom speed, this could indicate that they are using the more efficient timing strategy based on the loom's time before collision.

To see if the children showed their looming-related VEPs at a constant time-to-collision or not, standard deviations across all their looming-related VEPs, independent of loom speed, were investigated.

2.5.4 Time-frequency responses. In order to include only the marked looming-related peaks in the frequency analysis, event-files were made for each infant separately and appended to the raw EEG data. Time-frequency analysis was then performed in brain space using pre-defined multiple source dipoles that modelled activities in the parietal and visual cortex, the main brain regions of interest. To avoid mixed contribution from underlying brain sources, optimal separation of brain activity was achieved by a multiple source montage (Scherg & Berg, 1991; Scherg, Ille, Bornfleth & Berg, 2002). The source montage consisted of 17 sources that modelled activities in the visual pathways as well as any residual activities in other regions of the brain. More precisely, the regional sources of interest were the visual cortex lateral left (VClL), visual cortex radial left (VCrL), and visual cortex radial right (VCrR), as these are believed to be active in the visual processing of motion stimuli (Probst, Plendl, Paulus, Wist & Scherg, 1993; Van der Weel & Van der Meer, 2009; Zeki et al., 1991).

To analyze brain activities using these sources, a 4-shell ellipsoidal head model (Berg & Scherg, 1994; Hoechstetter et al., 2004) was created for each infant and the source dipoles were inserted while the artifact-corrected coordinate files were appended. When analyzing data from the first two test sessions, bone thickness and conductivity were adjusted to 3.0 mm and 0.02 σ, respectively, as recommended for infants, while 5 mm and 0.018 σ, were used in the last test session (Grieve, Emerson, Fifer, Isler, & Stark, 2003; BESA information). Settings for latency, filters, and average parameters used in the VEP analyses were maintained.

The resulting time-frequency displays (TSE plots) represent the change in amplitude over time in the regional sources of interest for each infant separately. Since the focus was on induced oscillatory activity only, averaged evoked response signals were subtracted from the single trial time series before computation of the TSEs. The three looming conditions (2, 3 and 4 s) were combined into one motion condition, and comparisons between the motion condition and a static control condition (blank screen) were then computed. To test for significant differences in the TSEs for each individual child, TSE probability maps with comparisons between the motion condition and the static control condition were computed. Bonferroni procedure was used to correct for multiple testing as described by Simes (1986) and applied to each set of time samples belonging to one frequency bin. In all three test sessions, both the TSE plots and the TSE probability maps were limited between frequency cut-offs of 4-80 Hz, frequency and time sampling were set at 1 Hz and 50 ms, respectively, and epochs were set from -300 to 300 ms.

In addition, probability of significant differences in frequency ranges and amplitude values in the TSE data was investigated. Paired sample t-tests were used to look for differences between the combined motion condition and the static control condition using BESA statistics 1.0 (BESA GmbH). Accordingly, significant time-frequency ranges at group level could be used as a guide when finding patterns of oscillatory activities in each child's individual TSE displays. To address the multiple comparisons problem, a combination of permutation tests and data clustering was employed in the statistical tests. Clusters alpha, which determines the significance level for building clusters in time and/or frequency, was set at $\alpha = 0.005$. Number of permutations was set at 512, while frequency cut-offs, frequency and time sampling, and epochs were the same as stated above.

2.5.5 Movement ABC. To address the children's motor skills, the Movement Assessment Battery for Children (M-ABC) (Henderson & Sugden, 1992) was included in the last test session at age 6. The performance test evaluates the children's motor skills as the child performs a series of motor tasks in a standard way. The test consists of eight tasks grouped under three different headings: Manual Dexterity, Ball Skills, and Static and Dynamic Balance. It takes 20-40 minutes for the child to complete the tasks, where points are given based on their performance. The total score can vary from 0 to 40 points, and a total score over 13.5 indicates clumsiness in the motor domain.

3.0 Results

Prominent visual looming-related VEP peaks were observed in the occipital and parietal areas of the cortex prior to the time the virtual loom would have made contact with the children. However, only data collected from the Oz channel were used for further analysis due to lack of responses in channel Pz in some of the children. On average, each child contributed 16 (SD = 6.4, range = 7-34) trials where looming-related VEPs occurred in the first test session, 15 (SD = 5.8, range = 10-37) in the second test session, and 19 (SD = 9.3, range = 12-37) in the third test session. The VEP peaks were approximately evenly distributed among the three looming conditions and between the full-term and preterm children.

3.1 VEP analyses

The full-term children showed their looming-related VEPs prior to the virtual collision on average -0.86 s (SD = 0.22) at 4-5 months, -0.54 s (SD = 0.14) at 11-12 months, and -0.21 s (SD = 0.07) at 6 years. The preterm children showed their looming-related VEPs on average -1 s (SD = 0.19) at 4-5 months, -1.02 s (SD = 0.12) at 11-12 months, and -0.41 s (SD = 0.16) at 6 years, prior to the virtual collision (see Figure 5).

A 2 (group: full-term vs. preterm) x 3 (age: 4-5 months vs. 11-12 months vs. 6 years) x 3 (loom speed: 2s vs. 3s vs 4s) mixed model analysis of variance was performed on average looming-related peak activation. Bonferroni correction was used to adjust for multiple comparisons. The results showed a three-way interaction effect of age, group and loom speed, $F(4, 162) = 2.60$, $p < 0.05$, indicating that the full-term children with increasing age showed their looming-related brain responses significantly closer to collision, while the preterm children only significantly reduced their time-to-collision from 11-12 months to 6 years. No significant difference was found between the three loom speeds, except in the full-term children at 4-5 months. As evident in Figure 5, the full-term children at 6 years displayed the most similar time-to-collision for looming-related VEPs across loom speeds, and with the lowest standard deviations.

The results also revealed a two-way interaction effect of age and group, $F(2, 162) = 23.01$, $p < 0.001$. This indicates that the full-term children, irrespective of loom speed, showed their looming-related VEPs closer to collision compared to the preterm children, at both 11-12 months and at 6 years. An additional two-way interaction effect was found for age and loom speed. However, since the main purpose of this study was to investigate the differences between full-term and preterm children, shared effects were not subjected to further analyses. Moreover, the results revealed significant main effects of age, loom speed, and group, but these effects are likely to have been caused by the underlying three-way and two-way interaction effects.

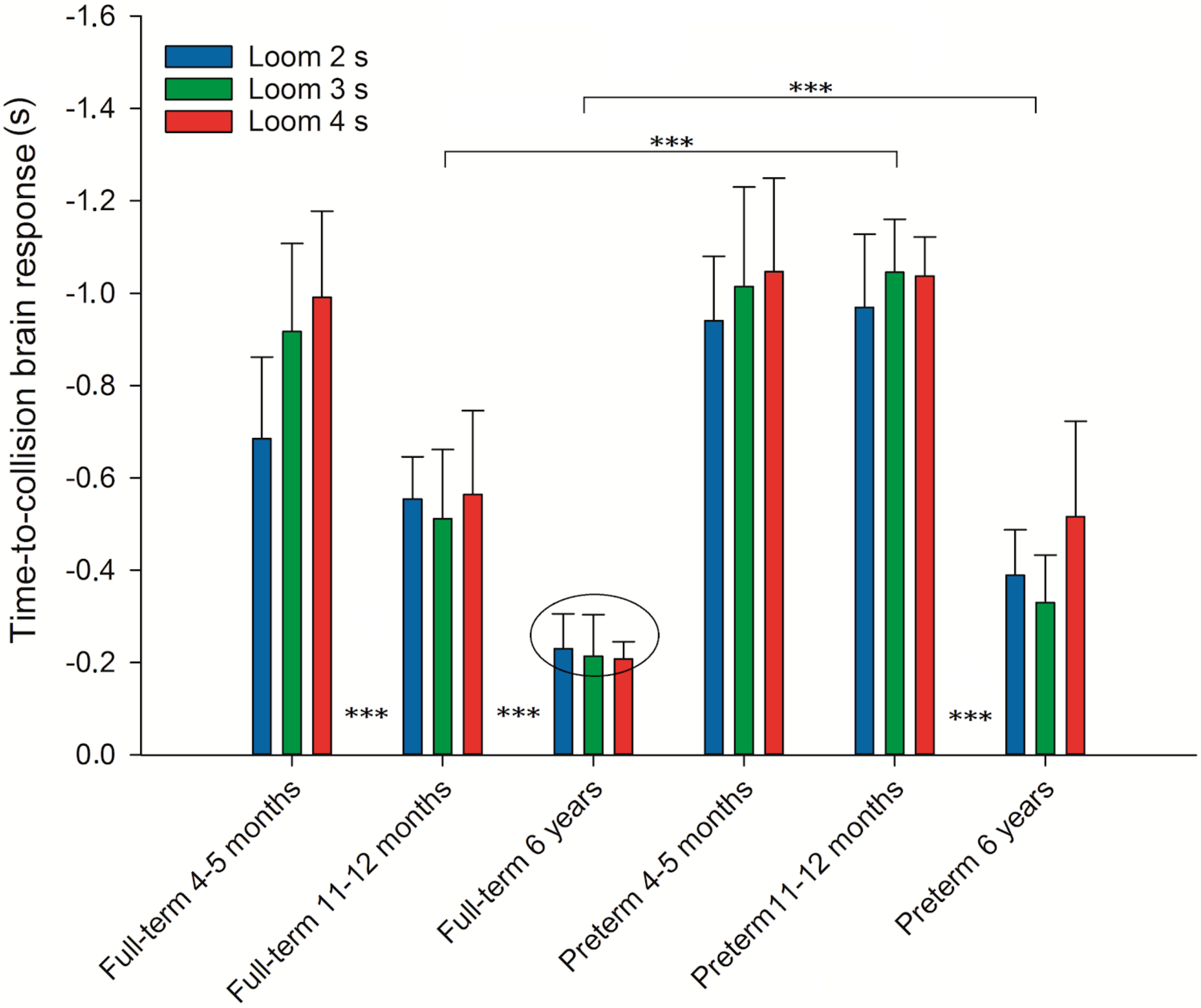

Figure 5. *Average time-to-collision for looming-related VEP peak activation (s) (including standard deviations) in the Oz electrode for the three loom speeds for both full-term and preterm children at the ages of 4-5 months, 11-12 months, and 6 years. ***significant at* $p < 0.001$*. The full-term children significantly reduced their values of time-to-collision from 4-5 months to 11-12 months and to 6 years, while the preterm children only reduced the time-to-collision at which their looming-related VEP occurred from 11-12 months to 6 years. At the age of 11-12 months and 6 years, the full-term children showed their VEPs at a significantly shorter time-to-collision compared to the preterm children. No significant difference in time-to-collision was found between the three loom speeds, except in the full-term children at 4-5 months, and is consistent with the use of a visual angle strategy. Note that the full-term children at 6 years displayed their looming-related VEPs at the most similar time-to-collision across loom speeds and with the smallest standard deviations.*

3.2 VEP duration

The average VEP duration (VEP_{start} – VEP_{end}) for looming-related peaks in the Oz electrode for the full-term children was 0.23 s (SD = 0.03) at 4-5 months, 0.20 s (SD = 0.02) at 11-12 months, and 0.17 s (SD = 0.02) at 6 years. For the preterm children, the average VEP duration for looming-related peaks in the Oz electrode was 0.22 s (SD = 0.02) at 4-5 months, 0.23 s (SD = 0.03) at 11-12 months, and 0.19 s (SD = 0.03) at 6 years (see Figure 6).

A 2 (group) x 3 (age) x 3 (loom speed) mixed model analysis of variance was performed on VEP duration. The results showed a two-way interaction effect of age and group, $F(2, 162) = 13.19$, $p < 0.001$, indicating that the full-term children significantly decreased their average VEP duration from 4-5 months to 11-12 months, and from 11-12 months to 6 years, while preterm children only decreased their VEP duration from 11-12 months to 6 years. The results also revealed significantly shorter average VEP duration for full-term compared to preterm children at both 11-12 months and at 6 years, irrespective of loom speed.

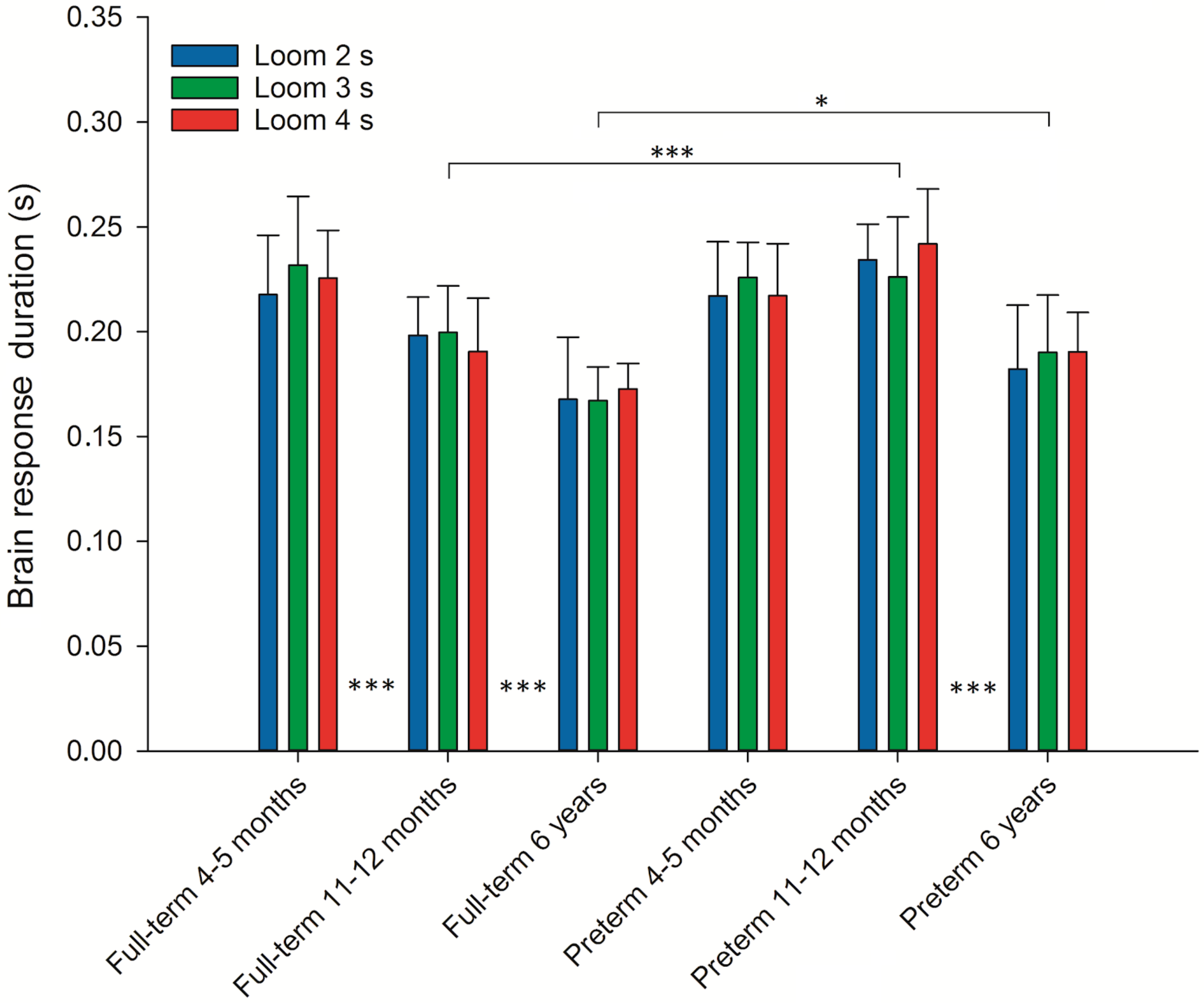

Figure 6. *Average VEP duration (VEP$_{start}$ – VEP$_{end}$) in the Oz electrode for looming-related VEP peaks (s) (including standard deviations) for the three loom speeds at the age of 4-5 months, 11-12 months, and 6 years for both full-term and preterm children. * significant at p < 0.05 and ***significant at p < 0.001. The average VEP duration significantly decreased with age for all three test sessions for the full-term children, but only from 11-12 months to 6 years for preterm children. Additionally, the full-term children showed significantly shorter VEP durations compared to the preterm children at both 11-12 months and 6 years.*

3.3 Timing strategies

In the analysis of looming-related VEP responses (see paragraph 3.1), full-term children reduced their time-to-collision with faster approaching looms at the age of 4-5 months. This response pattern is consistent with the use of a visual angle strategy. The same tendency was also evident for preterm children at 4-5 months, however this was not significant. Neither significant differences between the three loom speeds were found in full-term or preterm children at 11-12 months and 6 years. To further investigate differences between full-term and preterm children's variance in time-to-collision in the last two test sessions, standard deviations (SD) across all VEP responses independent of loom speed were analyzed. One tailed t-tests between full-term and preterm children at both 11-12 months, $t(18) = 1.85$, $p < .05$, and at 6 years, $t(12) = 2.31$, $p < .05$, showed significant differences in SD. This indicates that the full-term children showed looming-related VEPs at a more constant time-to-collision independent of loom speed compared to the preterm children at both test sessions.

Due to more variance in the preterm compared to full-term children's time-to-collision at 11-12 months and 6 years, individual SDs were further investigated to see if any of the preterm children used the less efficient timing strategy based on the loom's visual angle. As formulated by Field (2013), an outlier value can be defined as a value larger or smaller than the Mean +/- SD * 2.5. A large SD indicates that the looming-related VEPs occur at time-to-collision values more distant from the mean and therefore less likely at a constant time before collision. This could indicate use of a visual angle strategy if the children decrease their VEPs time-to-collision with increasing loom speed. In contrast, a low SD for a particular child means that it is responding at a relatively constant time-to-collision irrespective of loom speed, indicating use of the more efficient time-strategy.

Table 1 shows SD of all VEPs independent of loom speed for each child. Mean + SD * 2.5 was then calculated for the full-term children, and the preterm children having a SD above these criterion values were marked in yellow (see Table 1). At 11-12 months, the criterion based on the full-term children's SD resulted in 0.36. The preterm children fulfilling the criterion were AT and MS which stood out with extremely high SDs, while SK had a SD right under the criterion. At 6 years, the criterion based on the full-term children's SDs resulted in 0.29, where the preterm children AT, MS and SK stood out with extremely high SDs. When looking closer at these three children's mean time-to-collision for every loom speed, all three showed decreased time-to-collision with increasing loom speed at 11-12 months, consistent with a visual angle strategy. The same goes for two out of three children at 6 years, while the last child seemed to be about to shift from a visual angle strategy to a time strategy as he/she showed shortest time-to-collision for 3s loom and longest for 4s loom.

Table 1. Individual analysis of standard deviation in 11-12 months and 6-year-old children. *Standard deviation across all looming-related VEP responses independent of loom speed for both full-term and preterm children at 11-12 months and 6 years. The highlighted numbers show the preterm children with a standard deviation greater than the full-terms' Mean + SD * 2.5. The preterm children AT and MS at 11-12 months and AT, MS and SK at 6 years, showed unusually high standard deviations indicating great variation in their time-to-collision across the three loom speeds. Note that SK are right under the criterion at 11-12 months as well.*

11- to 12-month-old children				6-year-old children			
Full-term		**Preterm**		**Full-term**		**Preterm**	
VE	0.26	**AT**	0.36	**VE**	0.15	**AT**	0.31
SN	0.18	**DT**	0.29	**SN**	0.19	**DT**	0.21
ST	0.27	**EL**	0.34	**ST**	0.27	**EL**	0.26
LS	0.28	**MS**	0.38	**LS**	0.16	**MS**	0.49
GE	0.25	**SK**	0.35	**GE**	0.19	**SK**	0.52
JY	0.31	**TA**	0.30	**JY**	0.15	**TA**	0.15
BE	0.27	**WM**	0.28	**BE**	0.21	**WM**	0.27
SE	0.28	**MA**	0.25				
BK	0.20	**TU**	0.30				
ME	0.32	**DK**	0.19				
Mean	0.26			**Mean**	0.19		
SD	0.04			**SD**	0.04		
Mean + SD * 2.5 = 0.36				**Mean + SD * 2.5** = 0.29			

3.4 Time-frequency analyses

Figure 7 shows the results of the permutation test that presents the average of all children in each group at the three different test sessions when TSEs of the combined looming motion, including all three loom speeds, were compared with a static control condition (blank screen). The permutation test showed significant negative clusters (suggesting significantly smaller values in the motion condition than the static control condition) in every session for both full-term and preterm children in at least one of the three visual areas of interest VClL, VCrL or VCrR.

The permutation test revealed that the full-term children at 4-5 months (see Figure 7a) showed alpha- and theta-band activity. When they had reached 11-12 months (see Figure 7b), the frequencies increased, and the activity could then be observed in late beta- and early gamma-band range, while they at 6 years (see Figure 7c) showed more prominent beta-, but mostly gamma-band activity. In addition, the activity occurred over gradually shorter periods of time with increasing age for the full-term children. The preterm children, on the other hand, did not show the same developmental trend, since beta-band activity is observed at 4-5 months (see Figure 7d), alpha- and beta-band activity at 11-12 months (see Figure 7e), and alpha- and some theta-band activity at 6 years (see Figure 7f). Nor did they show oscillatory activity in gradually shorter periods of time with increasing age.

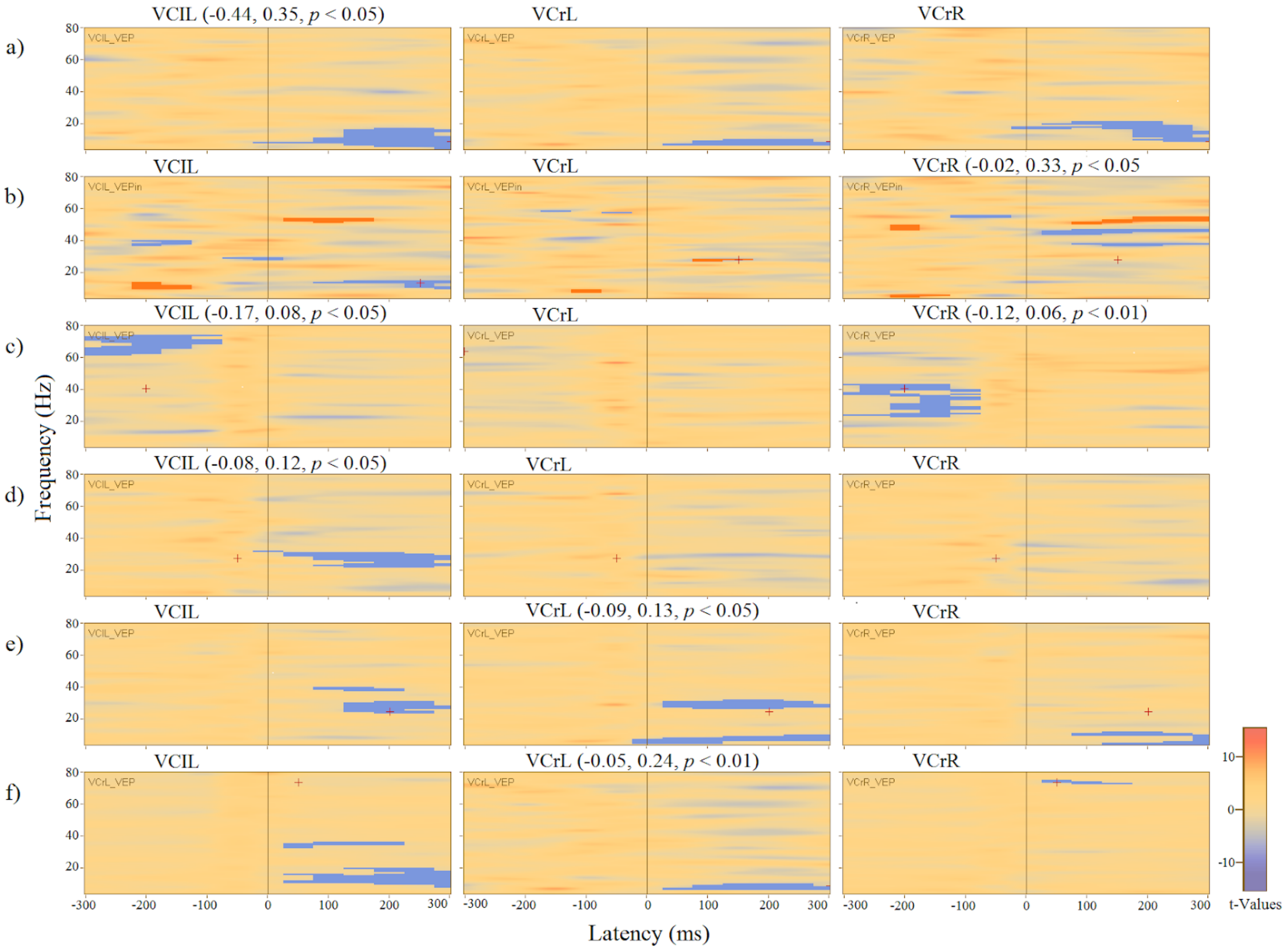

Figure 7. *Average visualization of significant data clusters in the visual sources of interest when looming was compared with a static control condition in full-term children at 4-5 months (a), 11-12 months (b), and at 6 years (c), and in preterm children at 4-5 months (d), 11-12 months (e), and at 6 years (f). Epoch is from -300 ms to 300 ms, and the vertical red line marks the top of the looming-related VEP peak. Red colors represent positive clusters (i.e., larger t-values for the motion condition than the static condition), while blue colors indicate negative clusters (i.e., smaller t-values for the motion condition than the static condition). In parentheses are the respective cluster means for the motion condition written on the left, cluster means for the static condition in the middle, and the probability level at which the specified cluster is significant written on the right. Mark that this information is only given for the significant clusters.*

As illustrated in Figure 8, individual TSE plots (a, c, e) for full-term children and matching TSE probability maps (b, d, f) correspond largely with the results from the permutation test (see Figure 7). When comparing the motion condition with the static control condition, the full-term children at 4-5 months individually showed activity in theta- and alpha-band range (a, b). At 11-12 months, activity could be observed in beta- and early gamma-band range (c, d), while at 6 years the activity was prevalent mainly in the gamma-band range (e, f). These activities appeared as desynchronized oscillations in at least one of the three visual areas of interest. See Appendix A for another illustration of full-term children's TSE plots and TSE probability maps.

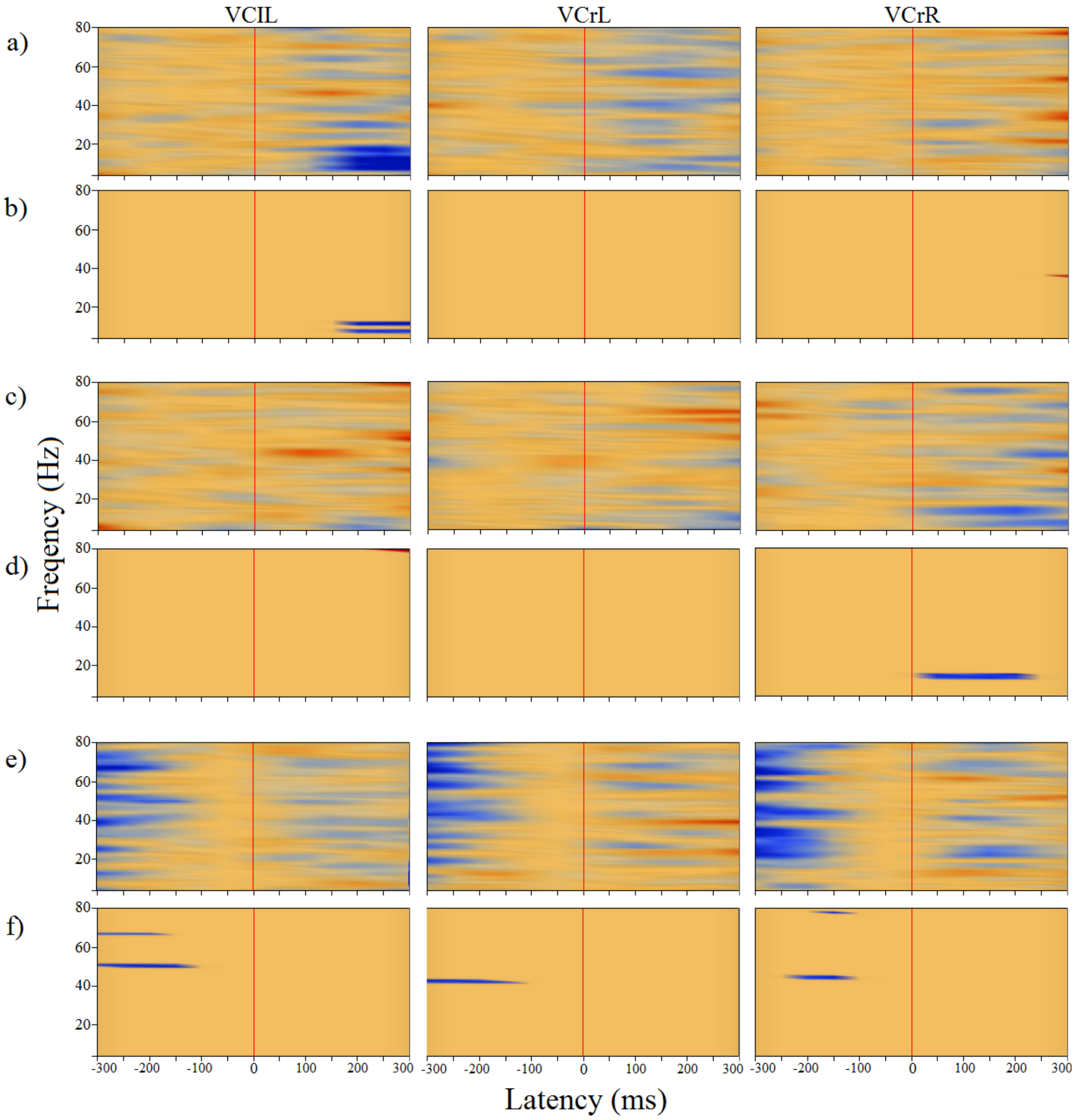

Figure 8. *TSE plots (a, c, e) and corresponding TSE probability maps (b, d, f) across brain regions of interest (VClL, VCrL, VCrR) when the motion condition was compared with the static control condition in typical full-term children at 4-5 months (a, b), 11-12 months (c, d) and at 6 years (e, f). Epochs from -300 ms to 300 ms, and the vertical red line marks the top of the looming-related VEP peak. In the TSE plots, red colored contours indicate increased spectral amplitude or induced synchronized activity, while blue colored contours represent decreased spectral amplitude or induced desynchronized activity. In the TSE probability maps, the red voxel marks show significant increase while the blue voxel marks show significant decrease of TSEs ($p < 0.05$) in the motion condition compared to the static control condition.*

In the individual TSE plots and matching TSE probability maps, more scattered activity was found over all three test sessions for the preterm children compared to the full-term children. See Figure 9 for illustration of typical preterm children's individual TSE plots (a, c, e) and matching TSE probability maps (b, d, f). When focusing on the same locations as the significant clusters in the permutation test (see Figure 7), the preterm children showed most activity in the beta-band range at 4-5 months (a, b), some modest beta-band activity but mostly alpha- band activity at 11-12 months (c, d), and primary alpha-band activity at 6 years (e, f). Virtually no gamma-band activity could be seen in any of the test sessions for the preterm children. The observed activities appeared as desynchronized oscillations in at least one of the three visual areas of interest when focusing on the same locations as the significant clusters in the permutation test. See Appendix B for another illustration of preterm children's TSE plots and TSE probability maps.

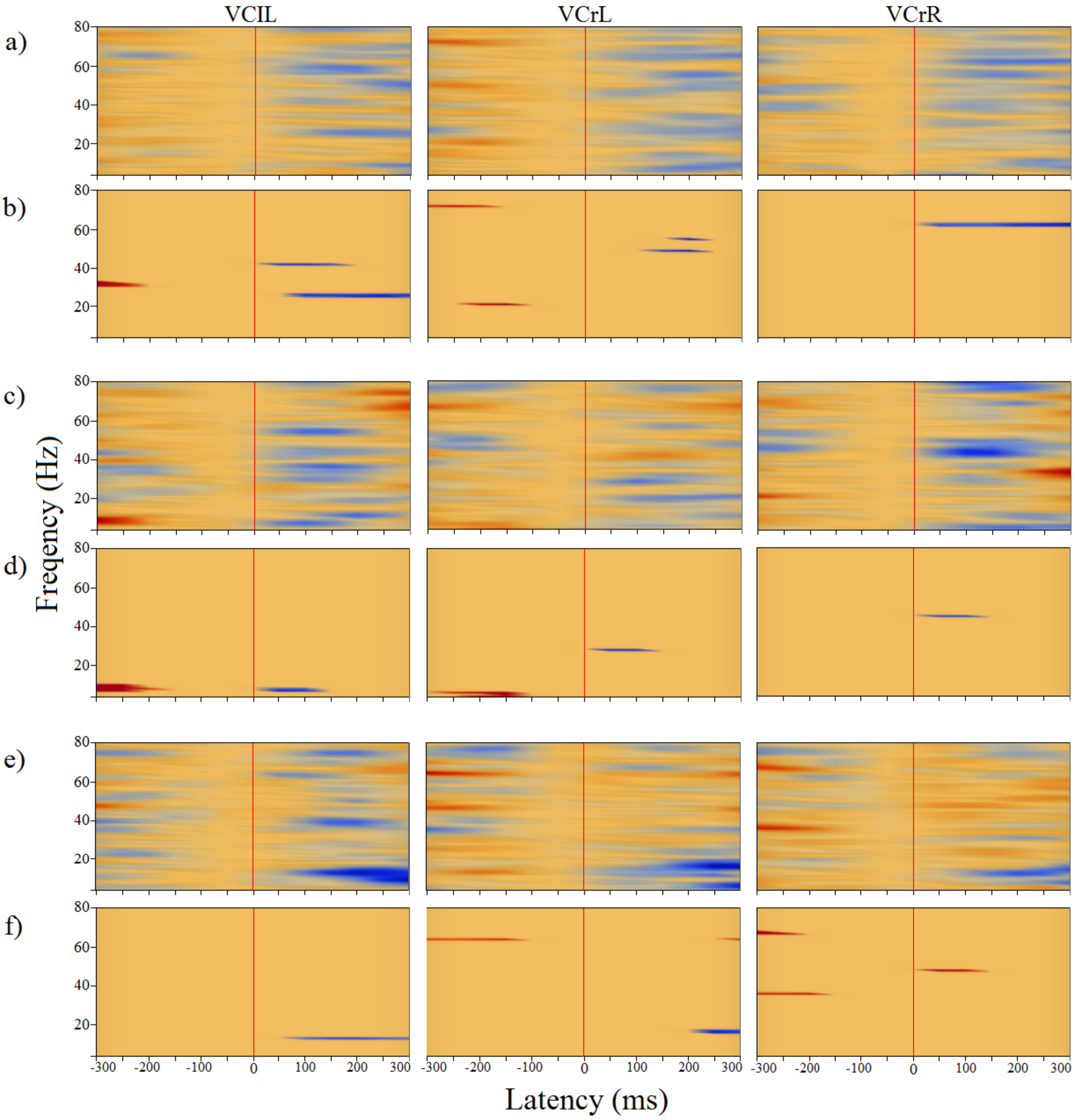

Figure 9. *TSE plots (a, c, e) and corresponding TSE probability maps (b, d, f) across brain regions of interest (VClL, VCrL, VCrR) when looming was compared with the static control condition in typical preterm children at 4-5 months (a, b), 11-12 months (c, d), and at 6 years (e, f). Epoch is from -300 ms to 300 ms, and the vertical red line marks the top of the looming-related VEP peak. In the TSE plots, red colored contours indicate increased spectral amplitude or induced synchronized activity, while blue colored contours represent decreased spectral amplitude or induced desynchronized activity. In the TSE probability maps, the red voxel marks show significant increase while the blue voxel marks show significant decrease of TSEs ($p < 0.05$) in the motion condition compared to the static control condition.*

3.5 Movement ABC

Table 2 shows each child's total score from the Movement ABC test. One full-term (VE) child and one preterm child (DT) had a total score above 13.5 (highlighted in Table 2), which indicates clumsiness in the motor domain.

Table 2. Individual score from the Movement ABC test. *Full-term and preterm children's total M-ABC scores. The full-term child VE and the premature child DT had scores above 13.5, highlighted in yellow.*

Full-term	Total score	Preterm	Total score
VE	14	**AT**	5.5
SN	12	**DT**	21
ST	8	**EL**	13
LS	10	**MS**	2
GE	0	**SK**	4
JY	5	**TA**	4
BE	6	**WM**	3.5

4.0 Discussion

In the present longitudinal study, high-density EEG was used to investigate developmental differences between full-term and preterm children when perceiving looming visual motion. The children were tested at 4-5 months, 11-12 months, and at 6 years of age. Analyses of evoked brain activity (VEP) were performed to see when the children displayed their looming-related VEPs in response to virtual looms approaching on a collision course. Further analyses were performed on the VEP duration, and which timing strategy the children used to time their VEPs to different loom speeds. Analyses of induced brain activity (TSE) were carried out as well in order to investigate event-related time-frequency responses. In line with the hypotheses, significant differences were observed between the full-term and preterm children when perceiving looming visual motion. While the full-term children showed significantly improved timing of brain responses with increasing age, the same developmental trend could not be found in the preterm children. Taken together, this study indicate that preterm children may have impaired visual motion perception, and do not show the same developmental trend as their full-term peers.

The VEP analysis revealed a significant decrease in time-to-collision when the average looming-related response occurred during the looming sequence with increasing age in the full-term children. The fact that the brain responses occur closer to the upcoming collision can be explained by the gradually more specialized nervous system during the first 6 years of life. As theorized by Johnson (2000), neuronal pathways are unspecialized at birth, leading to activation in several pathways when infants are engaged by task situations. Consequently, young infants' response actions are often directed after the first available brain pathway, especially when the task is challenging or complex. This will result in a large proportion of incorrect responses, while increased age and experience will lead to specialized brain pathways where an appropriate pathway is activated in response to a given task or stimulus. This will then result in more precisely timed responses (Johnson, 2000), as observed in the full-term children showing their VEPs closer to collision with increasing age.

In contrast, the preterm children only showed their looming-related response closer to collision from 11-12 months to 6 years. This could indicate that the preterm infants do not show the same developmental pattern with gradually more specialized pathways as term born infants do during the first year of life. These finding are in line with earlier studies investigating development of visual motion perception in infants born preterm (Agyei, Van der Weel & Van der Meer, 2016b). The absence of improvement could indicate a lack of pathway specialization which can reflect on behavior through varying and suboptimal responses (Johnson, 2000). Despite the finding that preterm children decreased their time-to-collision from 11-12 months to 6 years, they still showed a larger time-to-collision than their full-term peers at both test sessions. This could indicate that the preterm children at 6 years do not follow the same developmental trend as their full-term peers.

In addition to showing looming-related VEPs later in the looming sequence with increasing age, the full-term children also showed gradually shorter VEP durations with increasing age. Shorter brain responses with increasing age during infancy is in line with results from earlier studies (Van der Meer, Svantesson & Van der Weel, 2012; Van der Weel & Van der Meer, 2009). Several underlying mechanisms can explain this developmental trend, where myelination of axons is considered especially important for more efficient cortical processing (Grieve, Emerson, Fifer, Isler, & Stark, 2003; Webb, Long & Nelson, 2005).

Cerebral damage, particularly in white matter essential for neural connectivity between brain areas, has been associated with deficits in visual and visuocognitive development (Atkinson & Braddick, 2012). In line with the fact that preterm birth may disrupt normal brain development (Birtles, Braddick, Wattam-Bell, Wilkinson & Atkinson, 2007; Hammarrenger et al., 2003; Hammarrenger et al., 2007) it was expected that the preterm children would not show the same decrease in VEP duration with increasing age as the full-term children. This was confirmed as the preterm children only decreased their VEP duration from 11-12 months to 6 years, and had longer VEP duration compared to their full-term peers at both 11-12 months and 6 years. This is in line with their developmental trend found in their looming-related VEPs time-to-collision, and could reflect less white matter in the preterm brain.

The preterm children falling behind compared to the full-term children who are showing a clear developmental trend with increasing age, was further emphasized in the time-frequency analysis of induced brain activity (TSE). When comparing the combined looming condition with the control condition, desynchronized brain activity could be observed in significantly higher frequency-bands with increasing age in the full-term children. The preterm children, however, did not show the same developmental trend as they showed desynchronized brain activity in approximately the same frequency-bands during all three test sessions. In the TSEs, brain activity could be observed for gradually shorter periods of time with increasing age in the full-term children, while the preterm children did not show such an improvement. A gradual decrease in response duration with increasing age is in line with earlier studies (Langrová, Kuba, Kremláček, Kubová & Vít, 2006; Van der Weel & Van der Meer, 2009), and is assumed to be caused by synaptic maturation and myelination (Grieve, Emerson, Fifer, Isler, & Stark, 2003; Webb, Long & Nelson, 2005).

Considered as a general sign of immaturity in infancy, the observed brain activity in the theta-band range (4-7 Hz) in full-term children at 4-5 months is in line with earlier studies where brain activity in infants is found to be dominated by low frequency activity (Agyei, Holth, Van der Weel & Van der Meer, 2015; Agyei, Van der Weel & Van der Meer; 2016b; Orekhova, Stroganova, Posikera & Elam, 2006; Thierry, 2005; Pfurtscheller, Neuper & Mohl, 1994; Van der Meer, Fallet & Van der Weel, 2008; Van der Weel & Van der Meer, 2009). The characteristics of oscillatory networks depend on the networks' structure and delay in neuronal interactions, where a huge number of unconnected neurons and dendritic spines are prevalent in infants (Huttenlocher, 1990; Webb, Long & Nelson, 2005), essential for adaptation and plasticity of the immature brain. As theta-band rhythms are found to be related to successful encoding of memory (Khader, Jost, Ranganath & Rösler, 2010), the more widespread theta-band activity observed in the youngest full-term infants could reflect involvement of larger and less specialized neuronal networks, and formation of cortical synapses during perception of visual motion.

Higher amplitude values in alpha- (7-13 Hz) and beta-band (13-30 Hz) frequencies were further observed in the full-term children at 11-12 months. Activity in alpha frequency has been found to be important for memory consolidation (Suzuki et al., 2012) while activity in beta frequency is thought to be vital for visual motion perception (Carmeli, Knyazeva, Innocenti & De Feo, 2005; Van der Meer, Fallet & Van der Weel, 2008). In addition, both alpha and beta seem to be essential for spatial attention (Foster, Sutterer, Serences, Vogel & Awh, 2017; Wróbel, 2000), as well as for within-network connectivity and cross-network connectivity (Ganzetti & Mantini, 2013). The observation of alpha- and beta-frequencies could therefore indicate the emergence of more specialized neuronal networks in the visual areas and the use of higher cortical structures when processing visual motion in the full-term children (Agyei, Holt, Van der Weel & Van der Meer, 2015; Agyei, Van der Meer & Van der Weel, 2016b).

When the children were 6 years old, mainly gamma-band frequency (30-150 Hz) could be observed in the full-term children. The faster gamma-band frequency has shown to be a more advantageous way of establishing rapid couplings between cell assemblies essential for more specific and restricted information processing (Fries, 2005). Furthermore, gamma-frequency have also been linked to memory (Herrmann, Munk, & Engel, 2004; Jensen, Kaiser & Lachaux, 2007), attention (Jensen, Kaiser & Lachaux, 2007), and especially to feature binding processes (Herrmann, Fründ & Lenz, 2010). As gamma-frequency have been observed in adult participants processing visual motion (Hoogenboom, Schoffelen, Oostenveld, Parkes & Fries, 2006; Krishnan, Skosnik, Vohs, Busey & O'Donnell, 2005), it could indicate that full-term children at 6 years, have developed adult-like specialized neuronal networks tuned to more efficiently process looming visual motion.

The number of neurons firing in synchrony are found to be proportional to the amplitude of oscillations where faster oscillating cell assemblies contain less neurons than slowly oscillating cell assemblies (Pfurtscheller & Klimesch, 1992; Pfurtscheller & Lopes da Silva, 1999; Singer, 1993). The gradually increased frequency observed in the brain activity in response to visual looming could therefore indicate a progression to a more adult-like pattern where cell assemblies consist of fewer, more specialized and myelinated neurons in the full-term children. The preterm children on the other hand, did not show the same developmental pattern as the permutation test revealed beta-band frequency at 4-5 months, alpha- and beta-band frequencies at 11-12 months, and alpha- and theta-band frequencies at 6 years. No prominent gamma-band frequency in the preterm children's permutation test could be observed. In addition, the TSE plots and TSE probability maps showed scattered activity in different frequency bands within subjects, and great variation in activity between subjects. The great variation within the preterm groups makes it difficult to draw any firm conclusion. However, the fact that the preterm children in general showed more scattered activity in lower frequency bands could indicate slower cortical growth and lack of less specialized neuronal networks tuned to rapidly process looming visual motion.

As changes in visual perception during first year of life have been found to occur at the same time as infants start crawling, it has been suggested that a developmental trend could partially be due to increased locomotor experience (Agyei, Holt, Van der Weel & Van der Meer, 2015; Agyei, Van der Weel & Van der Meer, 2016b; Van der Meer, Svantesson & Van der Weel, 2012; Van der Weel & Van der Meer, 2009). This is in line with the notion that only self-generated locomotion helps the interaction between perception and action in the developing brain (James & Swain, 2011). While the infants at 4-5 months in the present study only had experience from being carried around, the infants at 11-12 months had started moving on their own. Consequently, the improved perception of looming visual motion observed in the full-term children with increasing age could partially be due to self-generated locomotion. However, the preterm children had the same experience with locomotion as the full-term children at the first and second test session, stressing the importance of both brain maturation and experience with self-produced locomotion for optimal development (Kayed, Farstad & Van der Meer, 2008).

The poorer development of visual motion perception observed in the preterm children compared to the full-term children are nevertheless mainly thought to be due to dorsal visual stream vulnerability associated with preterm birth (Birtles, Braddick, Wattam-Bell, Wilkinson & Atkinson, 2007; Hammarrenger et al. 2003; Hammarrenger et al. 2007). Since the dorsal visual stream has been found to develop in late prenatal and early postnatal life (Hammarrenger et al., 2007), this development may be disrupted by preterm birth, thus reducing specialization of neurons and their respective fibers (Hüppi et al., 1998; Kapellou et al., 2006; Mewes et al., 2006). Slower cortical growth in preterm children has also been suggested in other studies investigating the development of visual motion perception during the first year of life (Agyei, Van der Weel & Van der Meer, 2016a; Agyei, Van der Weel & Van der Meer, 2016b; Kapellou et al., 2006). Disruption of the dorsal visual stream and impeded efficient cortical growth in the preterm children could have contributed to the absence of gamma-band frequencies, lack of decreased time-to-collision in looming-related VEP responses, and modest decrease in VEP duration with increasing age. However, delayed development in preterm children has also been suggested to gradually decline with increasing age (Tremblay et al., 2014). The preterm children in the present study performed worse than the full-term controls at 6 years of age, however, they did show a significant improvement in perception of looming visual motion from 11-12 months to 6 years. It is therefore possible that the preterm children with increasing age will eventually catch up with their full-term peers.

Visual motion perception, and especially the ability to correctly respond to an imminent collision, are essential for prospective control, the ability to plan and perform movements to changing surroundings (Lee, 1993). In the present study, it was found that both full-term and preterm children at 4-5 months tended to show their looming-related VEPs closer to collision for faster approaching looms. This could indicate use of the less efficient timing strategy based on the loom's visual angle, found to be more prone to miscalculations (Kayed & Van der Meer, 2007). Smaller differences in time-to-collision between the three loom speeds were observed at 11-12 months and 6 years. However, investigation of standard deviations (SD) across all VEP responses independent of loom speed, showed more variance in the preterm compared to the full-term children's time-to-collision. Low SDs observed in the full-term children indicates that the children are responding at a relatively constant time-to-collision irrespective of loom speed. This is attributed to use of the more efficient timing-strategy based on the looms time away from collision leading to more accurate responses to the imminent collision (Van der Meer, Svantesson & Van der Weel, 2012). A shift from the less efficient visual angle strategy to the more efficient time strategy has been reported in earlier studies around 6 months of age (Kayed & Van der Meer, 2000, 2007). As the full-term children in the present study seemed to implement this shift between the ages of 4-5 months and 11-12 months, it could indicate increased accuracy of visual motion processing and development of prospective control (Kayed & Van der Meer, 2009; Van der Meer, Svantesson & Van der Weel, 2012).

Further investigation of individual SDs across loom speeds revealed that the same three preterm children showed highest SDs at both 11-12 months and at 6 years. When looking closer at the children's mean time-to-collision for each loom speed separately, it was clear that the they mostly showed their looming-related VEPs closer to collision for faster approaching looms. This could indicate that they still used the less efficient timing strategy based on the loom's visual angle, a strategy that is more prone to error. Earlier studies have also found some preterm infants not being able to shift from a less efficient timing strategy to a more efficient one (Kayed, Farstad & Van der Meer, 2008; Kayed & Van der Meer, 2009). Inability to shift strategy has been suggested to indicate lack of flexibility to properly adjust to the changing surroundings, and as an early sign of perceptuo-motor problems (Kayed, Farstad & Van der Meer, 2008; Kayed & Van der Meer, 2009).

Problems with visual motion perception prevalent in preterm children have been linked to reduced motor abilities (Braddick, Atkinson & Wattam-Bell, 2003; Van Braeckel et al., 2008). Earlier studies have found that preterm children at different ages perform worse compared to their full-term peers on different motor tasks (De Rose et al., 2013; Foulder-Hughes & Cooke, 2003a; Griffiths et al., 2017), while others have found no difference between full-term and preterm children's motor performance (Cserjesi et al., 2012). Despite clear developmental differences in perception of looming visual motion between full-term and preterm children in this study, no differences in performance on the M-ABC could be observed. The individual analyses of the children's performance on the M-ABC revealed that one child from each group stood out with scores above 13.5, which indicates clumsiness in the motor domain (Henderson & Sugden, 1992). For consideration, the full-term child with a score above 13.5 had just reached 7 years in the third test session and therefore performed a more challenging version of the test, which could explain the high test score.

Furthermore, others have argued that M-ABC does not differentiate well between high- and low-risk individuals (e.g., Aanondsen et al., 2007). Jongmans, Mercuri, de Vries, Dubowitz and Henderson (1997) have proposed that M-ABC should be combined with other measurements when testing motor functioning as only low correlations have been found between the test and other similar measurements, indicating that it does not examine all the aspects of the motor domain. Nevertheless, with the purpose of detecting mild to moderate movement difficulties in children, the M-ABC is thought to be one of the most widely used standardized assessment tests (Barnett & Henderson, 1998). If one assumes that the M-ABC can detect differences in motor functioning between full-term children and preterm children without neurological deficits or extremely low birth weight, the lack of group differences in this study could be due to increased support for preterm children. In line with advanced neonatal medical care in combination with better follow-up, the literature supports the notion that preterm children born after 2000 have better outcomes compared to earlier generations (Baron & Rey-Casserly, 2010). It has also been reported that preterm children often benefit from specialized resources (Marlow, Wolke, Bracewell & Samara, 2005). For instance, four out of seven preterm children tested at all three sessions in the present study received help from physiotherapy. This could be one possible explanation for the small differences between the full-term and preterm children's performance on the M-ABC.

The present study provides new insight into the development of visual motion perception from infancy to school age in both full-term and preterm children. However, some limitations have to be considered. For instance, the total sample size was relatively low, and the preterm group was not entirely homogeneous. Five children were born moderately preterm and five very preterm, where one had normal birth weight, four had low birth weight, and five had very low birth weight. Furthermore, follow-up of the participants in a longitudinal study can be challenging, especially over a period of six years. Unfortunately, two of the participants had not reached the age of 6 years when collecting data for the last test session and one refused to wear the EEG net, leading to the loss of three out of ten preterm participants in the last test session. Considering these limitations, future studies should address development of visual motion perception in a larger and more homogenous group of preterm children. It would also be of great interest to assess whether the observed differences persist into adolescence and early adulthood.

The current longitudinal study is the first to investigate perception of looming visual motion in full-term and preterm children from infancy to school age. By using high-density EEG, gradual shorter time-to-collision and VEP duration, and higher frequencies were observed in the full-term children as they got older (from 4-5 months to 11-12 months, and from 11-12 months to 6 years). The preterm children only showed shorter time-to-collision and VEP duration from 11-12 months to 6 years and showed longer time-to-collision and VEP duration compared to their full-term peers at both 11-12 months and at 6 years. Also, they did not show brain responses in gradually higher frequency-bands with increasing age, and three preterm children did not seem to shift from a less efficient timing-strategy to a more efficient one. The developmental trend observed in the full-term children is assumed to be a consequence of more specialized neuronal networks, myelination of axons, and experience with self-produced locomotion. The impaired development observed in the preterm children can be attributed to the dorsal visual stream vulnerability associated with abnormalities in white matter. Development of visual motion perception is essential for prospective control, the ability to plan and perform precisely timed and coordinated movements adapted to ever-changing surroundings, that are important for fundamental and everyday functions. Despite impaired development in brain responses in the preterm children, little difference was observed between the full-term and preterm children’s motor function. This is suggested to be related to increased prenatal care and specialized services helping the preterm children reach their true potential. In sum, the preterm children showed less efficient perception of looming visual motion compared to full-term children, thus they did not show the same developmental trend as the full-term peers with increasing age. Further studies are therefore necessary to investigate if the preterm children will eventually catch up at a later age, or if they continue to show delayed development of visual motion perception.

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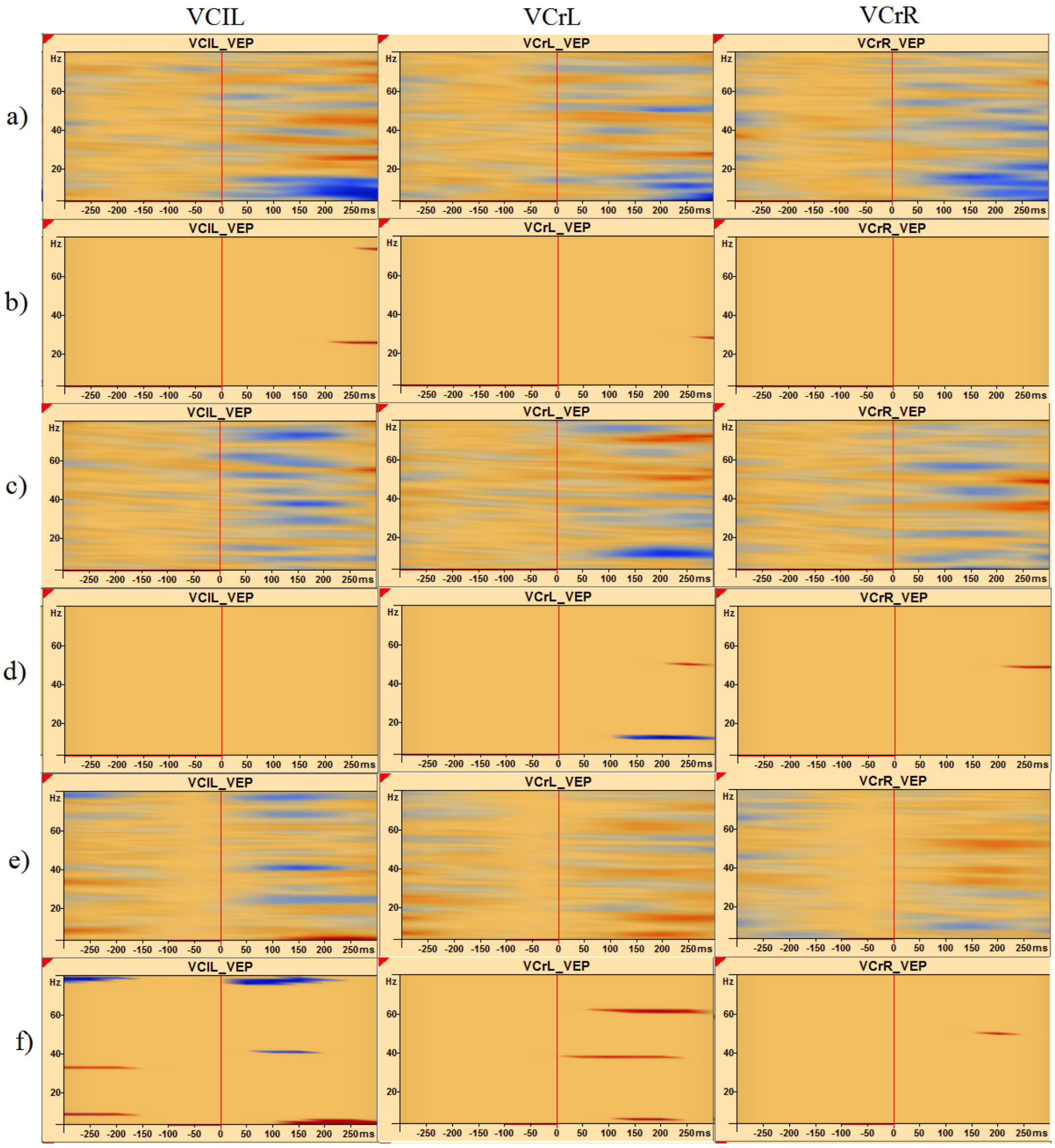
Appendices

Appendix A – TSE plots and TSE probability maps for full-term children

TSE plots (a, c, e) and corresponding TSE probability maps (b, d, f) across brain regions of interest (VClL, VCrL, VCrR) when the motion condition was compared with the static control condition in typical full-term children at 4-5 months (a, b), 11-12 months (c, d), and at 6 years (e, f). Epochs from -300 ms to 300 ms, and the vertical red line marks the top of the looming-related VEP peak. In the TSE plots, red colored contours indicate increased spectral amplitude or induced synchronized activity, while blue colored contours represent decreased spectral amplitude or induced desynchronized activity. In the TSE probability maps, the red voxel marks show significant increase while the blue voxel marks show significant decrease of TSEs ($p < 0.05$) in the motion condition compared to the static control condition.



Appendix B – TSE plots and TSE probability maps for preterm children

TSE plots (a, c, e) and corresponding TSE probability maps (b, d, f) across brain regions of interest (VClL, VCrL, VCrR) when looming was compared with the static control condition in typical preterm children at 4-5 months (a, b), 11-12 months (c, d), and at 6 years (e, f). Epoch is from -300 ms to 300 ms, and the vertical red line marks the top of the looming-related VEP peak. In the TSE plots, red colored contours indicate increased spectral amplitude or induced synchronized activity, while blue colored contours represent decreased spectral amplitude or induced desynchronized activity. In the TSE probability maps, the red voxel marks show significant increase while the blue voxel marks show significant decrease of TSEs ($p < 0.05$) in the motion condition compared to the static control condition.