

**A Longitudinal Study of Visual Looming in Pre-term and Full-term Infants  
using High-Density EEG**

by

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# TABLE OF CONTENTS

<b>ACKNOWLEDGEMENTS</b> .....	
<b>Abstract</b> .....	
<b>1.0 Introduction</b> .....	<b>1</b>
<b>2.0 Methods</b> .....	<b>9</b>
2.1 Participants .....	10
2.2 Apparatus.....	11
2.3 Stimuli .....	12
2.4 Procedure.....	13
2.5 Data analysis.....	14
2.5.1 VEP responses .....	14
2.5.2 VEP duration.....	17
2.5.3 Timing strategies .....	17
2.5.4. Frequency analysis.....	19
<b>3.0 Results</b> .....	<b>22</b>
3.1 VEP responses.....	22
3.2 VEP duration .....	24
3.3 Timing strategies .....	25
3.4 Individual analysis.....	25
3.5 Time-frequency analysis (TSE).....	26
<b>4.0 Discussion</b> .....	<b>30</b>
<b>References</b> .....	<b>36</b>
<b>APPENDICES</b> .....	<b>44</b>
Appendix A .....	44
Appendix B .....	50
Table 2.....	50
Table 3.....	54

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## Abstract

Electroencephalogram (EEG) was used in full-term and pre-term infants at the age of 4 to 5 and 11 to 12 months to longitudinally study brain electrical activity as a function of visual perception of looming motion stimuli. The aim of the study was to find evidence for developmental differences between normally developing full-term and pre-term infants' perception and processing of a virtual looming object approaching on a direct collision course with three different accelerations. Analyses of visual evoked potentials (VEPs) and temporal spectral evolution (TSEs) were used. VEP results showed full-term infants to significantly decrease their looming-related brain responses at the age of 11 to 12 months, where they showed their looming-related brain responses at a fixed time-to-contact irrespective of loom speed. The TSE results showed an increase in amplitudes observed as synchronized early beta band activity at the age of 11 to 12 months in full-term infants. The VEP and TSE results indicated that full-term infants have developed specialized neuronal networks for visual motion perception in the dorsal visual stream and are using a sophisticated and efficient timing strategy to time their brain responses to the virtual collision, indicating that they have developed prospective control at the age of 11 to 12 months. The pre-term infants, on the other hand, did not significantly decrease their looming-related brain responses at the age of 11 to 12 months where they did not time their looming-related brain responses closer to time-to-collision. The TSE results showed that two of the pre-term infants showed little to no synchronized early beta band activity at the age of 11 to 12 months. The results from the VEP and TSE analyses indicated that the pre-term infants may not have developed specialized neuronal networks for processing visual motion, are using a less efficient timing strategy to time their brain responses, and consequently may have problems with prospective control at the age of 11 to 12 months. Together, these findings suggest that pre-term infants at 11 to 12 months of age have problems with visual motion processing, a dorsal stream function. However, the results of VEP duration significantly decreased for both group of infants at the age of 11 to 12 months indicating that they need less time to process the looms and that they have a sufficient amount of myelination of neurons in the dorsal visual stream. More follow-up research is needed to further understand the neurobiological development in pre-term children early in development, since early measures could, in the long term, help pre-term children develop cognitive abilities that allow them to reach their true intellectual and social potential.

## 1.0 Introduction

Throughout the animal kingdom, the sight of a rapidly approaching object usually signals danger and elicits avoidance reactions (Dean et al., 1989; Schiff, Caviness & Gibson, 1962). It is important for both animals and humans to respond quickly when danger is approaching to avoid being hurt or injured. While the response may vary between species, the main function is to detect whether or not an object is approaching on a direct collision course and how imminent the collision is. If an object is approaching on a direct collision course, it will project an expanding image with a rapid symmetrical growth on the retina. This motion is called *looming* (Gibson, 1986; Van der Meer, Svantesson & Van der Weel, 2012) and provides information about the approaching object and how imminent the collision is.

Interaction with events in the surroundings, like avoiding being hit by an object, demands prospective control where action, perception, and cognition are tightly coupled together in a complex system (Lee, 1998; Von Hofsten, 2004, 2007). Prospective control requires perceiving the environment in relation to the bodily characteristics of the individual so that adaptive behavior can develop. The development of smooth visual pursuit of moving objects is one of the earliest indications of prospective control seen in infants. It involves infants' anticipation of a moving object's forthcoming motion, and this ability develops over the first three months of life (Von Hofsten, 2007; Von Hofsten & Rosander, 1996). The information needed for the perception of our own motion or object motion in the environment is available in the optical flow field (Gibson, 1986). In our visual field, perception of movement transforms the entire optic array into a flow field, which provides information of the direction of movement. It is important for humans to pick up information from the visual flow field so that they can calculate their next movement and thus guide their actions efficiently. Actions are directed into the future and their control is based on knowledge of what is going to happen next (Von Hofsten, 2007). Cognitive development has to do with expanding prospective control over and above the information available at any point in time by using rules and representations of events to guide our actions (Von Hofsten, 2004). Optic flow is crucial to guide our actions efficiently, and adults and infants can both perceive optic flow (Van der Meer, Fallet & Van der Weel, 2008), but prior to the onset of locomotion, infants can only discriminate large changes in heading during navigation (Gilmore, Baker & Grobman, 2004). This probably has to do with infants' less specialized neural networks for motion perception compared to adults caused by the infants' lack of experience with motion stimuli (Van der Meer et al., 2008).

The perception of looming has been widely investigated in locusts (Rind & Simmons, 1992; Rind & Simmons, 1997), flies (Holmqvist, 1994), pigeons (Sun & Frost, 1998; Wang & Frost, 1992), monkeys (Zeki, 1974, 2004) and humans (Kayed & Van der Meer, 2000, 2007; Van der Meer et al., 2012; Van der Weel & Van der Meer, 2009; Yonas, Pettersen & Lockman, 1979). These studies show that the middle temporal (MT) and medial superior temporal area (V5), also known as MT+ (MT/V5) (Morrone et al., 2000), are involved in the visual processing of motion and have neurons that react and respond to looming stimuli. The emergence of smooth-pursuit eye movements and sensitivity to motion direction (Atkinson, 2000) indicate that this area is functional at around 2 months of age (Von Hofsten, 2004). Sun and Frost (1998) identified three classes of neurons in the nucleus rotundus of the pigeon midbrain that respond to different kinematic properties of looming – tau, rho and eta. Neurons of the first class (tau) always initiate their responses at a fixed time before an object makes a collision. Neurons in the second (rho) and third (eta) classes both initiate their responses earlier in the looming sequence for larger or slower objects. However, there is one distinctive feature – rho neurons have a response threshold after which their responses remain unchanged with different object size and velocity, while eta neurons decrease their responses as the approaching object reaches a particular angular size (Sun & Frost, 1998).

The eye's perception of visual information propagates from the lateral geniculate nucleus (LGN) to the primary cortex. Two interconnected visual pathways distinguish the information in the primary visual cortex, either through a dorsal stream propagating information towards the parietal lobe or through a ventral stream directed towards the temporal lobe (Andersen, 1997). The ventral stream is important for object recognition and the dorsal stream is involved in the processing of motion and is associated with visual-motor transformations – that is, the routing of sensory information into motor areas for the purpose of action. This pathway has been referred to as the “where” or “how” pathway because it tells us where and how to perform visually guided movements (Andersen, 1997). The dorsal stream processes visual information for fast goal-directed action such as reaching and grasping using an egocentric frame of reference (Creem & Proffitt, 2001). A growing number of studies shows that the dorsal stream in the adult and infant cortex and its incorporated areas V1, V2 and MT+, have neurons that are selectively activated by motion stimuli (Braddick, Birtles, Wattam-Bell & Atkinson, 2005; Cheng, Fujita, Kanno, Miura, Tanaka, 1995; Rosander, Nyström, Gredebäck & Von Hofsten, 2007). Human infants are in need of neural structures allowing them to judge impending collisions adequately, especially as they become more mobile during the second half of the first year of life. In normally developing infants, the processing of motion stimuli

is shown to be localized in the occipito-parietal areas in the left and right visual cortex (Van der Meer et al., 2012; Van der Weel & Van der Meer, 2009). However, the functioning and development of these areas in pre-term infants are less known.

The human brain starts developing prior to birth and continues to develop during the first year of life. Infant neuronal networks are characterized by the vast excess of neurons and dendritic spines as part of the maturational process (Huttenlocher, 1990; Webb, Long & Nelson, 2005), and the number of dendrites and synaptic connections in the primary visual cortex reaches a peak level between the ages of 8 months and 2 years (Klaver, Marcar & Martin, 2011). This overproduction of neurons is advantageous in adaptation and plasticity of the brain. During the first year of life, the infant brain undergoes rapid changes and doubles in weight, where there is constantly strengthening of some connections and pruning of other connections. This strengthening and pruning of neural pathways might be a developmental change that affects processing speed and efficiency as a more restricted area of the brain gets activated due to specializations of neural pathways (Edelman, 1993; Johnson, 2000). Synaptic maturation of neuronal networks in the visual cortex (Huttenlocher, 1990) and myelination of neurons increases the speed of electrical impulse propagation from soma to dendrites (Dubois, Dehaene-Lambertz, Soarés, Cointepas, Le Bihan & Hertz-Pannier, 2008). Thus, during early infancy until adulthood synaptic maturation and myelination could affect the visual processing speed with age (Webb et al., 2005).

Research on infant perception was at its peak in the 1960s and 1970s. The experimenters caught an interest in looming stimuli and defensive responses, and wanted to examine how early infants could respond to motion stimuli (Bower, Broughton & Moore, 1971; Schiff et al., 1962; Yonas et al., 1979). Several studies have investigated infants' development of prospective control and how they process information of looming motion by looking at infants' defensive responses to looming stimuli (Bower et al., 1971; Kaye, Farstad & Van der Meer, 2008; Kaye & Van der Meer, 2000, 2007; Schiff et al., 1962; Yonas et al., 1979). Today, it is well established that blinking is the most reliable indicator of awareness to stimuli on a collision course in early infancy. If blinking occurs too early, the eyes will probably reopen before the collision takes place. On the other hand, if the blinking happens too late the eyes may be injured. Thus, the timing of the defensive blink has to be precise in order to protect the eyes when something is about to hit the face. The estimate of the response has to be made according to when an object is about to hit, referred to as the time-to-collision. Precise prospective control where the defensive action has to be perceived ahead in time is required so that the body is prepared to respond (Von Hofsten, 2004).

Kayed and Van der Meer (2000, 2007) investigated timing strategies used in defensive blinking to optical collisions in 5- to 7-month old infants. The stimulus used was programmed to loom symmetrically toward the infant's face so that the infant would get an experience of a visual collision. Infants mainly timed their defensive blinking by relying on one of three information variables based on the looms' visual angle, velocity, or the time away from the virtual collision. The results showed that infants initially used a strategy based on the loom's visual angle or velocity, and switched to a strategy based on time-to-collision around the age of 7 months. The results also showed that infants that relied on strategies based on the visual angle or velocity had a higher number of late defensive blinks than the infants who used a strategy based on time-to-contact. Their findings indicate a developmental trend where infants around 7 months of age shifted from a less efficient strategy to a more sophisticated strategy based on time that was less prone to misjudgments, allowing them to deal with more demanding perceptual tasks (Kayed & Van der Meer, 2000, 2007).

Blinking in response to visual collisions is first found in infants between 6 and 14 weeks of age, but blinking to visual stimuli is not an innate response. Recent developments in non-invasive, high-density electroencephalogram (EEG) with sufficiently high temporal resolution allow us to investigate how the young human nervous system extracts and processes information for impending collision, without the need for a blinking response (Van der Weel & Van der Meer, 2009; Van der Meer et al., 2012). EEG is a method of measuring electrical brain activity, and is often used when investigating the perception of motion. EEG can be used to measure visual evoked potentials (VEPs) which are electrical potentials initiated by a specific visual stimuli (Luck, 2005). Magnetoencephalography (MEG) and EEG studies measuring visual evoked potentials have been proven to be complementary techniques for the study of the neural basis of motion perception in the millisecond time scale (Van der Meer et al., 2008).

Recent EEG studies have investigated infants' brain responses to looming danger. Van der Weel and Van der Meer (2009) used high-density EEG in eighteen 5- to 11-month-old infants and a looming stimulus approaching under three different accelerations, to investigate how the young human nervous system extracts and processes information for impending collision. Their results showed that infants' looming-related brain responses are localized in the visual cortex. A prominent developmental trend was found, suggesting that 10- to 11-month-old infants, as opposed to 5- to 7-month-old infants, have well-established neural networks for registering impending collision, probably caused by postnatal improvement of synaptic maturation and myelination (Grieve, Emerson, Fifer, Isler & Stark, 2003; Webb et



al., 2005). The 8- to 9-month-old infants in the study displayed an in-between developmental stage, which could be interpreted as a sign that appropriate neural networks are in the process of being established at that age. Coincidentally, this is also the average age at which infants start crawling, and makes sense from a perspective where brain and behavioral development go hand in hand (Johnson, 2000). Thus, as infants gain better control of self-produced locomotion, their perceptual abilities of sensing looming danger improve (Van der Weel & Van der Meer, 2009).

Van der Meer, Svantesson, and Van der Weel (2012) did a longitudinal study on ten infants' brain responses and prospective control when responding to a looming virtual object on a direct collision course at the age of 5 to 6 months and at the age of 12 to 13 months. The results showed that the timing and the duration of the VEP responses differed with age. At the age of 5 to 6 months, infants showed VEP peaks earlier in the looming sequence and VEP responses with longer duration than when they were 12 to 13 months old. The results from the timing-strategy analysis showed that with age, four infants shifted from a less efficient timing strategy involving the loom's velocity to the more efficient strategy involving the loom's time-to-collision. Further, they found that peak VEP activation in the investigated areas propagated across the cortex, showing the highest observed activation in the occipital area at the age of 5 to 6 months, whereas the parietal area showed the highest activation when the infants were 12 to 13 months old. They concluded that their results indicate a developmental trend in infants' prediction of an object's time-to-collision. As infants grow older and become more mobile during the first year of life, one of the underlying causes of the developmental trend found in their study could be due to an increase in locomotor experience (Van der Meer et al., 2012).

In addition to VEP analyses, growing attention has been given to EEG studies in the time-frequency domain, which have permitted the investigation of perceptual and cognitive functions through the manifestations of the natural frequencies in EEG oscillations (Basar, Basar-Eroglu, Karakas & Schurmann, 1999). Several EEG studies have found that full-term infants' visual motion processing at the age of 3 to 5 months is dominated by theta oscillations in the visual cortex (Agyei, Holth, Van der Weel & Van der Meer, 2015; Van der Weel & Van der Meer, 2009) which in infancy are strongly related to cognitive and attentional processes (Orehova, Stroganova & Posikera, 1999). As infants grow older, studies have found that full-term infants' visual motion processing at the age of 12 months is characterized by higher frequency activities where the infants show a more adult-like specialization for motion where fast oscillating cell assemblies have fewer but more

specialized neurons, resulting in improved visual motion perception (Agyei et al., 2015; Van der Meer et al., 2008).

Kayed, Farstad and Van der Meer (2008) investigated timing strategies to optical collisions in eight pre-term infants when they were 5, 6 and 7 months of age. Their results showed that at 5 months of age, three of the infants used a timing strategy based on the virtual object's visual angle, causing them to have problems with fast, accelerating approaches. Four infants blinked when the virtual object was a certain time away, allowing them to blink in time on all approach conditions. One of the infants stood out as he relied on a timing strategy based on velocity on all three test sessions, causing him to blink late on a large number of trials even at 7 months of age. They concluded that their results might be an early indication of perceptuo-motor problems (Kayed et al., 2008). Pettersen, Yonas and Fisch (1980) also investigated pre-term infants blinking in response to impending collisions. They found that at 10 weeks after birth, pre-term infants responded less frequently to an approaching object than full-term and post-term infants, but when the pre-term infants were tested at the same age from conception as a group of full-term infants, the response rates were equal (Pettersen et al., 1980). However, the brain responses and prospective control when responding to a virtual looming object on a direct collision course in pre-term infants needs further investigation.

In Norway, approximately 5.6 % of infants were born prematurely in 2013 (Store Medisinske Leksikon, 2014). Pre-term birth is defined as labor prior to the completion of 37 weeks of gestation (Markestad & Halvorsen, 2007). Pre-term labor is the leading cause of infant mortality in the industrialized world after congenital anomalies (Swamy, Østbye & Skjærven, 2008), but the chances of survival have increased the last couple of decades due to the advancement in neonatal health care (Markestad & Halvorsen, 2007; Wilson-Costello, Friedman, Minich, Fanaroff, Hack, 2005). However, several studies have shown that pre-term infants who survive have higher risks than full-term infants of getting illnesses and injuries that may affect health and development. Despite the increased chances of survival, pre-term infants have higher frequencies of difficulties with learning, attention/concentration, language, social interaction, motor skills and mental health (Markestad & Halvorsen, 2007). Also, the risk of severe brain damage leading to cerebral palsy (CP) and mental retardation increases with decreasing gestational age (Larroque et al., 2008; Markestad & Halvorsen, 2007). Studies have shown that pre-term infants are at a higher risk of facing difficulties at school than their full-term peers (Larroque et al., 2008; Wolke & Mayer, 1999). A meta-analysis on cognitive and behavioral outcomes of school-aged children born pre-term found that pre-term birth is associated with lower cognitive scores and increased risk of ADHD and

other behaviors at school age compared to full-term infants (Bhutta, Cleves, Casey, Craddock & Anand, 2002). Increased rates of neuronal cell death could lead to volumetric losses in specific brain regions and may at least partially explain the cognitive and behavioral abnormalities noted in these children (Bhutta et al., 2002).

Counsell and Boardman (2005) stated that pre-term birth causes differential brain development that is evident from abnormalities in tissue microstructure and cerebral morphology measured with MRI (Magnetic Resonance Imaging). Differences between pre-term and full-term infants have been observed in the cerebral white matter, deep grey nuclei and cortical grey matter (Counsell & Boardman, 2005). At 40 weeks gestational age, diffusor tensor imaging (DTI) has shown that white matter fibers in areas of the brain through which the dorsal stream flows are shorter, thinner, and less organized in pre-term than full-term infants (Hüppi et al., 1998). At 11 years of age, DTI has suggested reduced thickness, fewer axons, and/or poorer myelination of white matter in these brain areas in pre-term children as compared to full-term control children (Nagy et al., 2003). Pre-term infants are at a particular risk of white matter damage due to anoxia or to infection, with abnormal white matter apparent on MRI in many infants who do not have overt brain lesions. Delayed maturation of visual motion processing in the first year of life is related to the degree of white matter damage in pre-term infants and predicts later neurological and cognitive status (Atkinson & Braddick, 2012). Pre-term infants have also shown prominent reductions in cerebral cortical grey matter volume, deep nuclear grey matter volume, and an increase in cerebrospinal fluid compared with full-term infants. These pre-term infants exhibited moderate to severe neurodevelopmental disability at 1 year of age (Inder, Warfield, Wang, Hüppi and Volpe, 2005).

Several studies have pointed to impairment of the dorsal visual stream as a cause of less efficient visuo-motor processing in pre-term infants without CP (Birtles, Braddick, Wattam-Bell, Wilkinson & Atkinson, 2007; Braddick, Atkinson & Wattam-Bell, 2003; MacKay, Jakobson, Elleberg, Lewis, Maurer & Casiro, 2005; Van Braeckel, Bos, Butcher, Geuze, Van Duijn & Bouma, 2008). Dorsal stream vulnerability has been shown in several genetic neurodevelopmental disorders as well, like Williams syndrome (Atkinson et al., 2001; Atkinson et al., 2006), autism spectrum disorders (Grinter, Maybery & Badcock, 2010; Spencer et al., 2000), Fragile X syndrome (Grinter et al., 2010) and developmental dyslexia (Hansen, Stein, Orde, Winter & Talcott, 2001). Specifically, it has been proposed that the larger magnocellular (M) cells in the dorsal stream are more at risk early in the disease process than parvocellular (P) cells in the ventral stream, since neurons with larger cell bodies

and axon diameters are more susceptible to damage (Quigley, Dunkelberger & Green, 1988). In addition, magnocellular pathway loss might be more readily detected because there are far fewer M cells than P cells (approximately 80 % of the ganglion cell population is P cells and 8-10 % is M cells) (Dacey & Petersen, 1992). Tremblay et al. (2014) suggest that 12-month-old pre-term infants have a ventral stream (occipito-temporal or P pathway) that is normally developing, whereas the dorsal stream (occipito-parietal or M pathway) is still immature in 12-month-old pre-term infants. The notion that the dorsal stream is more vulnerable to damage than regions more ventrally is supported (e.g., Back, Riddle & McClure, 2007; Back & Rivkees, 2004; Peterson et al., 2003). The mechanisms underlying this vulnerability are as yet unclear, but may in pre-term infants be related to premature stimulation of an immature visual system or to a high sensitivity for minor organic damage (Van Braeckel et al., 2008).

Since pre-term infants are born several weeks earlier than expected, their brain and other organs are not yet fully developed compared to full-term infants. Thus, the mapping and understanding of how the brains of pre-term infants differ from the brains of full-term infants are important for both assessment of different difficulties associated with premature birth and facilitation for an optimal development. Early measures should in the long term help pre-term infants develop cognitive abilities comparable to their term-born peers that allow them to reach their true intellectual and social potential (Atkinson & Braddick, 2012).

The aim of the present study was to use high-density EEG measurements of infants' brain electrical activity to find evidence for developmental differences between normally developing pre-term and full-term infants' perception and processing of a virtual looming object that approaches them on a direct collision course. VEP analysis was used to investigate whether there are any differences between the two groups of infants' brain responses to virtual collisions at the age of 4- to 5-months and 11- to 12-months. Based on previous studies it was expected that the pre-term infants would show significantly poorer performance than their full-term controls. An individual analysis was performed to compare the pre-term infants' brain responses with the full-term infants' brain responses at 11- to 12-months of age. A time-frequency analysis (TSE – Temporal Spectral Evolution) was also carried out to investigate induced oscillatory brain activities. Low frequency activity was expected to dominate the TSE maps in the brain areas of interest when the infants were 4- to 5-month-old, whereas higher frequency activity was expected at the age of 11- to 12-months. Since TSE has never been done on pre-term infants' looming data before, there were no expectations with regard to their induced oscillatory brain activities. The brain areas of interest were the

occipital and parietal areas of the so-called dorsal visual stream of the cortex and the V5/MT complex (MT+).

## 2.0 Methods

### 2.1 Participants

A total of ten healthy pre-term infants (7 boys) and ten healthy full-term infants (7 boys) were recruited for this study. The pre-term infants were recruited with the help of the pediatrician in charge of the Neonatal Intensive Care Unit at St. Olav's University Hospital (Trondheim, Norway). However, one of the pre-term infants was very uncomfortable during the second testing session when he was 12 months old and it was impossible to collect any data on him. He was therefore excluded from the study and, as a consequence, his matched full-term control was automatically excluded as well. Thus, the analyses were performed on 18 infants in total for two testing sessions.

The pre-term infants included in this study were born on average at 31 (SD = 1.8, range 28.3-33.0) weeks of gestation with average birth weight of 1622 (SD = 453, range 1000-2670) grams. They did not have any major problems such as severe brain damage, retinopathy of prematurity (ROP) and/or other prenatal issues requiring potentially serious medical interventions leading to abnormal development. However, the experimenters were unaware of the neurological status, birth history, and any other events during the infants' stay at the hospital. The full-term infants included in this study were either recruited through local newspaper birth announcements, or parents showing an interest and making voluntary contact with the laboratory. They were born on average at 39.7 (SD = 1.1, range 38.3-41.9) weeks of gestation with average birth weight of 3636 (SD = 824, range 3085-4250) grams. This study used a longitudinal design where both groups of infants were tested twice.

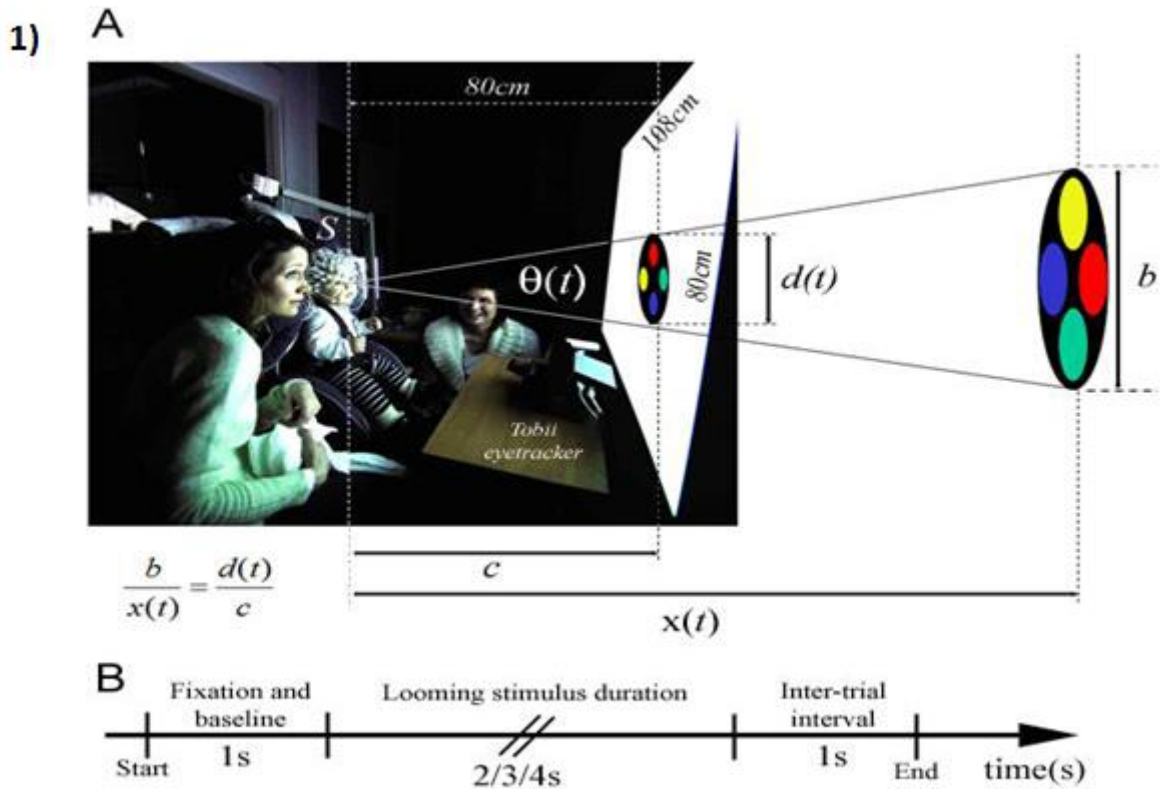
The pre-term and full-term infants were matched according to both their gender and age in full months. For valid matching of the participants, age corrected for prematurity was calculated for the pre-term infants. At the first testing session, the mean (corrected) age of the pre-term infants was 4.9 months (SD = 0.33) with a range of 140-158 days, and the mean age of the full-term infants was 4.7 months (SD = 0.84) with a range of 102-182 days. At the second testing session, the same pre-term infants' mean age was 12.2 months (SD = 0.6) with a range of 348-374 days, and the same full-term infants' mean age was 11.8 months (SD = 0.5) with a range of 339-386 days. At the time of the first testing session, 7 of the full-term infants were rolling over from back to stomach, or from stomach to back, or both ways. Two of these infants rolled over accidentally. One of the infants had some experience with backward movement. Five of the full-term infants were able to walk independently at the time of the second testing session, while the other full-term infants except from one were able to pull to stand or walk with help or while holding on to furniture. The motor development of the

pre-term infants was similar to that of the full-term infants. Except for three of the pre-term infants who had not started crawling or pulling to stand at the time of the second testing session, and were bottom shuffling instead.

Electroencephalogram recording as a psychophysical procedure is not associated with any physical harm or pain to the participants. All parents were informed about the experiment and their right to withdraw at any time, and signed an informed consent. The Norwegian Regional Ethics Committee and the Norwegian Data Services for the Social Sciences have approved the study. All testing was carried out at the Developmental Neuroscience Laboratory (NU-lab) at the Department of Psychology (NTNU) in Trondheim, Norway.

## **2.2 Apparatus**

The testing took place in a room with a large projection screen (108 cm wide and 80 cm high) hanging down from the ceiling. Stimuli were generated with E-Prime (Psychology Software Tools) and mirror-reversed projected onto the screen by means of an ASK M2 projector (see Figure 1A). Electroencephalogram activity was recorded with the Geodesic Sensor Net 200 (GSN) which consisted of 128 sensors that were evenly distributed across the infant's scalp. Triggers about the onset and offset of the stimulus were communicated from E-Prime onto the EEG-recording. As recommended for the high-input-impedance EGI amplifiers (Ferree, Luu, Russell & Tucker, 2001; Picton et al., 2000), all electrode impedances were kept under 50 k $\Omega$  to ensure an optimal signal-to-noise ratio. Net Station software recorded the amplified EEG signals on a Macintosh computer, using a sampling rate of 500 Hz with a low-pass filter of 100 Hz and a 0.1-Hz high-pass filter. An infrared Tobii X50 camera was used to track the infants' gaze. The visual feed was processed with Clear View software on an HP computer. Digital videos were recorded by two cameras positioned at different angles in front of the infants so that it was possible to observe the infants' attention and behavior during the experiment. The data were stored on a hard disc for off-line analyses.



**Figure 1.** Experimental setup with a diagram of stimulus configuration. **(A)** Each infant was shown an image of a flat circle approaching on a direct collision course. The looming stimuli simulated an object coming from far away approaching for a duration of 2, 3, and 4 seconds under three different constant accelerations ( $-21.1 \text{ m/s}^2$ ,  $-9.4 \text{ m/s}^2$ , and  $-5.3 \text{ m/s}^2$ ). The stimulus approached the infant as the image on the screen grew, and the loom stopped when the image filled the entire screen leaving a blank screen. In the bottom left corner is a mathematical equation describing the growth of the visual loom. **(B)** A timeline of stimuli sequence showing the approach of the looming disc and time duration during the phases of fixation, looming, and inter-trial interval from start to end in a single trial.

### 2.3 Stimuli

The stimulus consisted of a flat, black circle with 4 different colored inner circles of equal size (red, green, blue, yellow) rotating within it. The entire object rotated with a constant angular velocity of 300 degrees per second and was shown on a cream white background. The radius of the inner circles was 1/3 of the radius of the outer circle. The stimuli were programmed to loom towards the infant and coming up to the infant's face so that the infant would get an experience of a visual collision. The virtual object loomed towards the infant with a constant acceleration depending on the condition length. The image of the virtual object appeared on the screen and stayed at its smallest size for 1 s, at a virtual distance of 43.1 m, before it expanded during a looming phase and finally reached its largest size and disappeared, leaving a blank screen for 1 s. The image of the virtual object initially had a



visual angle of  $5^\circ$  (diameter of 6.5 cm), and grew to a maximum visual angle of  $131^\circ$  (diameter of 350 cm). The virtual object moved towards the infant under three different conditions with a constant acceleration over a period of 2 s ( $-21.1 \text{ m/s}^2$ ), 3s ( $-9.4 \text{ m/s}^2$ ), and 4 s ( $-5.3 \text{ m/s}^2$ ), respectively. The image of the virtual object had the same size/visual angle at the beginning and the end of the approach, independent of the virtual object's approach time. The virtual object moved over the same virtual distance (43.1-0.80 m) at a constant acceleration in all three conditions (see Figure 1B). The three looming conditions appeared on the screen in random order. In addition, a fourth reversed “zooming” condition was introduced as a control condition simulating the black circular disc moving away from the infant over 3 seconds. This control condition turned out to be great in (re)capturing the infant's interest but was not included in the analyses.

## 2.4 Procedure

The infant arrived with its parent(s) some time prior to the experiment. One of the experimenters informed the parent(s) about the experiment and played with the baby so that the baby became familiar and relaxed before the experiment started. An assistant measured the infant's head circumference to get the correct size selection of the GSN 200. Then, the electrode net was soaked in a solution of distilled water, saline and baby shampoo to ensure optimal contact with the scalp. The net was then placed on the scalp of the infant while he/she sat on the parent's lap, and small sounding toys and soap bubbles were used to distract the infant's attention from the net.

Immediately after the net was mounted, the infant was placed in front of the screen hanging 80 cm away from the infant in the experimental room. The infant was either sitting on the parent's lap (4- to 5-month-olds) or placed in a baby car seat (11- to 12-month-olds). One parent was always situated next to the infant in the experimental room to avoid any stress an absent parent may cause, but was instructed to not interfere unnecessarily. An assistant was also present to help the infant focus on the screen. The electrode net was then plugged into an amplifier and the impedance of the electrodes was checked. If electrodes had insufficient contact with the scalp, the electrodes were corrected by repositioning them slightly so that contact was improved.

The experimental room was divided by a window from the control room where the computers for stimulus generation and data acquisition were placed. During the experiment the infant was observed by the experimenters on a computer screen in the control room. The lights in the experimental room were turned off during the experiment to help the infant

concentrate on the screen. The stimulus was generated with E-prime, and the four different conditions were presented in a random order. Data acquisition was performed in one block, but pauses were made if the infant seemed to have lost interest. If pauses were made, the assistant and/or the parent played a little with the infant to retrieve interest, but if the infant seemed fed up or tired, the experiment was ended. Each infant was individually tested and the testing session lasted for about 20-30 minutes. The looming experiment was performed together with an optic flow experiment and an occlusion experiment, which provided data for other studies. The looming experiment was usually conducted after the optic flow experiment, about 5-7 minutes into the testing session, and took about 4-6 minutes on average. In both groups of infants, each infant completed on average 47 trials (SD = 4, range 39-53) at the first testing session, and on average 46 trials (SD = 9, range 33-68) at the second testing session. The reversed trials are not included in these numbers. The number of trials was equally distributed among the three looming conditions.

## **2.5 Data analysis**

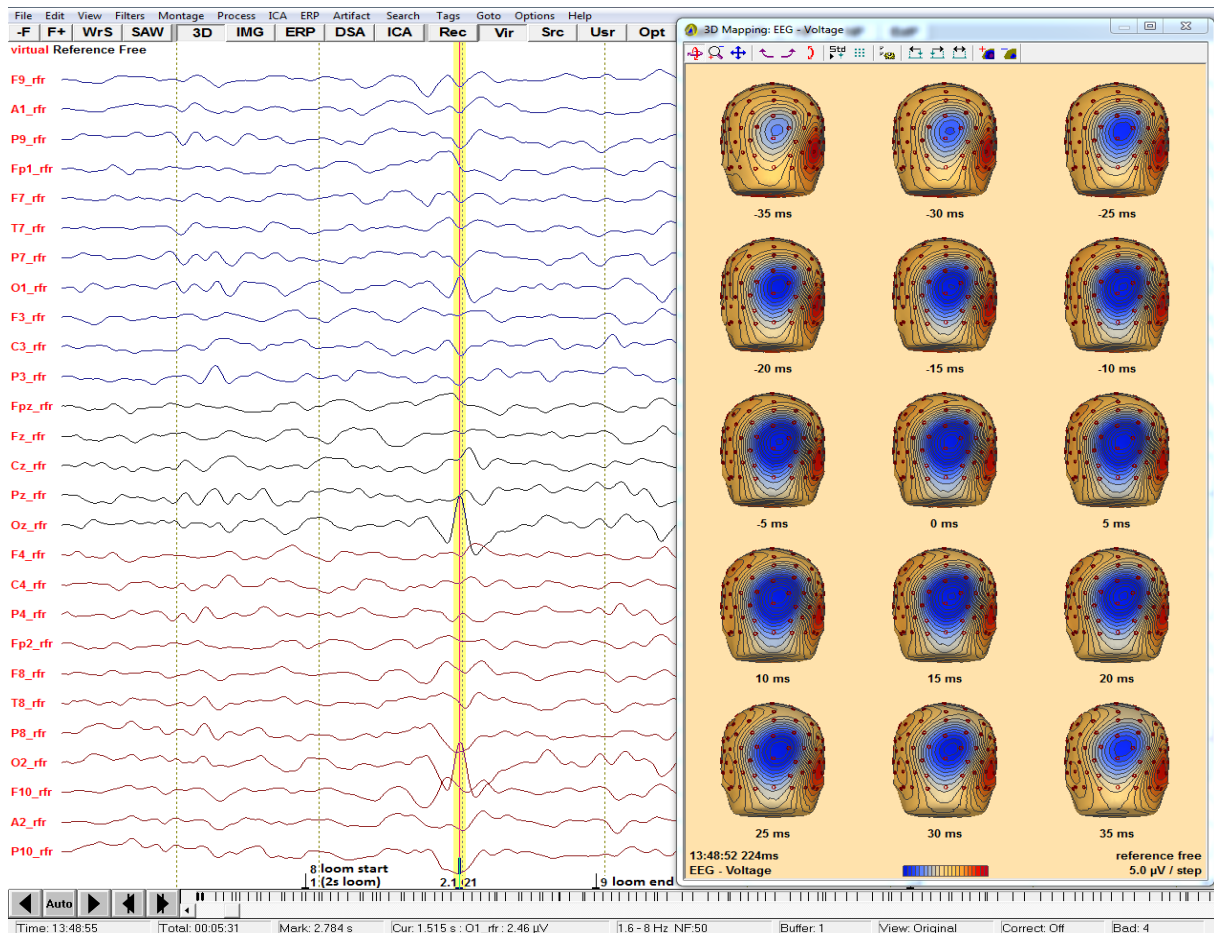
EEG data analyses were carried out in the software program BESA (Brain Electrical Source Analysis) version 6.0. The same methods were used to analyze the data for both testing sessions. As an initial pre-processing step, recordings were segmented with the Net Station software and exported as raw files to BESA for analysis. In BESA, a standard channel configuration and digitized head surface points were added to the raw data for each infant before processing began. By visual inspection, artefact-contaminated channels and trials resulting from head or body movements were excluded from further analyses or interpolated where necessary. None of the participants had more than 10 % of the channels defined as bad. Notch filter was set at 50 Hz to remove mainline noise interference in the EEG data, while low cut-off filter (high band pass) was set at 1.6 Hz to remove slow drift in the data, and high cut-off filter (low band pass) was set at 8 Hz. A reference-free montage showing EEG at 27 standard electrodes was used.

### **2.5.1 VEP responses**

An event-related potential (ERP) represents transient brain electrical activity generated by the summation of dendritic postsynaptic activity of neurons firing synchronously in response to a stimulus (Luck, 2005). The different arrangements (perpendicular or parallel) of the pyramidal neurons of the cerebral cortex create a dipolar field of positive and negative charges which enables flow of current through it (Luck, 2005). Visual evoked potentials (VEPs) represent the ERPs in the visual cortices. A VEP is the post-synaptic firing pattern of

neurons at a particular time in relation to a particular visual stimulus (Webb et al., 2005). It represents changes in the brain's electrical activity at a high temporal resolution by using high-density EEG.

A trial-by-trial investigation was performed on each infant's raw EEG recordings to find looming-related peaks. By looking at the reference-free channel distribution, highly prominent VEP peaks were marked at electrode sites Oz and Pz based on earlier studies investigating VEPs (Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002; Van der Meer et al., 2012). The marked VEP peaks provided information about the activity at the selected brain regions as a direct measure of amplitude channel activity. A 3-dimensional mapping of a build-up (negative) and a decline (positive) of voltage activity in the visual cortex could also visualize this activity over time. This 3D mapping and the trial-by-trial visual inspection were used to determine each VEP peak (see Figure 2). The time-to-collision of the looming stimulus was taken as the time with respect to the virtual collision at which a looming-related VEP peak occurred. At the time each VEP peak occurred, the time remaining to stimulus end, which coincided with the loom's time-to-collision, was recorded. To be sure that the infants actually were looking at the screen during the trial-by-trial investigation, the videos and gaze data were inspected.

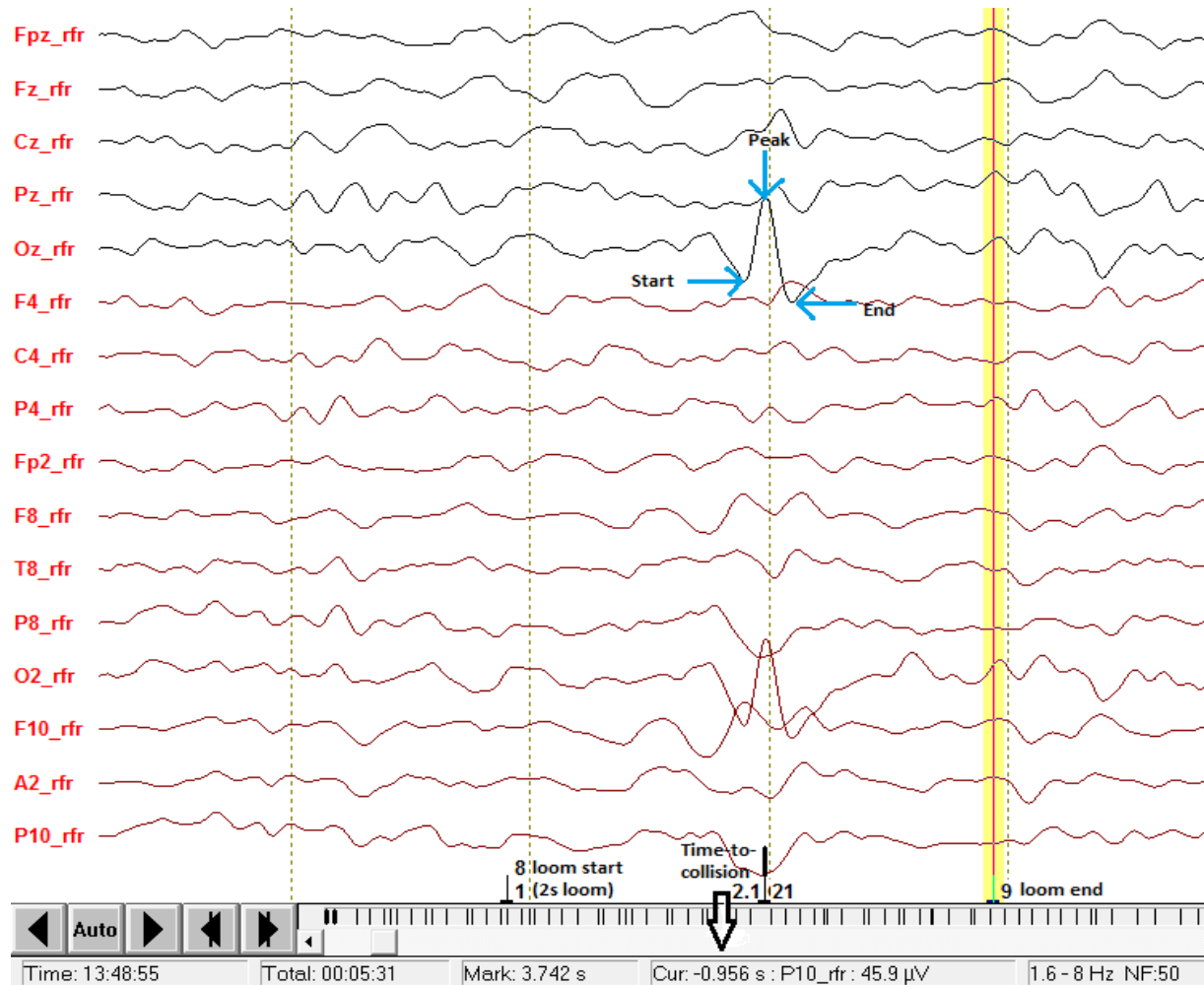


**Figure 2.** EEG data analysis showing a typical looming-related VEP response in the middle of the looming sequence. A reference free montage of 27 electrodes is shown. Prominent VEP peak activity at electrode Oz (and O1 and O2) in a 2 s looming trial is viewed as a direct response to the looming stimulus. The VEP peak is marked by a yellow vertical line. A 3D voltage mapping shows high activity in the visual cortex building up and declining over time.

Occasionally, several VEP peaks occurred in the same trial making it difficult to determine which peak represented the looming-related response. In case of multiple peaks, the peak occurring closest to the stimulus end or the peak that showed increased brain activity in the 3D mapping (a nice, blue circle of activity in the middle of the back of the head) was assumed to be more functionally related to the loom. Trials where looming-related peaks were not prominent or occurring too early or too late in the looming sequences were excluded from further analysis. Peaks too close to the end of stimulus or after the end of stimulus were assumed to represent other evoked potentials that were not related to the timing of the looming-related response.

### 2.5.2 VEP duration

In addition to recording the timing of the VEP peak with respect to the virtual collision, the duration of every looming-related VEP response was recorded:  $VEP_{duration} = VEP_{start} - VEP_{end}$  (see Figure 3). The VEP duration was defined as the difference in time between the start and the end of the looming-related peak (Van der Meer et al., 2012).



**Figure 3.** Marking and timing of a single looming-related VEP in raw EEG data showing how the start, peak and end of the VEP were marked manually in the Oz electrode of single trials. The yellow vertical line is aligned with the end of the looming sequence. Corresponding time-to-collision data were recorded from the lower tab.

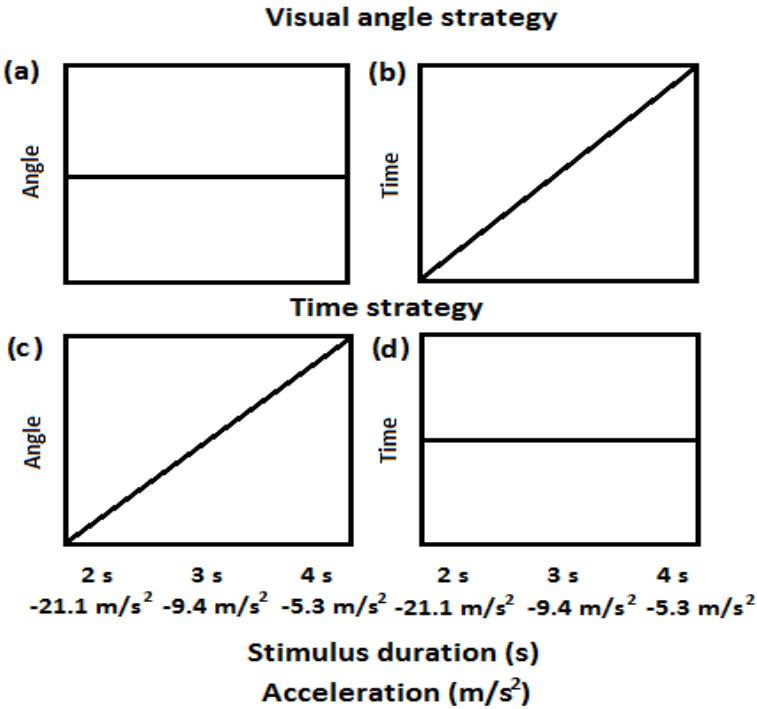
### 2.5.3 Timing strategies

Infants may depend on different optical variables of the visual looming stimulus to time their brain responses to the virtual collision. Therefore, the present study also investigated which timing strategies the infants used to time their looming-related brain responses.

Two different strategies were investigated, based on two variables of the visual looming stimulus: the loom's time-to-collision, and the loom's visual angle. These variables are a function of the looming stimulus' approach velocity and the duration of the looming

sequence. Any strategy used will depend on the variable the infant holds constant across trials.

A strategy based on the loom’s visual angle means that infants use the changes occurring in the angle subtended by the edges of the visual loom to time their looming-related brain responses (see Figure 4A). If the loom’s visual angle is held relatively constant (a) and the loom’s acceleration decreases, the time-to-collision would increase (b). If infants are using a strategy based on the loom’s visual angle, they are at risk of under- or overestimating the loom’s virtual collision because the loom’s visual angle does not accurately predict the loom’s time-to-collision. When looming stimuli with different speeds approach the infant, brain responses based on the visual angle of the looms would be influenced by the size of the looms. The approaching loom would then have reached a certain visual angle at a different time from virtual collision for each loom speed. Thus, this would create a problem for infants as they may not be able to accurately time the loom’s time-to-collision with changing approach loom speed.



**Figure 4.** A theoretical graph of the loom’s visual angle and time-to-collision as a function of the duration and acceleration of the looming sequence. As the acceleration of the loom decreases the strategies based on different information variables have different implications for the looming-related brain response. A visual angle strategy

*implies that as the loom's acceleration decreases the visual angle of the loom is held relatively constant (a), while the loom's time-to-collision increases (b). A time strategy implies that as the loom's acceleration decreases the loom's time away from the virtual collision is kept relatively constant (d), while the loom's visual angle increases (c). For simplicity, the lines are drawn as straight lines.*

A strategy based on the visual loom's time-to-collision is shown to be a more sophisticated and efficient strategy to time the looming-related brain responses to virtual collisions (Kayed et al., 2008; Kayed & Van der Meer, 2000, 2007). This strategy is based on showing brain responses at a specific time before the loom would have made contact with the infant (see Figure 4d). A time strategy implies that as the loom's acceleration decreases, the loom's time away from the virtual collision is kept relatively constant (b), while the loom's visual angle increases (c).

If the infants showed their looming-related VEP responses at a specific time before the virtual collision, irrespective of loom speed, this could indicate that they are using the most efficient timing strategy based on the visual loom's time-to-collision. If, however, the infants are differentiating their looming-related VEP responses between the three looming speeds, this could indicate that they are using a less efficient timing strategy based on the visual angle of the loom.

#### **2.5.4. Frequency analysis**

EEG studies in the time-frequency domain have permitted the investigation of perceptual and cognitive functions through the manifestations of the natural frequencies in EEG oscillations (Basar et al., 1999). Oscillatory activity is activity occurring with several oscillations in a narrow frequency band, and it can be divided into two distinct categories: evoked and induced activity. Evoked activity is brain activity that is both time- and phase-locked. The basic assumption is that evoked activity, or signal of interest, has a more or less fixed time-delay to the stimulus, while the ongoing EEG activity behaves as additive noise (Pfurtscheller & Lopes da Silva, 1999). Averaging techniques can be used to enhance the signal-to-noise ratio of such activities (Pfurtscheller & Lopes da Silva, 1999). Induced activity, on the other hand, is only time-locked to the event and not phase-locked. Thus, this activity cannot be extracted by a simple linear method, such as averaging, but may be detected by frequency analysis. These event-related phenomena represent frequency-specific changes of the ongoing EEG activity and may consist of either decreases or increases of power in given frequency bands. This may be due to a decrease or an increase in synchrony of the underlying neuronal populations. This decrease in synchrony is called event-related desynchronization (ERD) (Pfurtscheller, 1977; Pfurtscheller & Aranibar, 1977), and the increase in synchrony is called

event-related synchronization (ERS) (Pfurtscheller, 1992). ERD and ERS reflect changes in the activity of local interactions between main neurons and interneurons that control the frequency components of the ongoing EEG (Pfurtscheller & Lopes da Silva, 1999). ERD is associated with an increase of task complexity or attention (Boiten, Sergeant & Geuze, 1992), while ERS is associated with neurons in a deactivated state (Pfurtscheller & Lopes da Silva, 1999). Temporal spectral evolution (TSE) is used to investigate change in power or amplitude over time.

Before computing a TSE, event-files were made for each infant separately and appended to the raw EEG data. Event-files were made so that only the marked looming-related peaks for each infant were included in the frequency analysis.

Time-frequency analyses were performed in brain space using source dipoles that modelled the main brain regions of interest, the parietal and visual cortices. Scalp waveforms have mixed contributions from underlying brain sources due to the wide distribution of focal brain activity at the surface of the scalp. This is due to the nature of the dipole fields when recording remotely and due to the smearing effect of the volume conduction in EEG. Thus, an optimal separation of brain activity was obtained by a source montage derived from a multiple source model. The model is used to create an inverse spatial filter, i.e. a source montage, which separates the different brain activities. The regional sources which were used are believed to be active in the visual processing of motion stimuli (Probst et al., 1993; Van der Meer et al., 2012; Zeki et al., 1991). The regional sources were (with Talairach coordinates, Talairach & Tournoux, 1988) the visual cortex radial left (VCrL),  $x = -0.32$ ,  $y = -0.55$ ,  $z = 0.11$ , visual cortex radial right (VCrR),  $x = 0.32$ ,  $y = -0.55$ ,  $z = 0.11$ , and the visual cortex ventral midline (VCvM),  $x = 0.00$ ,  $y = -0.70$ ,  $z = -0.08$ . In analyzing these sources, a 4-shell ellipsoidal head model (Berg and Scherg, 1994; Hoehstetter et al., 2004) was created for each infant and the source dipoles were inserted in the head models. As recommended, bone thickness was adjusted for infants at 3.0 mm and conductivity at  $0.02 \sigma$  (Grieve et al., 2003). The same settings of epoch, filter, and average parameters were used as stated above (see Section 2.5).

The resulting time-frequency displays represented the change in amplitude over time for each infant separately. To focus on only induced oscillatory brain activity, averaged evoked response signals were removed from the single trial time series before computing a TSE. TSEs for each of the three looming conditions (2, 3 and 4 s looms) were computed. In addition, comparisons between the three looming conditions were computed including TSEs of a combined looming condition which included all the three looming speeds. TSE displays



were limited between frequency cut-offs of 4 Hz and 40 Hz, while frequency and time sampling were set at 1 Hz, 50ms. BESA Statistics 1.0 (BESA GmbH) was used to test for significant differences between the three looming conditions. A combination of permutation tests and data clustering was employed in the statistical tests to address the multiple comparisons problem. Cluster alpha (the significance level for building clusters in time and/or frequency) was set at 0.005, number of permutations was set at 512, and the frequency cut-offs were the same as stated above with epochs set from -300 to 300 ms.

### 3.0 Results

The infants in this study provided a total of 555 trials where prominent visual looming-related VEP peaks occurred. On average, each infant contributed 18 trials ( $SD = 5$ ) where looming-related VEP peaks occurred at the first testing session, and 14 trials ( $SD = 6$ ) where looming-related VEP peaks occurred at the second session. Looming-related peaks were more or less evenly distributed among the three loom speeds and among the full-term and pre-term infants. Looming-related VEP responses were observed in the occipital and parietal areas, especially in electrode Oz and Pz some time before the loom would have made contact with the infant. However, not every infant showed looming-related VEP responses in the parietal areas, and therefore the analyses were only performed on the looming-related VEP responses observed in the occipital electrode Oz. The occipital electrode Oz showed the most prominent looming-related VEP peaks in all the three looming conditions at both sessions for both groups of infants.

#### 3.1 VEP responses

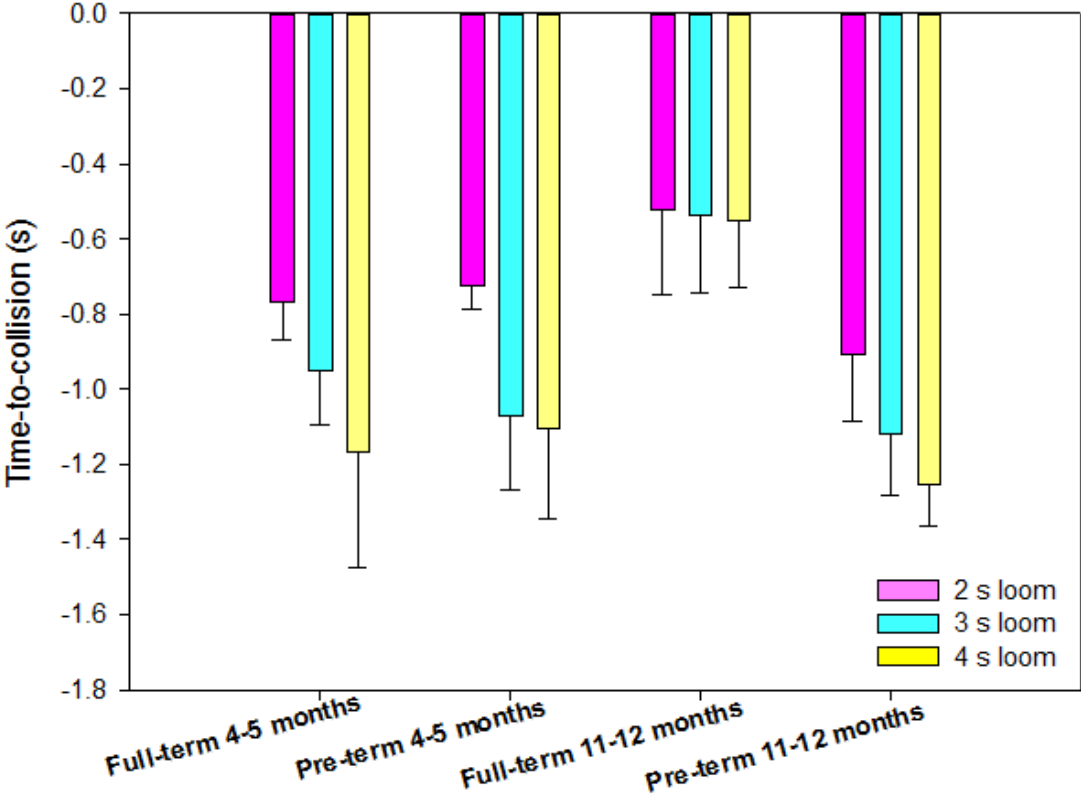
At the first testing session, the full-term infants showed their looming-related VEP responses on average  $-0.96$  s ( $SD = 0.25$ ) before contact, while the pre-term infants showed their looming-related VEP responses on average  $-0.97$  s ( $SD = 0.25$ ) before contact. With increasing age at the second testing session, the full-term infants showed their looming-related responses closer to the virtual collision, on average  $-0.54$  s ( $SD = 0.19$ ). However, the pre-term infants did not show their looming-related VEP responses closer to the virtual collision with age. At 11 to 12 months of age the pre-term infants showed their looming-related VEP responses on average  $-1.09$  s ( $SD = 0.21$ ) before the virtual collision (see Figure 5).

A 2 (group) x 2 (age) x 3 (loom condition) repeated measures ANOVA was performed on average looming-related peak activation. Adjustment for multiple comparisons was made by Bonferroni correction. The results showed a three-way interaction effect of age, group and looming condition,  $F(2, 32) = 3.53$ ,  $P < 0.05$ , indicating that the looming-related brain responses occurred closer to contact with increasing age only for the full-term infants, and that only the full-term infants at the age of 11 to 12 months showed their averaged looming-related brain responses at a fixed time-to-collision of about  $-0.54$  s ( $SD = 0.19$ ), irrespective of loom speed (see Figure 5). The pre-term infants, on the other hand, did not show their averaged looming-related brain responses at a fixed time-to-collision at the age of 11 to 12 months, and were showing their looming-related brain responses closer to contact for faster approaching looms. This indicated that the pre-term infants at the age of 11 to 12 months were

still using a timing strategy based on the loom’s visual angle, instead of the more advanced strategy based on the loom’s time-to-collision.

The results also showed a two-way interaction effect of age and group,  $F(1, 16) = 52.84, P < 0.001$ , indicating that irrespective of loom speed, the full-term infants at the age of 11 to 12 months responded significantly closer to time-to-contact than the 11- to 12-month-old pre-term infants.

In addition, the results showed a main effect of age,  $F(1, 16) = 15.15, P < 0.005$ , which could indicate that irrespective of loom speed, both the full-term infants and the pre-term infants showed their looming-related brain responses closer to contact with age. However, this effect is not real and is probably caused by the underlying two-way interaction of age and group since clearly only the full-term infants showed a significant decrease in their looming-related VEP responses with age.



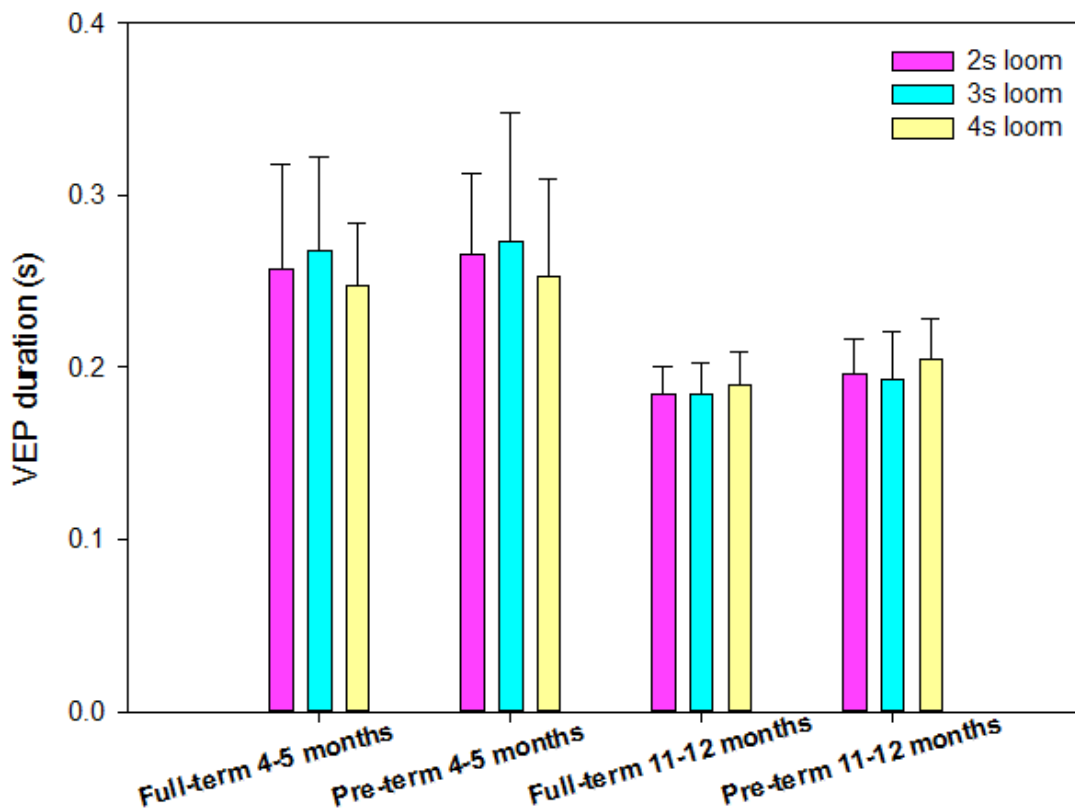
**Figure 5.** Averaged looming-related VEP peak activation (including SD bars) in the Oz electrode for the three loom speeds at the ages of 4 to 5 months and at the age of 11 to 12 months in both full-term- and pre-term infants. With increasing age, the full-term infants responded significantly closer to the loom’s time-to-contact than the pre-term infants. Only the full-term infants at the age of 11- to 12-months responded at a fixed time-to-contact of about -0.54 s irrespective of loom speed suggesting that the full-term infants, but not the pre-term

infants, had switched from a visual angle strategy to the more sophisticated time strategy during the time period studied.

### 3.2 VEP duration

Average VEP duration ( $VEP_{start} - VEP_{end}$ ) for looming-related peaks in the Oz electrode was -0.26 s (SD = 0.05) for 4- to 5-month-old full-term infants, and -0.26 s (SD = 0.06) for 4- to 5-month-old pre-term infants. Averaged VEP duration for 11- to 12-month-old full-term infants was -0.19 s (SD = 0.02), and -0.20 s (SD = 0.02) for 11- to 12-month-old pre-term infants (see Figure 6).

Another 2 (group) x 2 (age) x 3 (loom condition) repeated measures ANOVA was performed on average VEP duration. The results showed a main effect of age on average VEP duration,  $F(1, 16) = 44.01$ ,  $P < 0.001$ . This indicated that averaged VEP duration at 11- to 12-months of age was significantly shorter than averaged VEP duration at 4- to 5-months of age for both pre-term and full-term infants, irrespective of loom speed (see Figure 6).



**Figure 6.** Averaged VEP duration ( $VEP_{start} - VEP_{end}$ ) in the Oz electrode for looming-related VEP peaks (including SD bars) for the three loom speeds at the ages of 4 to 5 months and at the age of 11 to 12 months for both full-term and pre-term infants. The averaged VEP duration for looming-related VEP peaks across looms decreased significantly with age for both full-term and pre-term infants.

### 3.3 Timing strategies

When the infants were 4- to 5-months old, both the full-term and pre-term infants showed longer time-to-collision of their looming-related VEP responses with decreasing loom speed. This indicated that at the age of 4- to 5 months both the full-term and pre-term infants used a less efficient timing strategy based on the loom's visual angle to time their brain responses. At the age of 11- to 12 months the full-term infants showed their looming-related VEP responses at a fixed time-to-contact, which indicates that with decreasing loom acceleration, they showed their looming-related brain responses at relatively constant values of time-to-collision, while they allowed the visual angle to increase (see Figure 5). Thus, they appear to have switched from a less efficient timing strategy based on the loom's visual angle to the more efficient timing strategy based on the loom's time-to-collision with age. The pre-term infants at the age of 11- to 12-month, on the other hand, were showing their looming-related brain responses closer to contact for faster approaching looms, which could indicate that as the acceleration of the loom decreases, they were showing their looming-related brain responses at relatively constant values of the loom's visual angle, while they allowed the loom's time-to-collision to increase (see Figure 5). Thus, the pre-term infants appeared still to be using a less efficient timing strategy based on the loom's visual angle at the age of 11 to 12 months.

### 3.4 Individual analysis

Following that the pre-term infants did not improve the timing of their looming-related brain responses with age, the averaged looming-related VEP responses for both full-term and pre-term infants at 11 to 12 months of age were further explored to see whether there could be a criterion to distinguish the pre-term infants who were using a less efficient timing strategy when responding to the three looming speeds. Field (2013) formulated an outlier as values larger or smaller than the mean  $\pm$  SD\*2.5. The criterion values in this study were based on standard deviations of the time-to-collision values between the three looming conditions where high standard deviations could indicate that the infants are not using a timing strategy based on the loom's time-to-collision. Only criterion values for the 11- to 12-month-old full-term infants' averaged looming-related VEP responses were computed based on the mean and standard deviation of the time-to-collision values for the three looming conditions. The 11- to 12-month-old pre-term infants who showed averaged looming-related VEP responses above these criterion values were marked (see Table 1). The applied criterion pointed to only one pre-term infant, infant SP, who at 11 to 12 months of age showed an unusually high standard deviation in the averaged looming-related VEP responses between the three looming speeds.

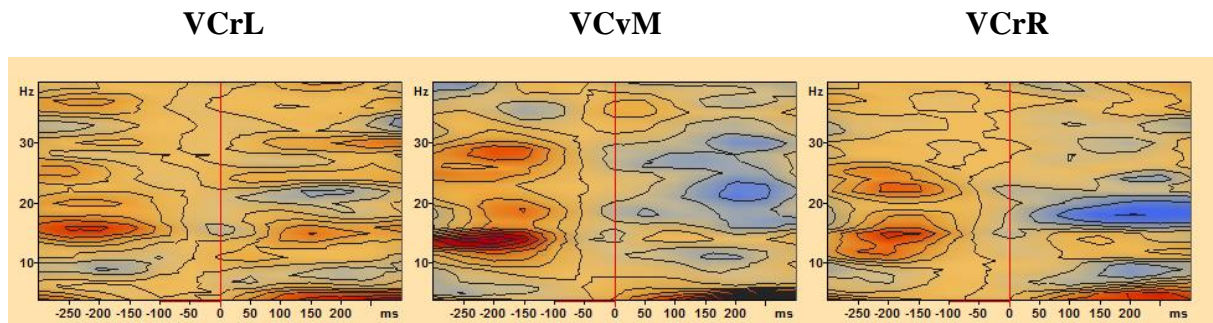
Full-term	2s	3s	4s	SD	Pre-term	2s	3s	4s	SD
AA	-0.811	-0.653	-0.529	0.142	AJ	-0.936	-1.102	-1.310	0.187
AB	-0.534	-0.635	-0.671	0.071	DK	-1.197	-1.326	-1.181	0.079
BC	-0.611	-0.708	-0.700	0.054	DL	-0.922	-1.113	-1.321	0.200
BD	-0.541	-0.268	-0.559	0.163	EM	-1.086	-1.424	-1.360	0.179
JE	-0.131	-0.132	-0.126	0.003	FN	-0.757	-1.088	-1.242	0.248
GF	-0.584	-0.640	-0.671	0.044	MO	-0.949	-1.063	-1.384	0.225
MG	-0.377	-0.562	-0.497	0.094	SP	-0.648	-1.033	-1.259	<b>0.309</b>
SH	-0.306	-0.711	-0.560	0.205	TQ	-0.701	-1.072	-1.211	0.264
SI	-0.819	-0.542	-0.656	0.139	WR	-0.977	-0.863	-1.025	0.083
<b>Mean</b>				<b>0.102</b>					<b>0.197</b>
<b>SD</b>				<b>0.065</b>					<b>0.077</b>
<b>Mean+SD*2.5</b>				<b>0.264</b>					

**Table 1.** Averaged time-to-collision values (ms) and standard deviations for the three looming conditions for both group of infants at the age of 11 to 12 months. The highlighted number indicate the pre-term infant who showed standard deviation greater than mean + SD\*2.5 of the standard deviations of the full-term group. Pre-term infant SP showed an unusually high standard deviation in response time to the three looming conditions which could be indicative of the infant gearing the looming-related VEP responses not to time-to-collision, but to the visual angle of the approaching looming object.

### 3.5 Time-frequency analysis (TSE)

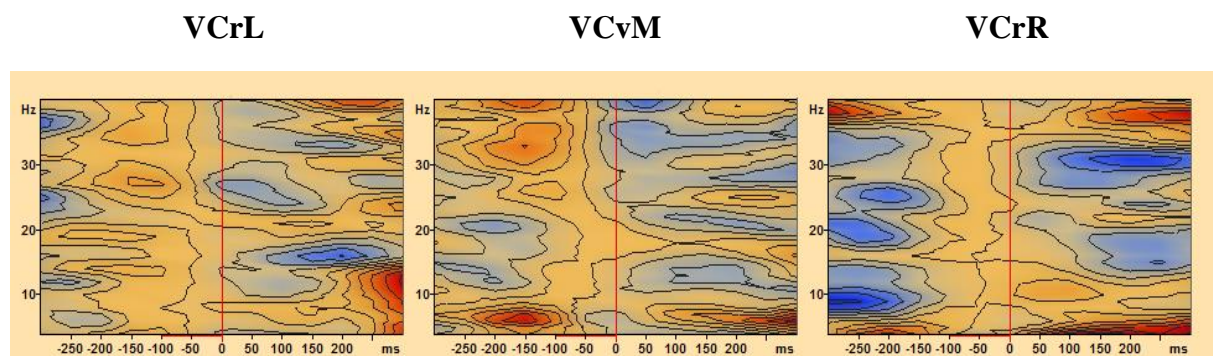
The TSE maps of the combined looming condition, which included all the three looming speeds, in full-term infants at the age of 4 to 5 months show synchronization in the theta frequency band in two or more visual sources of interest. The average latency of maximum induced ERS in the three visual sources VCrL, VCvM, and VCrR was 240 ms (SD = 61.3), while the average frequency of maximum induced ERS was 4.7 Hz (SD = 0.7). The combined looming condition also shows desynchronization in the alpha frequency band. The average latency of maximum induced ERD was 164 (SD = 77.4), while the average frequency of maximum induced ERD was 10.4 Hz (SD = 2.4) (see Figure 7 and also Appendix A and B). Figure 7 shows the results of one typical full-term infant's TSE map for the combined looming condition at the age of 4 to 5 months. No significant differences between the three

looming conditions were found with regard to induced activity when they were compared to each other.



**Figure 7.** TSE map of the combined looming condition for one typical full-term infant at the age of 4 to 5 months with an epoch length of -300 ms to 300 ms. VCrL, VCvM, and VCrR represent the visual areas of interest. The vertical red line marks the top of the looming-related VEP peak. Synchronization can readily be seen in the theta frequency band (red), and desynchronization can be seen in the alpha frequency band (blue).

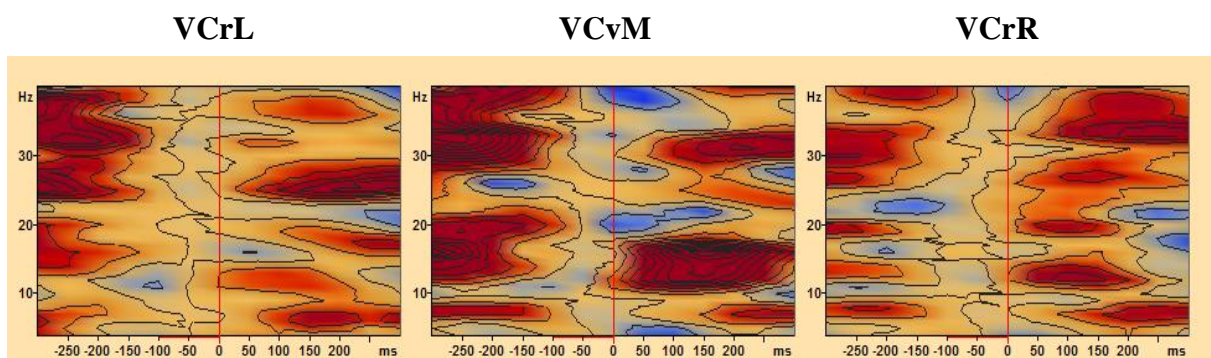
The TSE maps of the combined looming condition in pre-term infants at the age of 4 to 5 months show synchronization in the theta frequency band in one or more visual sources of interest in all but one infant who did not show any synchronization in any of the visual sources. The average latency of maximum induced ERS in the three visual sources VCrL, VCvM, and VCrR was 247 ms (SD = 69.8), while the average frequency of maximum induced ERS was 5.8 Hz (SD = 2.3). The combined looming condition also shows desynchronization in the alpha frequency band. The average latency of maximum induced ERD was 207 ms (SD = 76.1), while the average frequency of maximum induced ERD was 10.8 Hz (SD = 3.0) (see Figure 8 and also Appendix A and B). Figure 8 shows the results of one typical pre-term infant's TSE map for the combined looming condition at the age of 4 to 5 months. Again, no significant differences were found between the three looming conditions with regard to induced activity when they were compared to each other.



**Figure 8.** TSE map of the combined looming condition for one typical pre-term infant at the age of 4 to 5 months with an epoch length of -300ms to 300 ms. VCrL, VCvM, and VCrR represent the visual areas. A vertical

red line marks the top of the looming-related VEP peak. Synchronization can readily be seen in the theta frequency band (red), and desynchronization can be seen in the alpha frequency band (blue).

The TSE maps of the combined looming condition in full-term infants at the age of 11- to 12-months show synchronization in the theta frequency band in two or more visual sources of interest. The average latency of maximum induced ERS was 232 ms (SD = 75.3), while the average frequency of maximum induced ERS was 5.8 Hz (SD = 1.1). The combined looming condition also shows desynchronization in the late alpha frequency band. The average latency of maximum induced ERD was 244 ms (SD = 53.8), while the average frequency of maximum induced ERD was 11.1 Hz (SD = 3.0). Further, the combined looming condition shows synchronization in the early beta frequency band in one or more of the visual sources of interest. The average latency of maximum induced ERS was 249 ms (SD = 60.9), while the average frequency of maximum induced ERS was 17.5 Hz (SD = 5.1) (see Figure 9 and Appendix A and B). Figure 9 shows the results of one typical full-term infant's TSE map for the combined looming condition at the age of 11 to 12 months. There were no significant differences between the three looming conditions with regard to induced activity when they were each compared with each other.

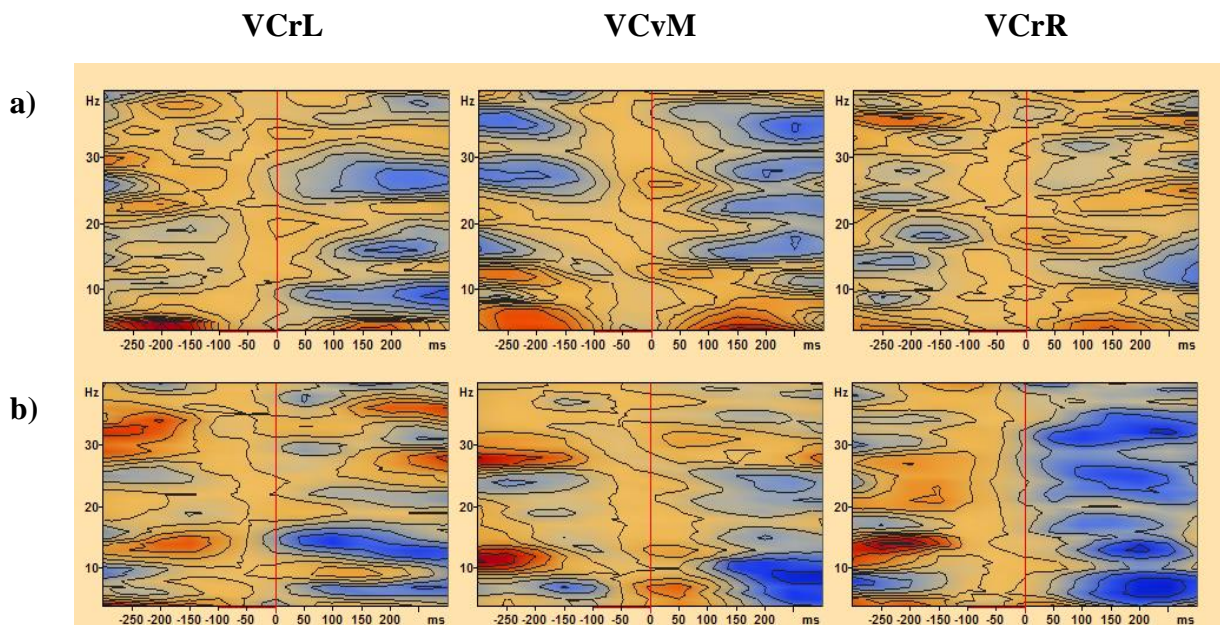


**Figure 9.** TSE map of the combined looming condition for one typical full-term infant at the age of 11 to 12 months with an epoch length of -300 ms to 300 ms. VCrL, VCvM, and VCrR represent the visual areas. A vertical red line marks the top of the looming-related VEP peak. Synchronization can readily be seen in the theta frequency band (red), desynchronization can be seen in the late alpha frequency band (blue), and synchronization can be seen in the early beta frequency band (red).

The TSE maps of the combined looming condition in pre-term infants at the age of 11 to 12 months show synchronization in the theta frequency band in two or more visual sources of interest. The average latency of maximum induced ERS was 229 ms (SD = 86.2), while the average frequency of maximum induced ERS was 6.0 Hz (SD = 2.1). The combined looming condition also shows desynchronization in the late alpha frequency band in two or more visual sources of interest. The average latency of maximum induced ERD was 218 ms (SD =



80.9), while the average frequency of maximum induced ERD was 10.8 Hz (SD = 3.4). Further, the combined looming condition shows synchronization in the early beta frequency band in one or more of the visual sources of interest. The average latency of maximum induced ERS was 217 ms (SD = 79.4), while the average frequency of maximum induced ERS was 18.4 Hz (SD = 5.0) (see Appendix A and B). Figure 10 shows the results of two pre-term infants' TSE maps of the combined looming condition which did not show the same results as the other infants' TSE maps in the pre-term group at the age of 11 to 12 months (see Figure 10 a and b and Appendix A and B). Again, no significant differences were found between the three looming conditions with regard to induced activity when they were compared to each other.



**Figure 10.** TSE maps of the combined looming condition for two pre-term infants that did not show the same results as the other infants in the pre-term group at the age of 11 to 12 months. The TSE maps have an epoch length of -300 ms to 300 ms and a vertical red line marks the top of the looming-related VEP peak. VCrL, VCvM, and VCrR represents the visual areas. **a)** shows the TSE map of pre-term infant AJ. Synchronization is observed in the theta frequency band (red) and desynchronization is observed in the late alpha frequency band (blue) as was observed in the other pre-term infants' TSE maps. However, the pre-term infant AJ's TSE map shows desynchronization in the early beta frequency band (blue) in the visual sources of interest VCrL and VCvM, and only a small amount of synchronization in the early beta frequency band (red) in the visual source VCrR. **b)** shows the TSE map of pre-term infant DL. Synchronization is observed in the theta frequency band (red) in only one visual source of interest (VCvM). Desynchronization is observed in the late alpha frequency band (blue) as was observed in the other pre-term infants' TSE maps, but the TSE map does not show any synchronization in the early beta frequency band as the other pre-term infants' TSE maps showed, except for a small amount of synchronization in the early beta frequency band (red) in the visual source VCrL.

## 4.0 Discussion

The present longitudinal study used high-density EEG measurements of infants' brain electrical activity to find evidence for developmental differences between normally developing pre-term and full-term infants' perception and processing of a looming virtual object that approaches them on a direct collision course under different accelerations. VEP analyses were used to investigate whether there are any differences between the two groups of infants' brain responses to virtual collisions at the age of 4 to 5 months and 11 to 12 months of age. VEP responses to the visual looming object, VEP duration of looming-related VEP peaks, and timing strategies were analyzed and compared between the pre-term and full-term infants. In addition, an individual analysis of the pre-term infants' brain responses to the virtual collision at the age of 11 to 12 months was carried out. A time-frequency analysis to investigate induced oscillatory brain activities as a function of visual motion perception in both pre-term and full-term infants was carried out.

In the course of development from 4 to 5 months to 11 to 12 months of age a significant improvement in looming-related brain responses where the brain responses occurred closer to contact with increasing age was only observed in the full-term infants. This result supports earlier findings of a longitudinal study which compared full-term infants at 5 to 6 months of age and 12 to 13 months of age with the same experimental paradigm (Van der Meer et al., 2012), and indicates that the full-term infants in the present study have developed prospective control when a virtual object is approaching them on a direct collision course. One possible contributing factor to the observed improvement in visual motion perception of a virtual looming object is possibly specialization of neuronal networks in the dorsal visual stream caused by increasing self-initiated locomotor experience during the first year of life (Edelman, 1993; Johnson, 2000), which causes the infants to use less time to process the looms allowing them to respond closer to the virtual collision. On the other hand, the pre-term infants did not show their looming-related brain responses closer to contact with increasing age, suggesting that they had not developed specialized neuronal networks in the dorsal visual stream at 11 to 12 months of age.

The results also revealed that only the full-term infants showed their looming-related brain responses at a fixed time-to-collision at the age of 11 to 12 months. This result indicates that the full-term infants by the age of 11 to 12 months had switched from a less efficient strategy based on the looms' visual angle to a more sophisticated and efficient strategy based on time. A timing strategy based on time is less prone to misjudgments and allows infants to deal with more demanding perceptual tasks. Full-term infants at the age of 11 to 12 months

showed their brain responses when the looming object reached a specific time before the optical collision, thereby allowing themselves the same amount of time to make a response irrespective of the loom's speed. This is also supported by earlier findings (Kayed & Van der Meer, 2000, 2007; Van der Meer et al., 2012). The fact that the pre-term infants at the age of 11 to 12 months showed their looming-related brain responses closer to contact for faster approaching looms, suggests that they are using a less efficient timing strategy based on the looms' visual angle. This timing strategy causes the pre-term infants to have problems with slow, accelerating approaches where they are showing a brain response too early in the looming sequence causing them to blink too early, which leads to a reopening of their eyes before the looming object would have made contact with them. This could lead to injury of the sensitive cornea of the eye and indicates that the pre-term infants have problems with prospective control.

The duration of the looming-related brain responses significantly decreased with increasing age in both pre-term and full-term infants. Shorter duration of looming-related VEP responses with growing age could indicate an increase in processing speed of visual information. A major contributing factor to this observed improvement could be myelination of neurons in the dorsal stream of the visual cortex which increases the speed of the electrical impulse propagation from soma to dendrites (Dubois et al., 2008, Webb et al., 2005). During early maturational stages until adulthood, white matter fibers increase in volume and density due to the ongoing axonal myelination (Webb et al., 2005). According to Johnson (2000), the infant brain during the first year of life undergoes rapid changes and also doubles in weight, suggesting that infants at the age of 4 to 5 months have less developed brains compared to when they are 11 to 12 months old. The fact that both the pre-term and full-term infants in this study showed shorter VEP duration with growing age could indicate a developmental trend. Shorter duration of VEP peaks with age could also indicate that as infants get older they need less time to process the looms.

In addition to VEP analyses, a time-frequency analysis was carried to study the changes in induced brain oscillations as a function of visual motion perception in both pre-term and full-term infants. The results from the TSE analyses of the combined looming condition showed desynchronization in the early alpha frequency band for both full-term and pre-term infants at the age of 4 to 5 months. This is consistent with the fact that normal infants' EEG is dominated by low frequency activity of large amplitudes (Orekhova et al., 2006; Thierry, 2005). Low frequency activity is considered to reflect the complex aspect of the motion stimuli (Pfurtscheller & Lopes da Silva, 1999). The desynchronization in the early

alpha frequency band could be an oscillatory mechanism for communication between underlining cortical networks when processing motion in infancy. The theta activity in the EEG of infants and young children is generally considered as a sign of immaturity (Orehova et al., 2006; Thierry, 2005). Thus, both the pre-term and full-term infants in the present study may have little specialization for motion (Dubois, Hertz-Pannier, Dehaene-Lambertz, Cointepass & Le Bihan, 2006; Edelman, 1993, Johnson, 2000; Mukherjee, 2002; Paus, 2001) at the age of 4 to 5 months where slowly oscillating cell assemblies have an abundance of neurons that are not specialized, resulting in an inefficient visual motion perception at the age of 4 to 5 months. This is supported by another longitudinal study of induced brain electrical activity in infants 3 to 4 months old and 11 to 12 months old where the infants were exposed to motion stimuli simulating ego-motion (Agyei et al., 2015). A possible explanation for this result could be that young infants have little experience with motion stimuli caused by their lack of experience with self-initiated locomotion at an early age.

Infants start to explore the world right after they are born either in a stroller or in the arms of their parents, and this gives them passive experience with the world. Self-produced locomotion is found to be superior to passive observation and turns out to be crucial for the normal development of visual motion perception (Held & Hein, 1963). With adequate neurobiological development and locomotor experience the full-term infants at 11- to 12-months of age showed a more adult-like specialization for motion (Carmeli, Knyazeva, Innocenti & De Feo, 2005; Van der Meer et al., 2008) where fast oscillating cell assemblies have fewer but more specialized neurons, resulting in improved visual motion perception. The results from the TSE analyses of the combined looming condition when the full-term infants were 11 to 12 months of age showed synchronization in the early beta frequency band. This means that the neurons are oscillating at higher frequencies which indicates a progressive shift in cortical coupling where slower early alpha band desynchronization network communication gradually makes way for a much faster and effective cortical coupling using synchronized high-frequency oscillations particularly in the early beta frequency band when processing looming motion at the age of 11 to 12 months. This is also supported by previous research (Agyei et al., 2015). The pre-term infants at the age of 11 to 12 months also showed synchronization in the early beta frequency band like the full-term infants at the same age. However, two of the pre-term infants showed little to no synchronization in the early beta frequency band in their combined looming condition TSEs. This indicates that these two pre-term infants at the age of 11 to 12 months have less specialized neuronal networks for processing motion than their full-term peers.

Both the results from the VEP and the TSE analyses revealed that pre-term infants have less specialized neuronal networks for processing motion stimuli on a direct collision course than their full-term peers. Another explanation of the results could be impairments in cerebral development such as neuronal loss or impaired differentiation with a reduction in dendritic and axonal development. In the absence of major sensory, physical, or intellectual disability, some pre-term infants have been referred to as ‘clumsy’ (Losse et al., 1991) or as having perceptual-motor dysfunction (Lazlo & Sainsbury, 1993; Jongmans, Mercuri, Dubowitz & Henderson, 1998), deficits in attention, motor control and perception (Landgren, Kjellman & Gillberg, 1998), and developmental coordination disorder (DCD; Wilson, Pollock, Kaplan, Law & Faris, 1992). DCD is defined as impairment of motor performance sufficient to produce functional performance not explicable by the child’s age, intellect, or other diagnosable neurological or psychiatric disorders (Polatajko, et al., 1995). Other features such as learning disabilities, attention deficit, poor social skills, low motivation, and poor self-esteem may be associated with DCD (Shaw, Levine & Belfer, 1982; Schoemaker & Kalverboer, 1994). Thus, several studies have linked prematurity to problems in perceptual-motor function. Although motor difficulties are less severe for pre-term children than those of children with CP, the ‘clumsiness’ experienced by pre-term children affects progress in school and adjustment in many pre-term infants. Vision-related problems have a major impact on the education and rehabilitation of pre-term children and may result in academic failure and cognitive deficits that persist into adolescence and adulthood (Luu et al., 2009).

Research has suggested that a vulnerable dorsal stream may be the explanation to as why motion perception is less efficient in pre-term infants even in the absence of brain damage (Guzetta et al., 2009). Tremblay et al. (2014) suggest that pre-term infants have a developmental delay for the dorsal stream (the M pathway) but not the ventral stream (the P pathway), and that this delay seems to resolve gradually with age. This confirms the developmental vulnerability of the M pathway compared to the P pathway in pre-term infants reported in previous studies (Hammarenger et al., 2007), which also showed that prematurity appears to disrupt the development of the M pathway in pre-term infants aged between 16 and 52 weeks compared to full-term infants. The M pathway development is thought to occur before birth in the intrauterine environment during the third trimester of pregnancy, whereas the P pathway is thought to develop several weeks later, after birth during the neonatal period in full-terms (Hammarenger et al., 2003). This explains why a premature birth more significantly affects the M pathway than the P pathway (Hammarenger et al., 2007). Braddick et al. (2003) also present a body of evidence suggesting that functioning within the ventral

visual stream matures earlier than dorsal visual stream functioning. The visual experience hypothesis states that because pre-term infants are born earlier than full-term infants, pre-term infants have more visual experience compared to age-matched full-term infants (Bosworth & Dobkins, 2013). This additional visual experience might accelerate the visual maturation of the P pathway. Bosworth and Dobkins (2009, 2013) showed that in healthy pre-term infants, P pathway maturation is positively influenced by the extra visual experience, but no significant effect was reported on the M pathway. Thus, the additional visual experience may compensate for the negative effect of prematurity on the P pathway, but not on the M pathway, which might explain why Tremblay et al. (2014) found a maturational delay for the M pathway, but not the P pathway. Overall, their results suggest that in 12-month-old pre-term infants, the ventral stream (occipito-temporal or P pathway) is normally developed, whereas the dorsal stream (occipito-parietal or M pathway) is still immature (Tremblay et al., 2014). Thus, the pre-term infants in the present study seem to be behind their full-term peers in development of visual motion processing. Even though they showed a decrease in the duration of their brain responses with age, which indicates that they have adequate myelination of neurons in the dorsal visual stream, their VEPs and TSEs indicate that they do not have specialized networks for visual motion perception at the age of 11 to 12 months.

Accurate processing of motion is critical for many aspects of visuo-motor planning and control (MacKay et al., 2005), for example when grasping a moving object, or avoiding an object on a direct collision course. Individual analysis can point out those infants that are more vulnerable to dysfunction in visual motion processing than other infants, and the outlier values of the individual analysis revealed that one infant had a larger standard deviation in response time to the three looming conditions which could be indicative of the infant gearing the looming-related VEP responses not to time-to-collision, but to the visual angle of the approaching looming object at the age of 11 to 12 months. To be able to utilize the criterion as an early screening tool for visual motion perception impairment, more longitudinal follow-up on these pre-term infants is necessary. As mentioned, the TSE revealed that two pre-term infants showed little to no synchronization in the early beta frequency band, which indicates that they may be more vulnerable during development of visual motion processing than their pre-term peers at the age of 11 to 12 months. More follow-up research on these pre-term infants is also necessary to see if their lack of synchronization in the early beta frequency band could be a normal developmental delay to be recovered as they grow older.

In conclusion, the results from the VEP analyses showed that with growing age, full-term infants responded to a visual looming object at a fixed time-to-collision close to virtual

contact and showed shorter duration of looming-related VEPs in the visual cortex. This indicates that they have developed prospective control when a virtual looming object is approaching on a direct collision course, where they use a strategy based on time to make the looming-related brain response. Thus, with adequate neurobiological development and locomotor experience they seemed to develop specialized networks for perception of visual motion. On the other hand, the pre-term infants at 11 to 12 months of age did not significantly decrease their looming-related brain responses as close to contact as their full-term peers and were showing their looming-related brain responses closer to contact for faster approaching looms using a timing strategy based on the looms' visual angle. This could be caused by impairments in cerebral development such as neuronal loss or impaired differentiation with a reduction in dendritic and axonal development, and indicates that they may have a vulnerable dorsal stream which could be an early indication of perceptuo-motor problems later on in development. However, the pre-term infants did show shorter VEP durations with age, indicating that they have an adequate amount of neuronal myelination. More longitudinal research should be carried out to gain a better understanding of the developmental progress of visual motion perception in pre-term infants before the results can be used to aid an early diagnosis. Future research should include more participants as the groups of participants in this study were quite small. It is still important to look at the neurobiological development in pre-term children early in development, since early measures should, in the long term, help pre-term children develop cognitive abilities that allow them to reach their true intellectual and social potential. It would also be interesting to test the same infants at the age of 5 years to see whether they have improved their perception of visual motion or not, since this is the age at which the children are starting at school and they may encounter problems with perceptual-motor actions which may influence both their achievement in school and self-esteem or have other potential effects on their everyday lives.

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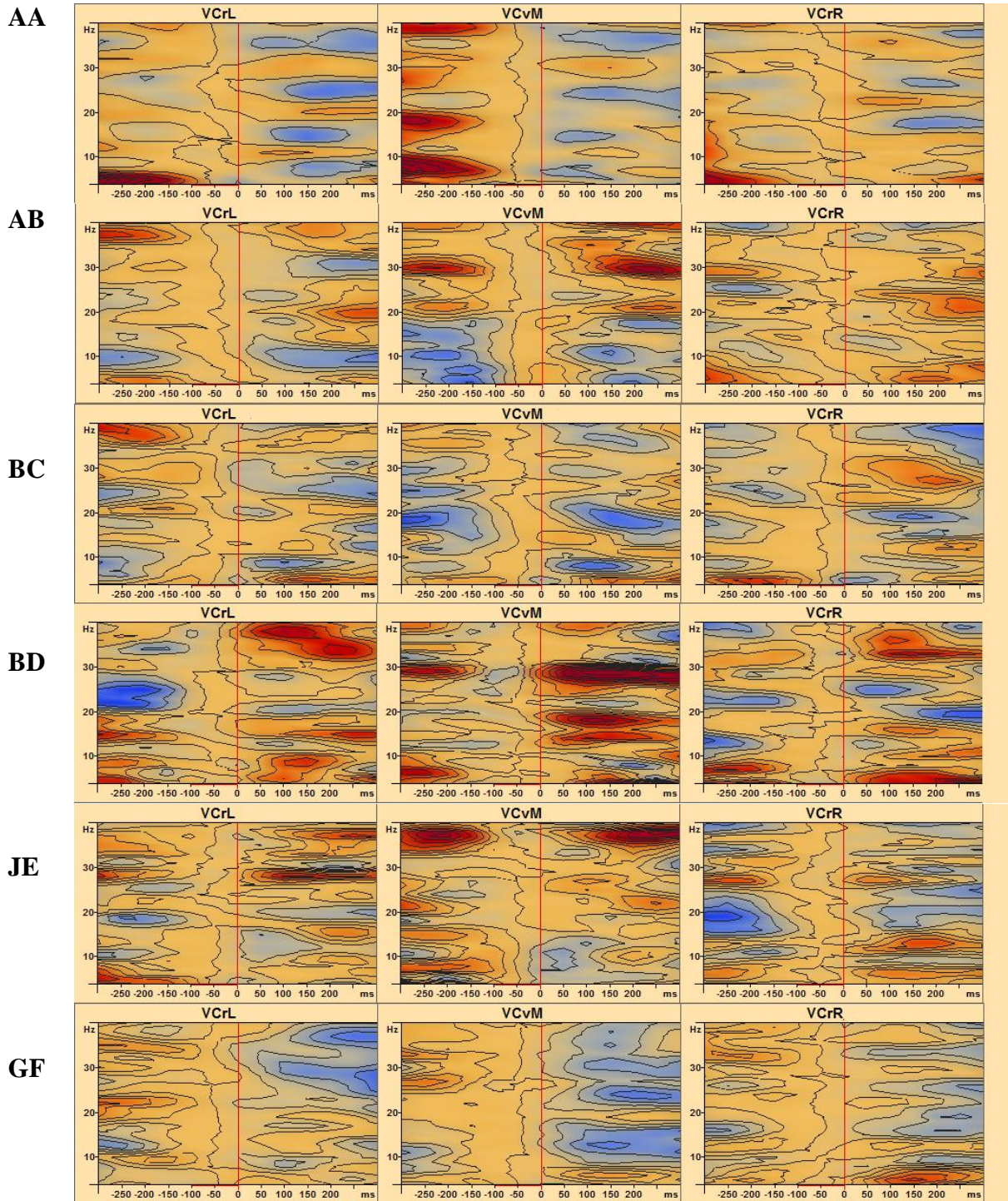
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## APPENDICES

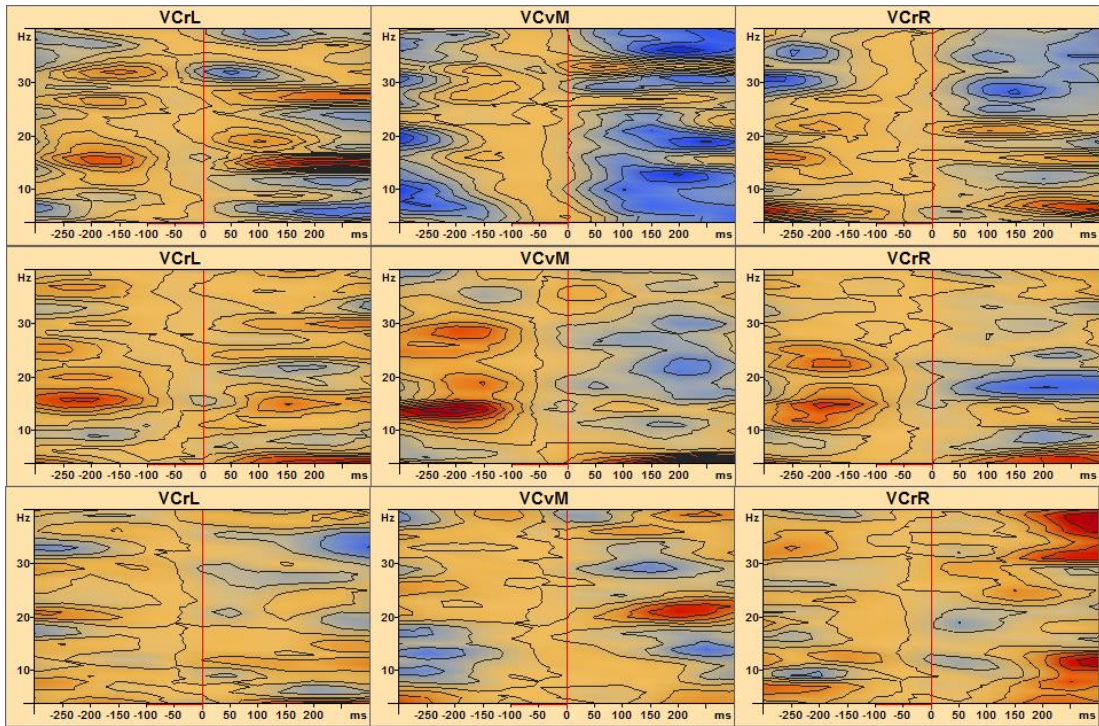
**Appendix A:** TSE maps of the combined looming condition over brain regions VCrL, VCvM, and VCrR in 4- to 5-month-old full-term and pre-term infants. Induced desynchronized and induced synchronized activities are shown in blue and red contours, respectively. Low amplitudes (induced theta-band synchronized activities) can be seen in one or more visual areas. At higher frequencies (alpha frequency band), induced desynchronized activities can also be observed. Epoch is from -300 ms to 300 ms and the frequency is from 4 Hz to 40 Hz.

### Full-term infants

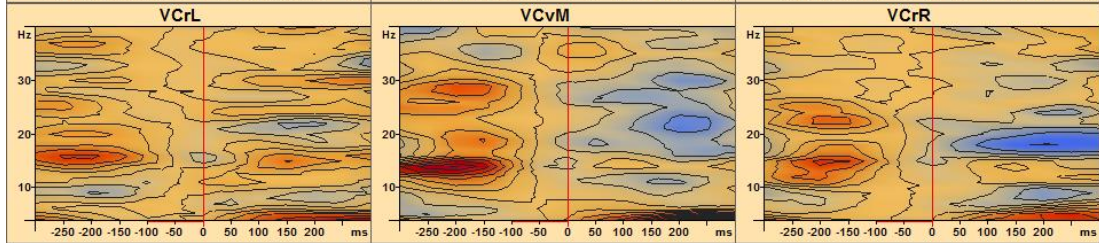




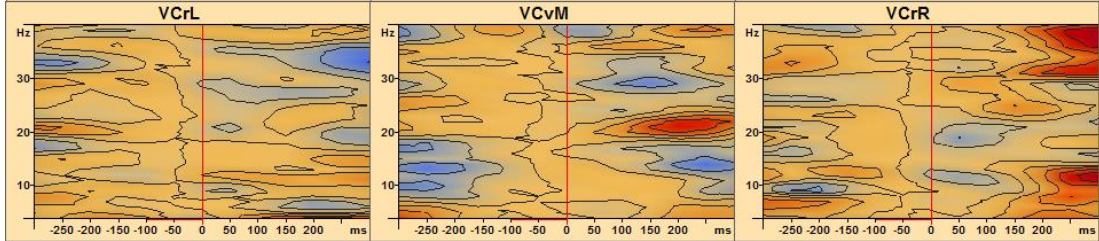
**MG**



**SH**

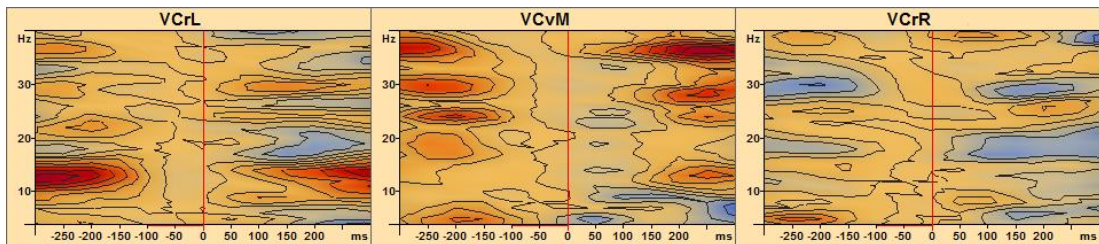


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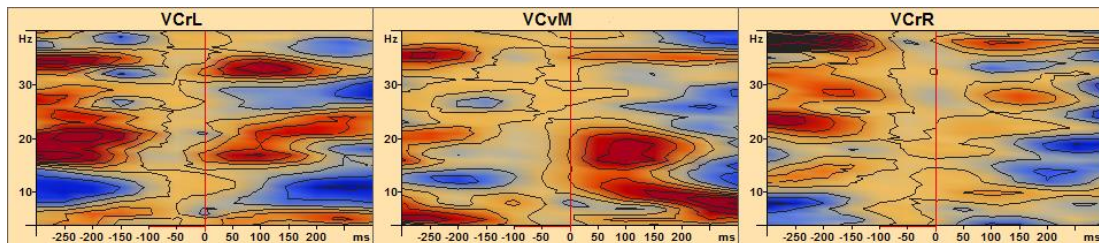


**Pre-term infants**

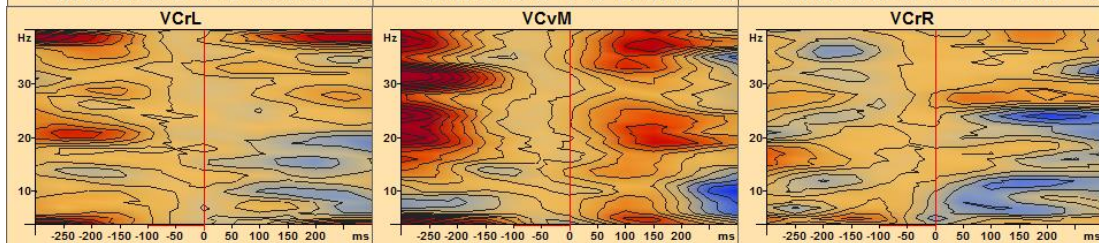
**AJ**



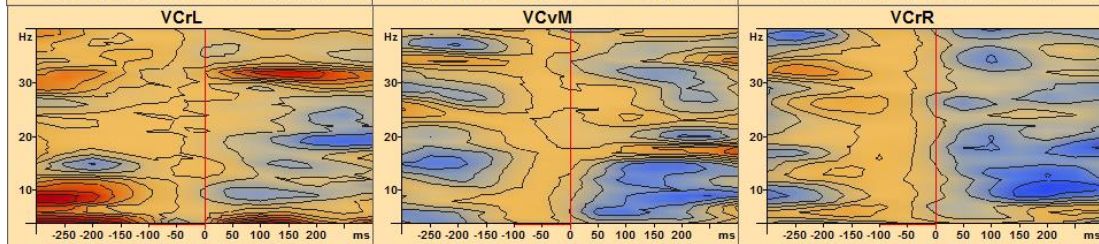
**DK**



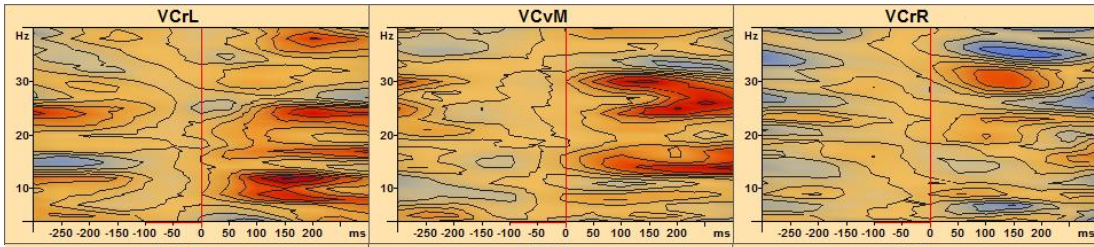
**DL**



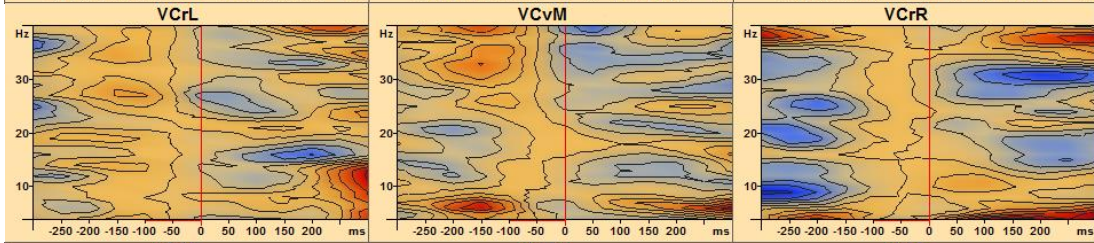
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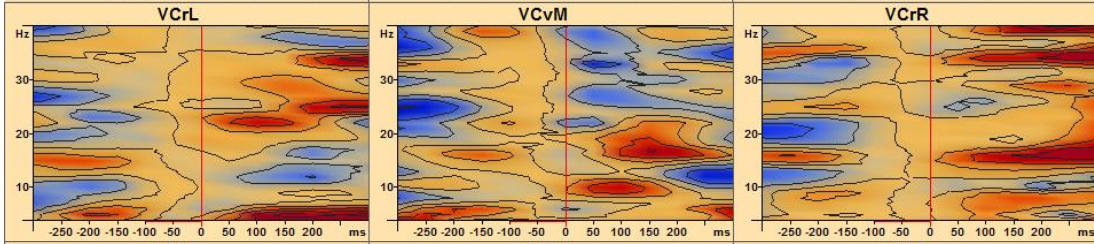
**FN**



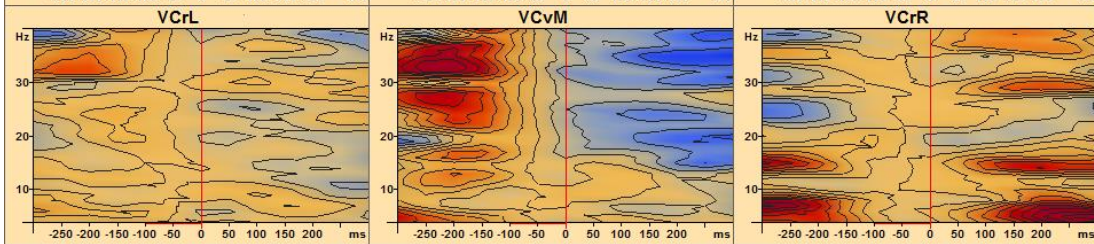
**MO**



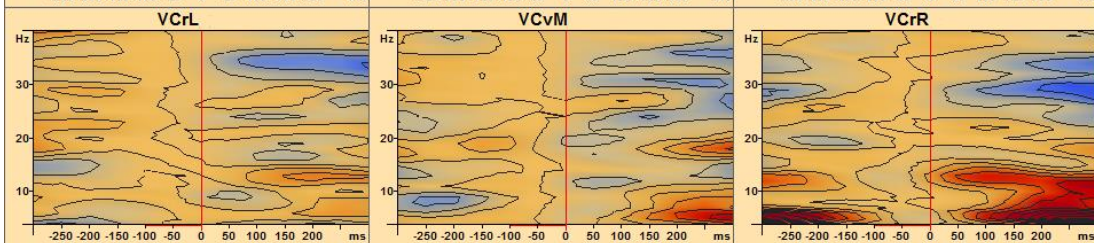
**TQ**



**SP**

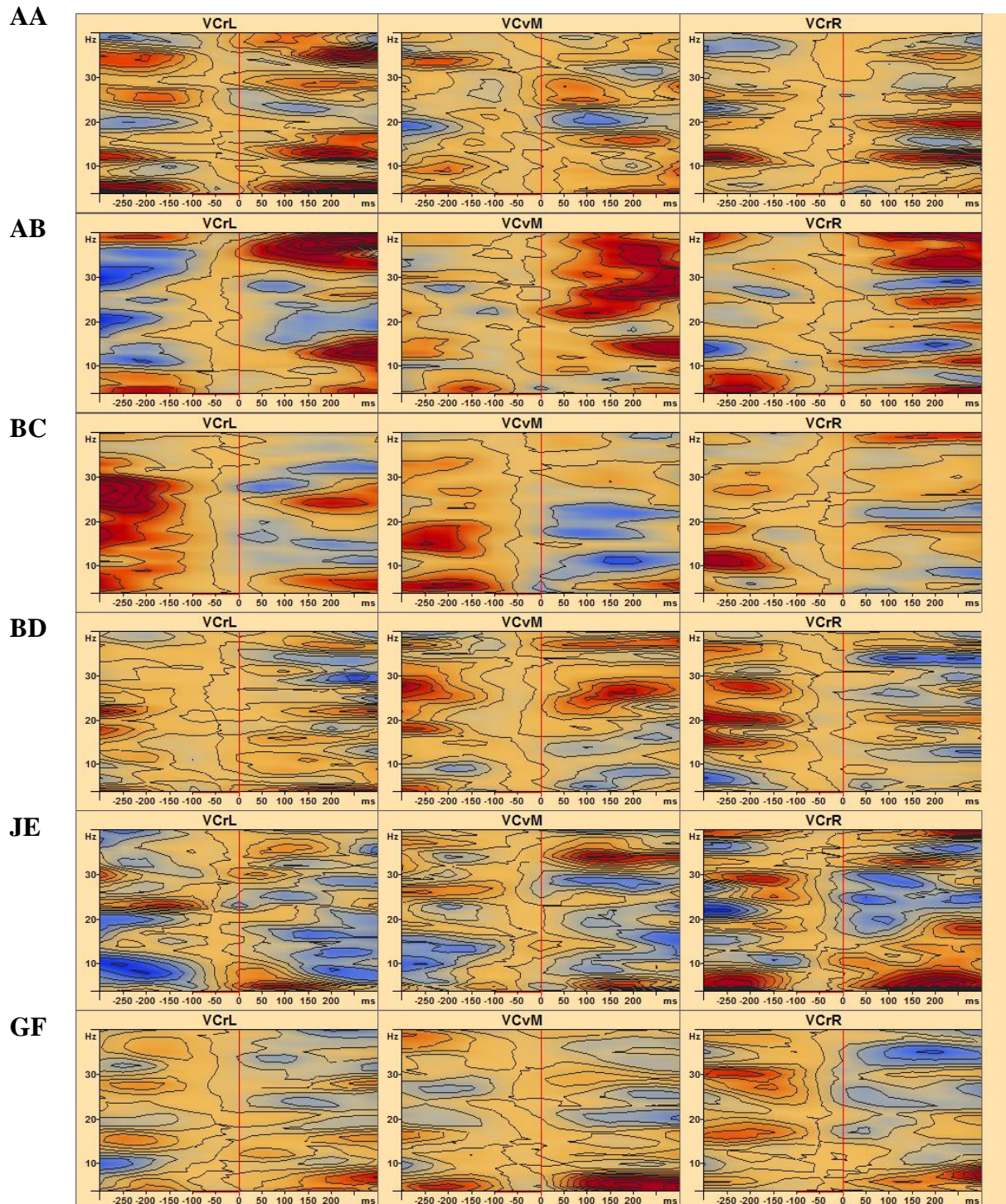


**WR**

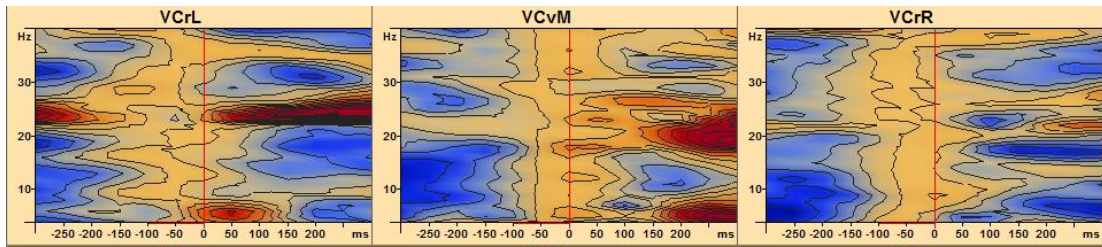


TSE maps of the combined looming condition over brain regions VCrL, VCvM, and VCrR in 11- to 12-month-old full-term and pre-term infants. Induced desynchronized and induced synchronized activities are shown in blue and red contours, respectively. Low amplitudes (induced theta-band synchronized activities) can be seen in one or more visual areas. At higher frequencies (late alpha frequency band), induced desynchronized activities can also be observed, and at even higher frequencies (early beta frequency band), induced synchronized activities can be observed again. Epoch is from -300 ms to 300 ms and the frequency is from 4 Hz to 40 Hz.

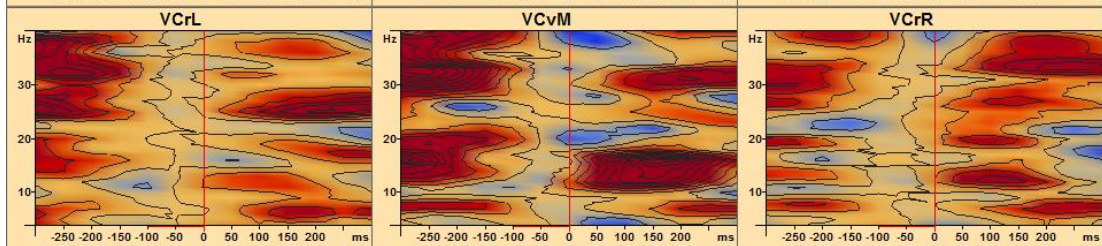
### Full-term infants



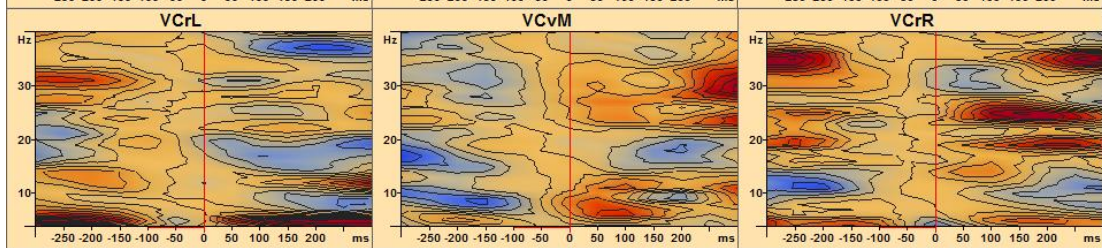
**MG**



**SH**

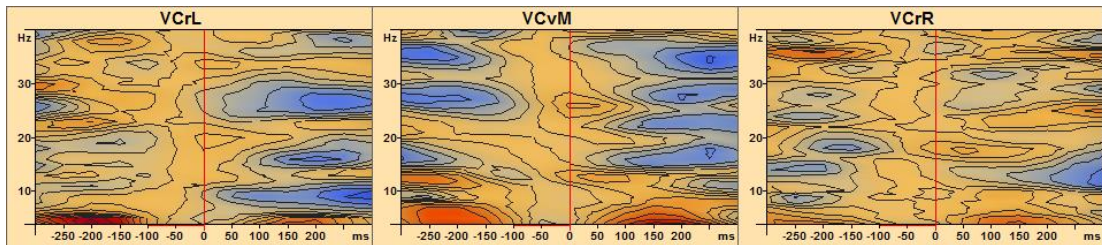


**SI**

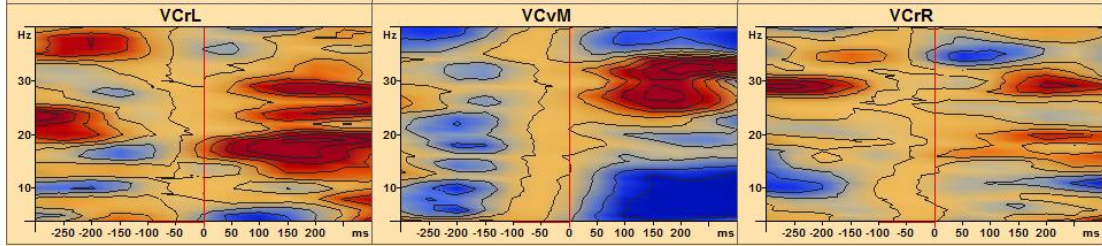


**Pre-term infants**

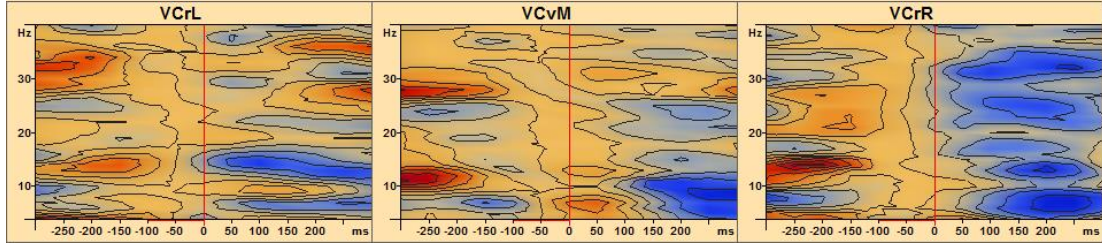
**AJ**



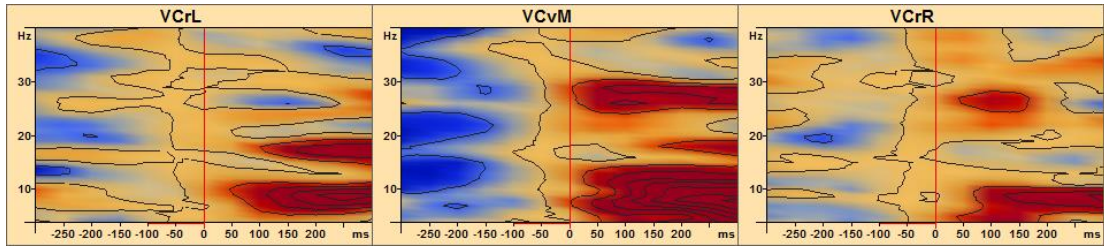
**DK**



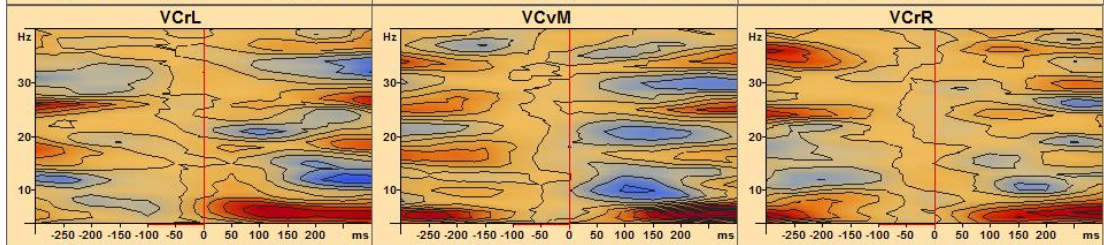
**DL**



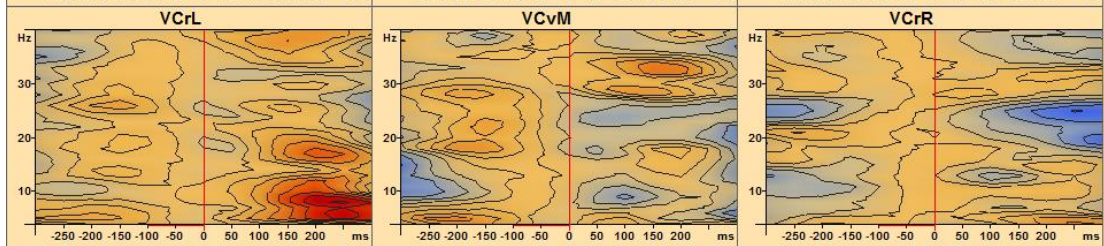
**EM**



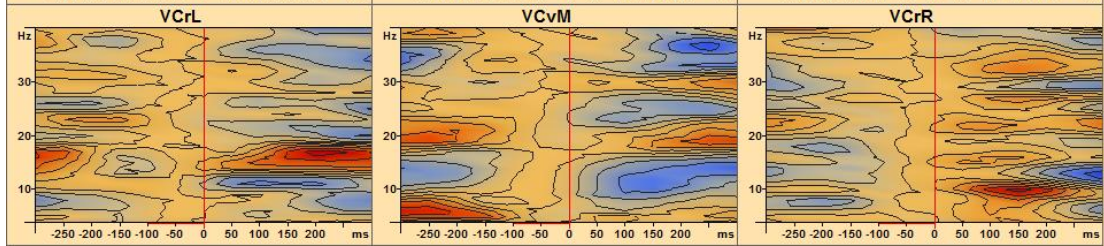
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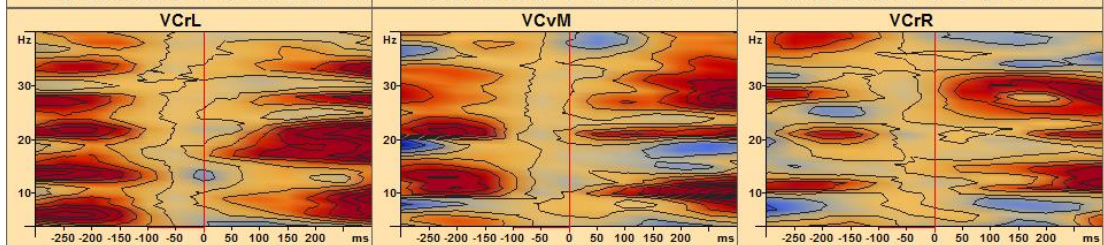
**MO**



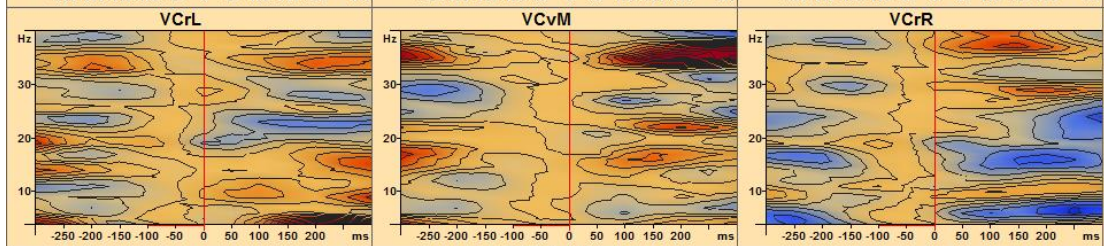
**SP**



**TQ**



**WR**



-63% | | | | | 63%

## Appendix B

**Table 2:** Frequency band, latencies and greatest percentage change in TSE of combined looming condition in both 4- to 5-month-old full-term and pre-term infants. Synchronized activities (positive percentage values) can be observed in the theta frequency band in one or more visual areas. Desynchronized activities (negative percentage values) can be observed in the alpha frequency band.

Full-terms/visual area	VCrL	VCvM	VCrR
AA	4.9 Hz, 300 ms, 25 %; 7.9 Hz, 151.5 ms, -30.2 %	5.9 Hz, 100 ms, -24.5 %	4.9 Hz, 300 ms, 42.1 %; 7 Hz, 199 ms, -9.6 %
AB	4 Hz, 300 ms, 15.6 %; 10 Hz, 300 ms, -35.2 %	10.9 Hz, 149.5 ms, -31.3 %	5.1 Hz, 199 ms, 34 %; 13.9 Hz, 44.3 ms, -15.1 %
BC	5.1 Hz, 149.5 ms, 37.4 %; 9 Hz, 102.1 ms, -30.8 %	5.1 Hz, 297.9 ms, 35.9 %; 8.1 Hz, 100 ms, -38.4 %	5.1 Hz, 256.7 ms, 14.5 %; 8.1 Hz, 172.2 ms, -13.8 %
BD	4.9 Hz, 300 ms, 40.7 %; 12.8 Hz, 100 ms, -16.2 %	4 Hz, 149.5 ms, 69.5 %; 8.1 Hz, 201 ms, -32.4 %	4 Hz, 293.8 ms, 82.5 %; 13.1 Hz, 50.5 ms, -18.9 %
JE		5.9 Hz, 149.5 ms,	5.1 Hz, 161.9 ms,

	13.1 Hz, 300 ms, -27.3 %	27.4 %; 12.8 Hz, 147.4 ms, -43.3 %	51.9 %; 9.2 Hz, 199 ms, -27.2 %
GF	12 Hz, 54.6 ms, -18.9 %	10.9 Hz, 46.4 ms, -25.3 %	5.9 Hz, 145.4 ms, 28.2 %; 9 Hz, 264.9 ms, -15.3 %
MG	12 Hz, 248.5 ms, -37 %	12.8 Hz, 199 ms, -60.3 %	6.2 Hz, 300 ms, 50.6 %; 12 Hz, 201 ms, -30 %
SH	4 Hz, 300 ms, 76 %; 8.1 Hz, 201 ms, -20.9 %	4 Hz, 250.5 ms, 136 %; 10.9 Hz, 199 ms, -27.4 %	4.2 Hz, 250.5 ms, 53.5 %; 9 Hz, 199 ms, -34.1 %
SI	4 Hz, 199 ms, 40.3 %; 7.2 Hz, 205.2 ms, -29.2 %	4.2 Hz, 250.5 ms, 23.8 %; 13.9 Hz, 246.4 ms, -36 %	4 Hz, 244.3 ms, 32.7 %; 11.8 Hz, 50.5 ms, -20.6 %
Pre-term/visual area	VCrL	VCvM	VCrR
AJ			

	4 Hz, 300 ms, -34.2 %	7 Hz, 295.9 ms, -34.9 %	5.9 Hz, 149.5 ms, -24.8 %
DK	5.1 Hz, 250.5 ms, 42.6 %; 11.1 Hz, 250.5 ms, -63.6 %	7.9 Hz, 300 ms, 102.9 %; 12.8 Hz, 295.9 ms, -45.1 %	10 Hz, 120.6, 23.3 %; 13.9 Hz, 201 ms, -43.9 %
DL	4 Hz, 250.5 ms, 42.5 %; 9 Hz, 250.5 ms, -26.7 %	4.6 Hz, 149.5 ms, 41.5 %; 10 Hz, 295.9 ms, -49.2 %	12 Hz, 151.5 ms, -35.4 %
EM	4 Hz, 100 ms, 63.8 %; 9.2 Hz, 100 ms, -25.6 %	9 Hz, 246.4 ms, -39.7 %	10.3 Hz, 201 ms, -45.1 %
FN	4 Hz, 250.5 ms, 26.7 %	10.9 Hz, 100 ms, -14.7 %	7 Hz, 149.5 ms, -30.3 %
MO	12.2 Hz, 300 ms, 52.2 %;	5.9 Hz, 300 ms, 55.9 %;	4.2 Hz, 300 ms, 60.5 %;



	16.1 Hz, 196.9 ms, -39.7 %	13.7 Hz, 190.7 ms, -22.4 %	15 Hz, 248.5 ms, -31.2 %
TQ	4.9 Hz, 155.7 ms, 85.7 %; 12 Hz, 199 ms, -41.4 %	5.9 Hz, 300 ms, 50.6 %; 12 Hz, 269.1 ms, -56.2 %	4 Hz, 300 ms, 35.3 %; 10 Hz, 201 ms, -30.7 %
SP	10.9 Hz, 269.1 ms, -22.3 %	15 Hz, 250.5 ms, -40.1 %	5.1 Hz, 295.9 ms, 95.2 %
WR	6.2 Hz, 252.6 ms, 22.6 %; 9.2 Hz, 50.5 ms, -15.5 %	5.1 Hz, 300 ms, 57.3 %; 12 Hz, 52.6 ms, -19.5 %	5.1 Hz, 264.9 ms, 124 %

**Table 3:** Frequency band, latencies and greatest percentage change in TSE of combined looming condition in both 11- to 12-month-old full-term and pre-term infants. Synchronized activities (positive percentage values) can be observed in the theta frequency band in one or more visual areas. Desynchronized activities (negative percentage values) can be observed the late alpha frequency band in one or more visual areas. Synchronized activities can also be observed in the early beta frequency band.

Full-terms/visual area	VCrR	VCvM	VCrR
AA	5.1 Hz, 267 ms, 79.3 %; 10 Hz, 295.9 ms, -16.9 %; 13.1 Hz, 201 ms, 64.1 %	4 Hz, 300 ms, 55.8 %; 10 Hz, 199 ms, -12.5 %; 15.9 Hz, 201 ms, 37.3 %	4 Hz, 300 ms, 44.5 %; 9.8 Hz, 300 ms, -11.3 %; 12 Hz, 252.6 ms, 65.7 %
AB	4 Hz, 295,9 ms, 58.3 %; 9 Hz, 149.5 ms, -9.1 %; 13.1 Hz, 283.5 ms, 104 %	4 Hz, 250.5 ms, 36.3 %; 7 Hz, 151.5 ms, -22.3 %; 14.8 Hz, 269.1 ms, 73.5 %	4 Hz, 258.8 ms, 73.5 %; 7 Hz, 300 ms, -29.9 %; 11.1 Hz, 300 ms, 48.5 %
BC	5.5 Hz, 300 ms, 50.3 %; 11.1 Hz, 287.6 ms, -28.4 %; 24 Hz, 205.2 ms,	5.9 Hz, 297.9 ms, 48.2 %; 11.1 Hz, 163.9 ms, -43.8 %; 29 Hz, 149.5 ms,	8.1 Hz, 293.8 ms, -32.6 %; 18.7 Hz, 250.5 ms,

	52.1 %	20.2 %	28.2 %
BD	4 Hz, 201 ms, 57.7 %; 13.1 Hz, 297.9 ms, -24.6 %; 21.9 Hz, 287.6 ms, 31.4 %	4 Hz, 297.9 ms, 15.3 %; 16.1 Hz, 248.4 ms, -25.5 %; 26 Hz, 151.5 ms, 52.5 %	5.1 Hz, 300 ms, 15.3 %; 13.1 Hz, 300 ms, -32 %; 20 Hz, 293.8 ms, 28.9 %
JE	7 Hz, 300 ms, 51.8 %; 10.9 Hz, 199 ms, -16.2 %; 15.9 Hz, 287.6 ms, 24.5 %	5.1 Hz, 199 ms, 83.7 %; 10 Hz, 234 ms, -13.1 %; 12 Hz, 291.8 ms, 18.2 %	7.9 Hz, 297.9 ms, 67.9 %; 11.1 Hz, 194.8 ms, -19.2 %; 20 Hz, 300ms, 16.4 %
GF	5.1 Hz, 100 ms, 54.6 %; 8.7 Hz, 199 ms, -40.3 %	5.1 Hz, 291.8 ms, 94.9 %; 15 Hz, 300 ms, -39.6 %	5.1 Hz, 201 ms, 92.2 %;  18 Hz, 258.8 ms, 43.3 %
MG	5.9 Hz, 50.5 ms, 52.3 %;	5.1 Hz, 291.8 ms, 94.9 %;	

	18 Hz, 207.2 ms, -49.7 %; 24.7 Hz, 300 ms, 105 %	11.1 Hz, 199 ms, -39.5 %; 19.1 Hz, 300 ms, 100.7 %	16.9 Hz, 236.1 ms, -57 %; 22.1 Hz, 297.9 ms, 33.2 %
SH	5.9 Hz, 151.5 ms, 67.2 %; 12.8 Hz, 295.9 ms, -18.3 %; 16.9 Hz, 300 ms, 61.2 %	7 Hz, 254.6 ms, 64.4 %; 10 Hz, 300 ms, -33.6 %; 15.9 Hz, 149.5 ms, 244 %	7 Hz, 250.5 ms, 68.7 %;  12 Hz, 100 ms, 85 %
SI	4.9 Hz, 203.1 ms, 87 %; 8.3 Hz, 250.5 ms, -31.9 %; 12 Hz, 300 ms, 56.4 %	6.2 Hz, 87.6 ms, 43.2 %; 9.4 Hz, 199 ms, -24.4 %; 10.9 Hz, 300 ms, 40.1 %	4.9 Hz, 199 ms, 34 %; 10.9 Hz, 300 ms, -31.8 %; 19.1 Hz, 205.2 ms, 53.7 %
Pre-terms/visual area	VCrL	VCvM	VCrR
AJ	4 Hz, 155.7 ms, 44.5 %; 9 Hz, 300 ms, -52.7 %	4 Hz, 151.5 ms, 64.4 %; 17.8 Hz, 250.5 ms, -41.5 %	4.2 Hz, 149.5 ms, 41.1 %; 11.1 Hz, 300 ms, -43 %;

			24.9 Hz, 300 ms, 34 %
DK	7.9 Hz, 300 ms, 52.3 %; 10 Hz, 151.5 ms, -19.9 %; 19.1 Hz, 199 ms, 108.6 %	5.9 Hz, 209.3 ms, -77.3 %; 32 Hz, 201 ms, 113 %	4 Hz, 300 ms, 50.8 %; 10.9 Hz, 297.9 ms, -55.4 %; 20 Hz, 209.3 ms, 46 %
DL	7 Hz, 252.6 ms, -39.4 %; 9.2 Hz, 141.2 ms, 18 %	7 Hz, 48.5 ms, 33.4 %; 9 Hz, 281.4 ms, -55.1 %; 13.1 Hz, 50.5 ms, 18.8 %	4 Hz, 48.5 ms, 25.9 %; 7 Hz, 248.5 ms, -57.5 %
EM	9 Hz, 250.5 ms, 178.8 %; 15 Hz, 100 ms, -12.4 %; 17.1 Hz, 300 ms, 109.8 %	7.9 Hz, 297.9 ms, 284.8 %; 16.1 Hz, 48.5 ms, -16.2 %; 18 Hz, 297.9 ms, 74.8 %	9 Hz, 300 ms, 124.5 %; 15.4 Hz, 250.5 ms, -26.4 %; 26.9 Hz, 102.1 ms, 60.4 %
FN	5.9 Hz,	5.9 Hz,	5.9 Hz,

	124.7 ms, 60.3 %; 12 Hz, 254.6 ms, -43.6 %; 18 Hz, 300 ms, 35.6 %	275.3 ms, 94.8 %; 10 Hz, 110.3 ms, -39.1 %; 16.9 Hz, 289.7 ms, 18 %	300 ms, 67 %; 10.9 Hz, 172.2 ms, -27.1 %; 16.1 Hz, 250.5 ms, 11.3 %
MO	8.1 Hz, 248.5 ms, 70.6 %;  16.9 Hz, 201 ms, 44.2 %	9 Hz, 97.9 ms, -32.7 %; 18 Hz, 199 ms, 15.3 %	4 Hz, 250.5 ms, 32.5 %; 13.1 Hz, 104.1 ms, -25 %
TQ	7.9 Hz, 300 ms, -29.2 %; 16.9 Hz, 201 ms, 55.2 %	5.1 Hz, 300 ms, 17.2 %; 13.9 Hz, 300 ms, -38.1 %; 19.1 %, 293.8 ms, 36.2 %	4 Hz, 135.1 ms, 20.8 %; 13.1 Hz, 300 ms, -44.8 %; 15.9 Hz, 102.1 ms, 21.5 %
SP	9 Hz, 300 ms, 122.7 %;	10 Hz, 295.9 ms, 187.4 %; 15 Hz, 199 ms, -27.2 %;	4.9 Hz, 300 ms, 38.6 %; 7.9 Hz, 149.5 ms, -31.3 %;

	21 Hz, 200 ms, 135 %	21 Hz, 300 ms, 72.7 %	21 Hz, 300 ms, 60.9 %
WR	4 Hz, 201 ms, 92 %;  15 Hz, 300 ms, 29 %	4 Hz, 297.9 ms, 24.6 %;  7 Hz, 300 ms, -26.3 %;  16.1 Hz, 149.5 ms, 33.3 %	6.2 Hz, 250.5 ms, -51.8 %;  10 Hz, 106.2 ms, 20.5 %