A longitudinal EEG study of visual motion perception in full–term and preterm infants and children

by

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Abstract

High-density electroencephalogram (EEG) was used to longitudinally study evoked and induced brain electrical activity in full-term and preterm infants and children at 4-5 months, 11-12 months and at 6 years of age as a function of visual motion perception. The participants watched simulated structured forwards and reversed optic flow, as well as non-structured random visual motion. Analyses of visual evoked potentials (VEPs) and temporal spectral evolution (TSE) were performed on EEG data, recorded with a 128/256-channel sensor array. Motor functions were also investigated through Movement Assessment Battery for Children (M-ABC). VEP results revealed that at 11-12 months and at 6 years of age, the full-terms significantly increased their sensitivity with shorter latencies to optic flow and thus detected structured optic flow more efficiently than random visual motion. The TSE analyses revealed increased synchronized activity, especially in late alpha- and early beta-band, but also in some gamma-band frequencies, for the full-term participants with increasing age. However, the preterm participants followed a different development where they only showed increased sensitivity to optic flow at 6 years of age, but at that age, they were still not capable of detecting structured optic flow more efficiently than random visual motion. Frequency analyses revealed that the preterm participants showed less high-frequency synchronized activity in late alpha- and early beta-band ranges at 11-12 months and at 6 years of age compared to the full-terms, and most of them did not show any synchronized activity at all. M-ABC showed that most of the preterm children seemed to do well in perceptual-motor tasks related to the visual dorsal stream at 6 years of age. The study concluded that the observed progression in visual motion processing for the full-term participants during the first year of life to primary school age can be attributed to an increase in self-produced locomotor experience, and neural maturation. The results show that with age, full-terms rely more on structured optic flow and show a more adult-like specialization for motion, with fewer but more specialized neurons. The preterm participants' delayed development of visual motion perception can be related to a dorsal stream vulnerability caused by premature birth. The poorer differentiation between radial motions suggests that they still have an immature or altered network for processing visual motion information by the age of 6 years. Because premature children do seem to have caught up on some but not all areas for visual motion perception by the time they started school, further studies will reveal whether the observed dorsal stream impairments are just a sign of developmental delay or will follow them through life.

1.0 Introduction

When navigating through the environment, a wealth of information about self-motion is registered by the perceptual systems of the observer. Gibson (2015) argued that perception and behaviour are mutually dependent on each other; when we move, our behaviour is guided by what we perceive, while what we perceive is affected by our movements. Thus, perception and action cannot be separated in the understanding of visual motion perception.

According to Gibson (2015), self-motion produces flow patterns of visual information, referred to as *optic flow*, which describes the stream of visual information we receive about the environment and our own motion when we navigate through the surroundings. The complex patterns of motion provide rich perceptual information about the speed and direction of the observer´s motion, and the surface and layout of the environment (Gibson, 2015). The continuous perceptual information from the environment is proven essential for controlling walking direction (Bruggeman, Zosh & Warren, 2007; Warren, Kay, Zosh, Duchon & Sahuc, 2001), stabilizing posture, and estimating the time it takes to make contact with or avoid objects in the surroundings (Bertenthal, Rose & Bai, 1997; Higgins, Campos & Kermoian, 1996; Kayed & Van der Meer, 2009; Vaina & Rushton, 2000; Van der Meer, Van der Weel & Lee, 1994; Wilkie & Wann, 2003).

The relationship between perception of the visual scene and behaviour is also essential for our ability to effectively navigate and execute forthcoming actions. Integrating perceptual information, cognition, and motor performance of intended actions are tightly coupled together in a complex system. This system is referred to as *prospective control* and is our ability to make and plan these movements precisely according to the continuously changing environmental and bodily characteristics (Adolph, Eppler, Marin, Weise & Clearfield, 2000; Turvey, 1992). The ability of controlling speed and direction during locomotion is depending on the complexity and the familiarity of the visual flow information to the observer. Although many movements are highly automatized and repetitive such as walking, they must be constantly modified to fit the present demands of the context in which the movements unfold (Adolph et al., 2000). Individuals without sufficient prospective control, may experience difficulties in responding to environmental changes, in performing everyday tasks and in avoiding injuries. Considering the relevance and importance of these abilities to everyday life, it is important to comprehend how infants learn to make use of visual information for perception.

Visual information is argued to be processed in two separate, yet interacting cortical streams, known as the ventral and the dorsal stream. The ventral stream is referred to as the "what" pathway and is associated with object recognition. The ventral pathway leads from the occipital lobe to the temporal lobe. The dorsal stream is referred to as the "where" or "how" pathway, because it informs us where and how to perform visually guided movements (Andersen, 1997). It is associated with aspects such as direction, speed, timing, movement planning, and motion perception. The dorsal pathway leads from the primary visual cortex to the medial temporal (MT) and medial superior temporal (MST) area, together known as the V5/MT+ area, and further to the parietal lobe (Andersen, 1997; Morrone et al., 2000; Smith, Wall, Williams & Singh, 2006). Research of the neuronal mechanisms involved in visual motion processing has shown that the V5/MT+ area has neurons selectively activated for processing of radial motion (De Jong, Shipp, Skidmore, Frackowiak & Zeki, 1994; Dukelow et al., 2001; Morrone et al., 2000) and that cells in the MST area of the dorsal stream are especially implicated in the processing of optic flow (Duffy, 1998; Holliday & Meese, 2008; Smith et al., 2006; Vaina & Rushton, 2000; Yu, Page, Gaborski & Duffy, 2010). This is supported by studies showing that motion perception is impaired when transcranial magnetic stimulation (TMS) is applied in the MT/V5 area approximately 150 ms after onset of the motion stimulus (Sack, Kohler, Linden, Goebel & Muckli, 2006; Stevens, McGraw, Ledgeway & Schluppeck, 2009).

Sensitivity to radial optic flow seems to improve with age, but is still immature at age 16, indicating that the higher cortical areas such as MST have yet to mature (Joshi & Falkenberg, 2015). Since radial optic flow is the most common flow experience during self-motion, the immaturity seen in infants and children will also affect any functioning depending on its input (Joshi & Falkenberg, 2015). Human infants need to develop neuronal structures to be able to move around in the environment, especially when they become more mobile during the second half of the first year of life. Gilmore, Hou, Pettet and Norcia (2007) report that adults easily distinguish between different forms of motion such as expansion/contraction, rotation (left/right), and translation (horizontal/vertical). Compared to adults, young infants are far less capable and efficient in detecting optic flow (Gilmore, Baker & Grobman, 2004; Van der Meer, Fallet & Van der Weel, 2008). However, fundamental perception of optic flow patterns is seen in infants already in the first weeks and months after birth, and even newborns are to some extent able to track a horizontally moving object, which indicates that perception for motion is present right after birth (Hait, 1966). This ability to continuously pursue a moving target, is one of the earliest indications of prospective control behaviour. During the first year of life, infants show rapid perceptual development in response to visual motion. Von Hofsten and Rosander (1996) found how 3-month-old infants are able to stabilize gaze on the visual flow field by using basic abilities such as head and body movements. Moreover, behavioural studies have found that infants younger than one month of age show defensive responses including backward head tilting and blinking in response to structured motion. These responses suggest that young infants use perceptual information to execute adaptive motor responses (Jouen, Lepecq, Gapenne & Bertenthal, 2000; Kayed & Van der Meer, 2007; Shirai & Yamaguchi, 2010).

In normally developing full-term infants, information for motion is reported to be processed in the occipito-parietal areas in the left and right visual cortex (Van der Meer, Svantesson & Van der Weel, 2012; Van der Weel & Van der Meer, 2009), but for preterm born infants the functioning and development of these areas are less known. Unlike normally developing full-term infants, preterm infants show differential brain development. Studies have shown that infants born preterm are at a higher risk of neurological deficits and developmental disorders. In the recent years, impairments of the dorsal stream have been suggested to cause less efficient visuo-motor processing in preterm born infants (Birtles, Braddick, Wattam-Bell, Wilkinson & Atkinson, 2007; Braddick, Atkinson & Wattam-Bell, 2003; MacKay et al., 2005; Van Braeckel et al., 2008). Atkinson and Braddick (2007) report in a number of studies that preterm born children show delays in particularly three brain domains that all have links to the dorsal stream: selective attention, spatial function, and executive control. When compared to full-term children, preterm children seem to fall short when it comes to perception of global motion, global form, and biological motion, possibly reflecting that these forms of visual motion processing develop at different rates, and may be vulnerable to atypical neurodevelopment (Taylor, Jakobson, Maurer & Lewis, 2009).

Infants born before 37 completed weeks of gestation are defined as preterm. In Norway, approximately 5.2 % of infants are born before completed 37 weeks of gestation every year, and the lower limit for viability in Norway is considered week 24, or 500 grams of weight (Markestad & Halvorsen, 2007; Norsk Helseinformatikk, 2018). Preterm birth is a major cause of infant morbidity, and preterm labour is the next leading cause of infant mortality in the industrialized world, after congenital anomalies (Swamy, Østbye & Skjærven, 2008). Fortunately, due to the improvements in neonatal care in the 1970s, the chances of survival have increased during the last decades (Markestad & Halvorsen, 2007; Wilson-Costello, Friedman, Minich, Fanaroff & Hack, 2005).

However, despite the increased chance of survival, preterm infants that survive show a higher risk than their full-term peers to suffer from illnesses and injuries that can lead to health and developmental problems. Preterm birth shows a greater risk of developing major handicaps such as cerebral palsy, blindness, and hearing loss, compared to full-term infants (Platt et al., 2007). Several studies of preterm children have shown that not only has the prevalence of preterm children with cerebral palsy increased, but also more children have been identified with subtle perceptual-motor difficulties. Some of the areas of motor skill abnormalities reported in preterm born children are postural control (Van der Fits, Flinkweert, Stremmelaar, Martijn & Hadders-Algra, 1999; Van der Heide et al., 2004), kicking movements (Fetters, Chen, Jonsdottir & Tronick, 2004), and eye-hand coordination (Goyen et al., 2006). Although preterm children without cerebral palsy have less severe motor difficulties, the *"clumsiness"* experienced by these children affects their progress in school (Hall, McLeod, Counsell, Thomson & Mutch, 1995; Jongmans, Mercuri, De Vries, Dubowitz & Henderson, 1997; Klein, Hack & Breslau, 1989; Rosenbloom, 1995; Saigal, Szatmari, Rosenbaum, Campbell & King, 1990; Veen et al., 1991). The frequency of reported difficulties with language, learning, social interaction, concentration, attention, motor skills, and mental health in preterm children raises concerns (Markestad & Halvorsen, 2007). It has been calculated that approximately 15-45% of the very preterm (VPT) infants have some sort of milder disability (Hack et al., 2002; Roberts, Anderson, De Luca & Doyle, 2010; Saigal & Doyle, 2008; Stjernqvist & Svenningsen, 1999). Moreover, when compared to term borns, very preterm individuals have been found to score significantly lower on behavioural, motor and cognitive measures, and minor motor impairments have been shown to have an impact on overall school performance despite intelligence within the normal range (Foulder-Hughes & Cooke, 2003). In a study by Jongmans et al. (1997) preterm children were reported to have a higher prevalence of neurological signs and perceptual-motor problems at school age than their peers. Their study showed that preterm children with the lowest birth weight and the lowest gestational age were the ones that were the most affected at the age of 6 in their neurological and perceptual-motor development. In general, preterm or low birth weight (LBW) children seem to have an increased risk of having attention-deficit/hyperactive disorder (ADHD), as well as more cognitive and psychiatric disorders (Foulder-Hughes & Cooke, 2003; Linnet et al., 2006). It seems clear that despite considerable improvement in perinatal care and survival of preterm infants, many will experience learning, behavioural and motor difficulties in school age, adolescence and early adulthood (Botellero et al., 2017; Foulder-Hughes & Cooke, 2003).

Deficits in visual motion perception, which is a dorsal stream function, have also been reported in VPT born children as well as several genetic neurodevelopmental disorders, including Williams syndrome (Atkinson et al., 2001; Atkinson et al., 2006), autism spectrum disorders (Grinter, Maybery & Badcook, 2010; Spencer et al., 2000), developmental dyslexia (Hansen, Stein, Orde, Winter & Talcott, 2001), and Fragile X syndrome (Grinter et al., 2010), supporting the notion of a susceptibility of the dorsal stream to a wide range of different neurodevelopmental disorders (Braddick et al., 2003). It has been proposed that the vulnerability in developmental disorders may stem from loss of the larger magnocellular (M) cells in the dorsal pathway. M-cells have larger cell bodies than parvocellular (P) cells found in the ventral pathway, which make them more at risk since their cell-body and axon diameters are more susceptible to damage (Quigley, Dunkelberger & Green, 1988). Further, a study by Tremblay et al. (2014) suggests that preterm born infants at 12 months of age have a ventral stream (occipito-temporal or P-pathway) that is normally developed at this age, but that the dorsal stream (occipito-parietal or M-pathway) is still immature or altered at the same age. In general, the notion that the dorsal stream is more vulnerable than the ventral regions to damage, is supported by several studies (e.g., Back, Riddle & McClure, 2007; Back & Rivkees, 2004; Peterson et al., 2003). Guzzeta et al. (2009) reported that school-age preterm born children when compared to full-term controls, regardless of the presence of brain damage, showed impaired dorsal-stream related functions. The results indicate that dorsal stream vulnerability may not be restricted to developmental disabilities, but that also preterm birth may result in impaired dorsal-stream related functions.

At birth, the human brain is equipped with 100 billion single neurons. During the first year of life, the infant brain doubles in size, and the neurons will make specialized connections due to maturation and experience, forming complex networks. These networks become specialized to rapidly process perceptual information. This process is modulated by fibre volume of white matter that in healthy infants increases during early infancy until adulthood due to ongoing axonal myelination. This process will increase the speed of neural communication (Dubois, Hertz-Pannier, Dehaene-Lambertz, Cointepas & Le Bihan 2006; Mukherjee et al., 2002; Paus et al., 2001).

However, a body of literature has pointed to a different pattern of early brain development in the functioning and anatomy of premature infants (e.g., Ajayi-Obe, Saeed, Cowan, Rutherford & Edwards, 2000; Inder, Warfield, Wang, Hüppi & Volpe, 2005; Padilla, Alexandrou, Blennow, Lagercrantz & Ådén, 2014). The human brain consists of organized dynamic networks of interconnected neurons and associated synapses that work together in such a way that dysfunctions within the networks can result in adverse effects on behavioural patterns. With magnetic resonance imaging (MRI), Counsell and Boardman (2005) reported that being born preterm causes differential brain development that is evident from abnormalities in tissue microstructure and cerebral morphology. Among others, Padilla et al. (2014) have found that extremely preterm born infants show significant global reduction in brain tissue, especially reduced grey matter, and significantly increased cerebrospinal fluid (CSF) volume. In a brain growth study, Kapellou et al. (2006) used magnetic resonance imaging (MRI) to take 274 images from 23 to 48 weeks of gestation on 113 extremely preterm infants born between 23 to 29 weeks of gestation. Kapellou et al. (2006) reported that preterm infants showed slower cortical growth with decreased gestational age at birth. The differences observed in preterm infants seem to persist into young adulthood and adolescence, as an MRI study found that significant cortical thinning was observed in very low birth weight (VLBW) adolescents for the parietal and temporal lobe when compared to a term-born control group (Martinussen et al., 2005).

Preterm infants with VLBW are shown to have a higher risk for cortical and subcortical grey matter abnormalities, white matter alterations, as well as neurodevelopmental problems, including fine and gross motor problems, that persist into young adulthood (Botellero et al., 2017; Counsell & Boardman, 2005; Hollund et al., 2018; Lund et al., 2012; Padilla et al., 2014). Earlier studies have reported that white matter organizations are still affected in late childhood and adulthood from VLBW and preterm birth (Skranes et al., 2007; Vangberg et al., 2006). Diffusor tensor imaging (DTI) has shown that at 40 weeks of gestational age, white matter fibres in areas of the brain through which the dorsal stream flows are shorter, thinner, and less organized in preterm infants (Hüppi et al., 1998). The same results have later been confirmed in a MRI study (Mewes et al., 2006), illustrating that preterm infants corrected for prematurity compared to full-term infants had less unmyelinated and myelinated white matter at 42 weeks of gestational age. Myelination deficits like this may affect the structural and functional connectivity and lead to slower signalling in the brain (Hollund et al., 2018). Motor pathways such as the corticospinal (CST) tract and the corpus callosum (CC) seem to be some of the several white matter tracts that are affected by premature birth (Eikenes, Løhaugen, Brubakk, Skranes & Håberg, 2011; Groeschel et al., 2014). The abnormal cerebral white matter observed in preterm infants may explain some of the neurodevelopmental impairments reported in preterm born individuals (Atkinson & Braddick, 2005, 2012; Skranes et al., 2007).

To study the neural basis of motion perception and the functional specialisations of cortical structures, electroencephalogram (EEG) is used in visual perception tasks. EEG records electrical activities of pyramidal neurons with high temporal resolution (in millisecond scale) (Agyei, Holth, Van der Weel & Van der Meer, 2015; Dukelow et al., 2001; Sakkalis, Tsiaras, Michalopoulos & Zervakis, 2008; Tucker, 1993). Studies using EEG have revealed that infants younger than 6-8 weeks are not able to efficiently discriminate between different motion directions and do not efficiently pursue small moving objects, but that these kinds of abilities rapidly improve from 6-14 weeks of age (Gilmore et al., 2007; Rosander, Nyström, Gredebäck & Von Hofsten, 2007). Among the different types of optic flow-related motions, one of particular interest is expansion because it best defines motion during forwards locomotion (e.g., crawling/walking). An optic flow study by Ptito, Kupers, Faubert and Gjedde (2001) reports that both contraction and expansion activate visual and nonvisual cortical areas, but that expansion shows a greater cerebral activation than contraction. Also, a longitudinal study by Brosseau-Lachaine, Casanova and Faubert (2008), by using a forced-choice preferential looking technique, reported that infants showed a significantly improved sensitivity to expanding versus contracting radial motion during the first months of life. This dissociation may suggest that sensitivity to expansion (simulating forwards locomotion) develops at a faster rate than contraction (simulating reversed locomotion). This probably reflects the natural maturation of cerebral areas underlying motion integration in infancy, as the same dissociation is found in adults, showing a greater response to expanding radial motion than to contracting radial motion (Holliday & Meese, 2005).

Visual evoked potentials (VEPs) is a term describing event-related potentials (ERPs) elicited by visual stimuli, measured by EEG (Woodman, 2010). Motion-sensitive VEP waveforms in EEG are found to be dominated by negativity (N2), which is thought to originate from V5/MT+ in the occipital and parietal visual area. This latency peak occurs in adults around 130-200 ms post stimulus, while in infants at 11-12 months around 270-290 ms post stimulus (Agyei et al., 2015; Fielder, Harper, Higgins, Clarke & Corrigan, 1983; Heinrich, Renkl & Bach, 2005; Kobayashi, Yoshino, Kawamoto, Takahashi & Nomura, 2004; Probst, Plendl, Paulus, Wist & Scherg, 1993).

Studies using EEG to investigate VEPs have shown that optic flow is more rapidly processed than random visual motion both in infants and adults. A possible explanation is that humans more frequently experience optic flow through locomotion in their everyday lives (Agyei et al., 2015; Agyei, Van der Weel & Van der Meer, 2016; Van der Meer et al., 2008). Furthermore, these studies report a longer latency N2 visual component with higher amplitude in infants compared to adults (Van der Meer et al., 2008), and that N2 latency improves with infants' age during the first year of life (Agyei et al., 2015, 2016). Van der Meer et al. (2008) reported that infants who had not yet started to walk by themselves process optic flow slower, but that the processing time decreased with increased experience with optic flow through self-produced locomotion in the environment. The same was also confirmed in a later longitudinal study by Agyei et al. (2015), reporting that infants' processing time for optic flow at 3-4 months was significantly decreased by 11-12 months of age in normal term-born infants. These findings could thus be attributed to the increased experience infants have with self-initiated locomotion at the end of the first year.

However, although experience with self-initiated locomotion in full-term infants showed faster processing of visual information with age, the same tendency has not been observed in preterm born infants. In a study by Agyei et al. (2016), preterm infants did not improve their processing time to optic flow through their first year of life, even though they had the same amount of locomotor experience as full-term born infants. It was suggested that the poorer responses observed in preterm infants may be related to an impairment of the dorsal stream specialization for the processing of visual motion (Agyei et al., 2016).

EEG studies have shown that adults easily discriminate between forwards optic flow, reversed optic flow, and random visual motion (Van der Meer et al., 2008). Moreover, adults also show the ability to detect forwards and backwards optic flow at both high and low speeds, but with significantly shorter latencies for both directions at low speed (Vilhelmsen, Agyei, Van der Weel & Van der Meer, 2018). When it comes to studies with EEG on VEPs in primary school children, the amount of research is very limited. However, a EEG study by Gilmore, Thomas and Fesi (2016) reported that children at 4-8 years of age show clusters of brain activity in response to different patterns and speeds of optic flow, similar to what was observed in adults. Further, a non-EEG study has reported that children at the ages from 6 to 17 years seem to gradually improve at discriminating between direction of motion and by 14 years of age show a mature level of visual motion perception (Bogfjellmo, Bex & Falkenberg, 2014).

In conjunction with the use of VEPs, attention to EEG studies in the time-frequency domain has grown. This has allowed perceptual and cognitive functions to be investigated through the manifestations of the natural frequencies in EEG oscillations (Basar, Basar-Eroglu, Karakas & Schurmann, 1999). Oscillations in the ongoing EEG can be understood by evoked and induced activity. An evoked VEP response is defined as the post-synaptic firing pattern of neurons at a specific time point in relation to the stimulus evoking the potential (Webb, Long & Nelson, 2005). Since evoked potentials are both time- and phase-locked to the stimulus onset, averaging techniques are commonly used as they increase the signal-to-noice-ratio (Pfurtscheller & Lopes de Silva, 1999). In addition to studying the evoked activity such as VEPs, analysis of induced activity can be performed to get a better understanding of the complexity of the brain response to visual motion. Frequency analyses can detect events that simple linear methods such as averaging techniques in VEPs cannot detect, as these frequency changes are time-locked and not phase-locked (Pfurtscheller & Lopes da Silva, 1999). The frequency changes are observed as either event-related synchronization (ERS) or event-related desynchronization (ERD). ERS and ERD oscillations suggest either an increase or decrease in power or amplitude of given frequency bands, indicating the increase or decrease in synchrony of underlying neuronal populations (Hoechstetter et al., 2004). Frequency analysis is therefore a better method for analysing induced activity as it uncovers event-related time-frequency responses that are believed to represent local cortical neuronal interactions related to the ongoing EEG activity (Pfurtscheller & Lopes da Silva, 1999).

Adults are reported to show motion-induced gamma-band, beta-band and alpha-band frequencies in the occipital and parietal areas (Hoogenboom, Schoffelen, Oostenveld, Parkes & Fries, 2006; Van der Meer et al., 2008; Vilhelmsen, Van der Weel & Van der Meer, 2015). Van der Meer et al. (2008) reported that 8-month-old infants show theta-band ERD when presented with visual motion stimuli, compared to a static non-flow pattern where theta-band ERS was found. In the same study, when motion stimuli were compared to a static non-flow pattern, a beta-band ERS for adults was observed, while a beta-band ERD was observed in the static non-flow condition. Theta-band activity is a lower-band frequency, which may indicate that a larger amount of neurons is coherently activated, compared to higher-band frequency such as beta-band activity (Pfurtscheller & Lopes da Silva, 1999). These low-frequency EEG rhythms, that are often observed in infants, are primarily attributed to signs of immaturity (Orekhova, Stroganova, Posikera & Elam, 2006). Later, Agyei et al. (2015, 2016) reported that infants show an increase in alpha-band ERS with age, which indicates progression towards a more adult-like visual motion processing of specialized and effective neuronal networks in the brain. Other studies have reported a transition of EEG spectral amplitudes from lower to higher frequency during development, which is also considered a sign of maturation (Hudspeth & Pribram, 1992). These findings are consistent with studies reporting that low-frequency rhythms undergo systematic development from early childhood to adulthood (Stroganova, Orekhova & Posikera, 1999).

In connection with the above findings on the relation between behavioural changes and underlying brain changes, the present study aimed to investigate the development of visual motion processing in the brain during the first year of life and at 6 years of age. This in an attempt to understand the development of visual motion processing and the effects of preterm birth. When born premature, infants are experiencing the visual environment at a time when the visual system is extremely immature and while their brains are in a period of rapid maturation. With an increasing number of premature infants surviving, it is important to gain knowledge about the impact of such early visual experience on later development. The present study contributes to a further understanding of the normal development of visual motion perception from early infancy into school-age, and the possible developmental impairments due to premature birth. This knowledge is essential to facilitate an optimal development and to reduce the difficulties observed as a result of premature birth in childhood, adolescence and early adulthood. Brain electrical activity in full-term and preterm infants and children at 4-5 and 11-12 months, and at 6 years of age, in response to optic flow and random visual motion, was investigated using high-density EEG in a longitudinal design. VEP and frequency analyses were applied to the data to investigate whether there were any significant differences in brain responses to visual motion perception between full-term and preterm participants at the different ages. In addition, individual analyses were applied in order to detect if any of the preterm participants showed abnormalities in visual motion processing and/or motor development. Based on earlier research, the present study expected perception of optic flow, especially forwards motion, to rapidly develop with increasing age and locomotor experience for full-term participants, with less improvement for random visual motion. Further, it was predicted that preterm infants would show a delayed development of visual motion processing between the ages of 4-5 and 11-12 months compared to their full-term peers, but that by the age of 6 years they would have caught up with the full-terms. Induced ERS at higher frequency-bands was expected to increase with increasing age especially for the full-term group.

2.0 Method

2.1 Participants

A total of 20 healthy infants, 10 full-term and 10 preterm (5 boys and 5 girls in both groups), were recruited for this study. The full-term infants were recruited by contacting parents through birth announcements in the local newspaper. The preterm infants were recruited through the Neonatal Intensive Care Unit at St. Olav's University Hospital in Trondheim with the help of the paediatrician in charge.

The full-term infants had a mean gestational age of 40 weeks (SD = 1.4, range 38-42 weeks) with an average birth weight of 3621 g (SD = 595, range 3085-5120 g). The preterm infants (moderate to very preterm) were born at 31weeks of gestation (SD = 1.7, range 28-33 weeks), with an average birth weight at 1591 g (SD = 453, range 1000-2670 g). The preterm infants did not have retinopathy of prematurity or obvious neurological deficits, but one boy was diagnosed with a mild form of cerebral palsy (CP) at age 2.

The study was longitudinal, testing infants first at 4-5 months, followed by a second testing approximately at 11-12 months, and a third testing during early childhood at 6 years of age. Preterm and full-term infants were matched according to sex and age. Three of the preterm children were not able to participate in the third testing session. Two girls had not yet reached the age of 6 years and the boy with CP was uncooperative. Their matched full-term controls were therefore omitted from the third testing session in order to ensure equal group sizes for each testing session. Hence, longitudinal analyses included 10 infants in each group for the two first testing sessions, while the third testing session included 7 children in each group (3 girls in each group). To ensure valid matching, preterm ages were corrected for prematurity. For the first testing session, the full-term infants had a mean age of 4 months and 4 days (SD = 18, range 100-164 days), while the mean age of the preterm infants was 5 months (SD = 11.2, range 141-177 days). At this stage, none of the infants had any crawling experience. For the second session, the mean age was 11 months and 17 days (SD = 13.1, range 330-372 days) for the full-term infants, and 1 year and 5 days (SD = 19.5, range 341-415 days) for the preterm infants. At this stage, all infants could crawl, and some could independently pull to stand, walk alone or walk with help, except three preterm infants who were bottom shuffling instead (parental report). For the third testing session, the mean age of the full-term children was 6 years and 7 months (SD = 6, range 73-88 months), and the preterm children had a mean age of 6 years and 9 months (SD = 1, range 81-85 months). At this age, all the children had started primary school.

Electroencephalography is a physiological procedure that causes no physical harm or pain to the participants. Prior to the experiment, parents gave their informed written consent and had the right to withdraw from the testing at any time. The study has been approved by the Norwegian Regional Ethics Committee and the Norwegian Data Services for the Social Sciences. All testing for the study was carried out at the Developmental Neuroscience Laboratory (NU-lab) at the Department of Psychology at the Norwegian University of Science and Technology (NTNU) in Trondheim, Norway.

2.2 Experimental stimuli and paradigm

An ASK M2 projector was used to project visual stimuli onto a rectangular display (108 cm wide, 80 cm high) at a fixed distance of 80 cm in front of the participant sitting in a chair (see Figure 1). Psychological software tool, E-prime, was used to generate the stimuli. The optic flow stimuli consisted of 100 black dots (5 mm virtual radius) positioned randomly on the white screen, with a red fixation point at the centre of the screen to attract attention. To discriminate between coherent and incoherent radial motion, three motion conditions were used: forwards optic flow, reversed optic flow, and random visual motion. Each condition was presented in random order for 1500 ms. In addition, to reduce motion adaption, a static non-flow condition occurred for 1500 ms between each motion condition. At the centre of the screen, the reference fixation point of 1.7 mm in diameter subtended an angle of 0.16°. With reference to the position of the fixation point, the black dots increased or decreased in size at a rate of 0.025 pixels per pixel. This made the particles appear small when far away from the eye in virtual space, and larger when closer.

In the forwards optic flow condition, the black dots seemed to coherently flow towards the participant, moving outward from the centre of the screen. Movement was parallel to the z-axis towards the eye with velocities in the x- and y-axes remaining zero. In the reversed optic flow condition, the dots coherently moved away from the participant. Here the movement was also parallel to the z-axis, but away from the eye with velocities in the x- and y-axes also at zero. In the random motion condition, the dots moved in completely random directions in virtual space and with the same properties as in the two structured optic flow conditions. Finally, in the static non-flow condition, the dots were frozen, and remained in the same position for the duration of the trial with a zero velocity in all directions. To maintain a constant number of dots during the motion trials, dots were automatically repositioned to compensate for dots moving out of the screen. The optic flow experiment was followed by two other experiments on looming and occlusion, providing data for other studies.

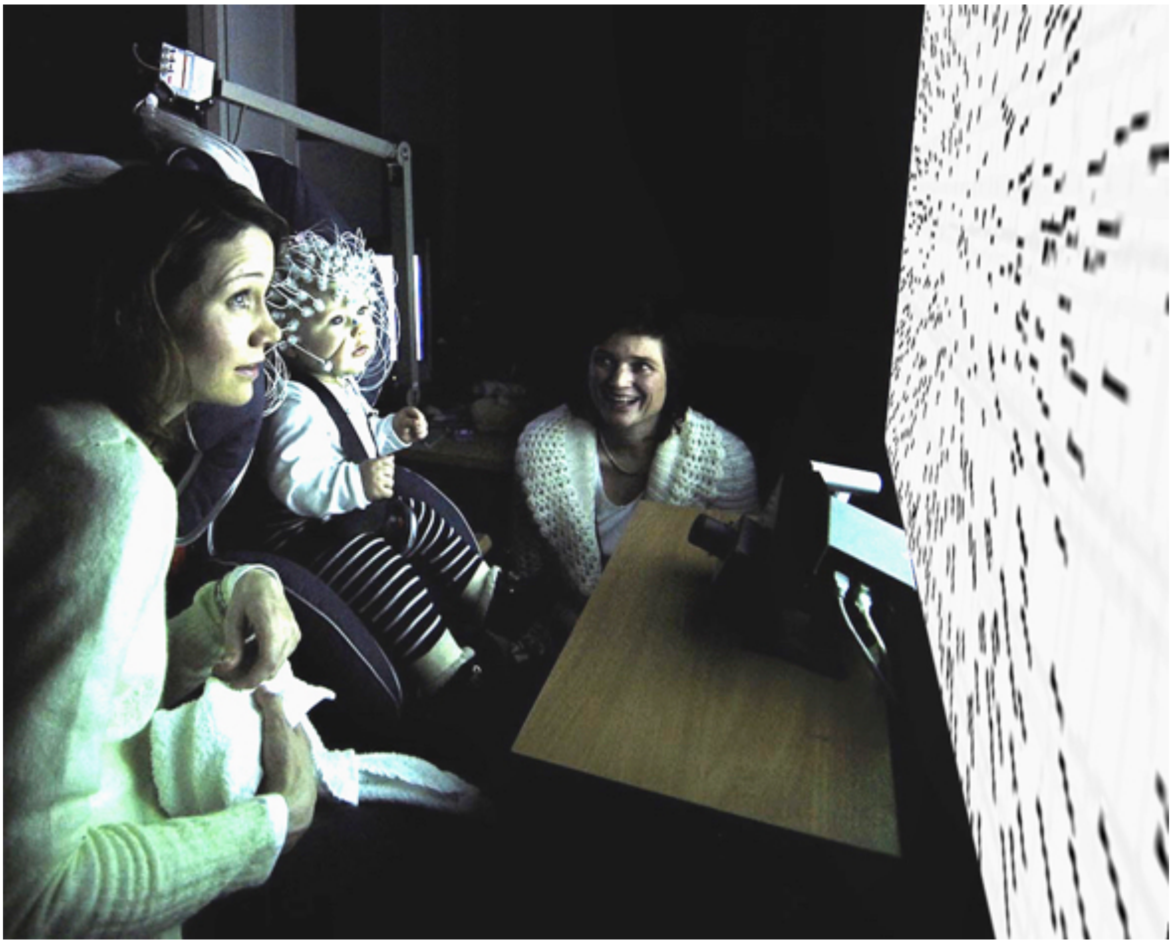

Figure 1. *Experimental set-up with a 12-month-old infant sitting in a baby car seat wearing the 128-sensor Geodesic Sensor Net. The parent is sitting on the right side and the assistant on the left side of the infant. On the screen in front of the infant, moving dots are projected, simulating optic flow and random visual motion. The eye tracker is placed on the table in front of the infant together with two digital video cameras filming the infant from two different angles.*

2.3 Data acquisition

EEG activity was recorded with a Geodesic Sensor Net (GSN) 200 (Tucker, 1993; Tucker, Liotti, Potts, Russell & Posner, 1994). The net was evenly distributed on the participant's head, and consisted of an array of 128 sensors for infants and 256 for children. To ensure signals were amplified with maximum impedance at the recommended value of 50 kΩ for optimal signal-to-noise ratio, a high-input amplifier was connected to the net (Budai, Contento, Locatelli & Comi, 1995; Ferree, Luu, Russell & Tucker, 2001; Picton et al., 2000). Amplified EEG signals were recorded at a sampling rate of 500 Hz with Net Station software on a Macintosh computer. To track the participants' gaze, a Tobii X50 camera was used to control for whether they were looking at the screen. The visual feed was processed with Clear View software on a HP computer. To track off-line the behaviour during the experiments, two additional cameras were positioned at different angles in front of the participant. Recorded data were subsequently stored for offline analyses.

2.4 Procedure

Parents would arrive with their infant or child some time prior to the experiment. In this time space, the parents signed the consent form and the infant or child was allowed some time to get used to the laboratory surroundings. An assistant measured the participant's head circumference to select the correct size of the net. To optimise electrical conductivity, the net was soaked in saline electrolyte and partially dried before being mounted on the infant or child's head while seated on the parent's lap or in a chair. To distract the infant's attention from the net, the assistant was blowing soap bubbles and small sounding toys were used. After the net was mounted, the infant or child was moved into a dimly lit experimental room, while other assistants moved to the control room next door, where they operated the computers necessary for data acquisition. The rooms were separated by a transparent glass partition that was soundproof. The infants were seated in front of the screen on the parent's lap during the first testing session, or in a baby car seat during the second session, and in a chair at age 6. One parent was sitting next to the infant/child to avoid any stressful effect resulting from the parent's absence, while an assistant was sitting on the other side to help the infant or child focusing on the screen. The net was connected to the amplifier and the impedance of the electrodes was checked, and electrode contact was improved if necessary.

After calibrating the eye movement in virtual space to the Tobii X50 infrared camera, the experimental session began. The optic flow experiment lasted for 5-7 minutes. Between 90 and 140 trials were presented to each participant, with half of those being the static non-flow trials. Data acquisition was carried out in one block, but the presentation was paused if the infant or child showed signs of boredom or disinterest. In this situation, the assistant and/or the parent would try to revive the level of interest before resuming the session. If the infant or child showed considerable level of disinterest, fussiness or tiredness, the session was ended.

2.5 Analyses

2.5.1 Data analyses. EEG data were analysed with Brain Electrical Source Analysis (BESA) research software version 6.0. The EEG recordings were first segmented with the Net Station software and then exported as raw files for further offline analyses. The same methods of analysis were applied to all the three testing sessions for both groups. By visual inspection, artefact-contaminated channels resulting from head or body movements, including instances where participants were not looking at the screen, were excluded from further analyses or their signals were estimated using spherical spline interpolation (Perrin, Pernier, Bertrand & Echallier, 1989; Picton et al., 2000). A maximum limit of channels defined as bad was set to 10%.

Averaging epochs were from -200 to 800 ms with a baseline definition of -100 to 0 ms. To remove electrical noise from the recorded data, the notch filter was set at 50 Hz. A high-pass filter was set at 80 Hz and a low pass filter was set at 1.6 Hz to remove slow drift in the data. Physiological artefacts caused by blinking or eye movements were corrected manually or by using a semi-automatic artefact correction designed to separate brain activities from artefacts (Berg & Scherg, 1994; Fujioka, Mourad, He & Trainor, 2011; Ille, Berg & Scherg, 2002). In scanning for artefacts, based on recommended BESA settings, channels and trials with amplitudes higher than 200–220 μV, gradients higher than 75 μV, and signals below 0.1 μV were excluded for further analyses.

The mean numbers of accepted motion trials for full-term infants at 4-5 months, 11-12 months and children at 6 years were 57 (SD = 16), 55 (SD = 17) and 59 (SD = 15), respectively, while those for preterm participants at 4-5 months, 11-12 months and 6 years were 55 (SD = 20), 60 (SD = 14) and 62 (SD = 4), respectively. Accepted trial numbers were approximately evenly distributed across the three motion conditions in all testing sessions. Further, the static control condition had mean numbers of accepted trials of 59 (SD = 18), 54 (SD = 18) and 58 (SD = 12) for full-term infants at 4-5 months, 11-12 months and children at 6 years. Corresponding accepted trials for preterm infants and children were 57 (SD = 12), 59 (SD = 12) and 61 (SD = 1), respectively.

2.5.2 Peak analyses at the electrode level. To obtain individual averages, EEG data were exported into the standard 81-electrode configuration of the 10-10 international standard electrode system after re-referencing to an artefact reference calculated from the average potentials over the scalp. The individual averages were combined creating a total of six grand averages, one for each group at each testing session. Grand average VEP's gave approximate time intervals that worked as a reference for selecting individual N2 components at different electrode sites. The N2 components of the individual VEP waveforms were then selected by using 3D spherical spline whole-head voltage maps of EEG scalp signal distributions. This helped to visualize maximum N2 activity in occipito-parietal areas for the most dominant VEP waveform. Peak latencies (time from stimulus onset to peak of the scalp N2 component) of the individual averages were recorded for further VEP analyses.

2.5.3 Time-frequency analyses in brain space. Time-frequency analyses, using multiple source dipoles, were performed in brain space, modelling the parietal and visual cortices, which were the main brain regions of interest. Since scalp waveforms receive mixed contributions from underlying brain sources, measuring brain oscillatory activities using surface electrodes may not be ideal. This is because the focal brain activity is widely distributed as a result of the nature of dipole fields and the smearing effect of brain volume conduction in EEG. Optimal separation of brain activity was achieved by using a source montage derived from a multiple source model, where source waveforms separate different brain activities (Scherg & Berg, 1991; Scherg, Ille, Bornfleth & Berg, 2002). The regional sources that were used, were the visual cortex lateral left (VClL), visual cortex lateral right (VClR), and the parietal midline (PM), argued to be active in the visual processing of motion stimuli (Probst et al., 1993; Zeki et al., 1991). A 4-shell ellipsoidal head model was created for each participant and used to convert data from electrode level to source montage dipoles to analyse the sources (Berg & Scherg, 1994; Hoechstetter et al., 2004). In inserting the source dipoles, the artefact-corrected coordinate files were appended. Bone thickness was adjusted to 3.0 mm and conductivity to 0.02 σ, as recommended for infants, and adjusted for children to 5.0 mm and 0.018 σ, respectively (BESA information; Grieve, Emerson, Fifer, Isler & Stark, 2003). Settings for latency, filter, and average parameters were the same as in the VEP analyses.

Time-frequency displays exhibit the changes in amplitude over time (TSE, temporal spectral evolution), which were generated from single trials by averaging spectral density amplitude over trials. Each graph displayed was a plot of spectral amplitude density of one montage channel over time and frequency normalized to the baseline for each frequency. (Hoechstetter et al., 2004; Pfurtscheller, Neuper & Mohl, 1994; Pfurtscheller, Stancak & Neuper, 1996). Before calculating TSE, signals from average evoked responses were removed from the single trial time series in order to have only displays of induced oscillatory brain activities. Independent TSEs for the three different motion conditions (forwards optic flow, reversed optic flow and random visual motion), and comparisons between each of the motion conditions and the static non-flow condition, as well as between the combined motion conditions and the static condition were carried out. Further, bootstrapped statistics were computed to explore significant differences between the TSE of motion conditions and the static non-flow condition for each participant for each of the three sessions. This produced probability maps that made it possible to look for differences in the TSE when comparing conditions separately for each infant and child. The approach permits the observation of significantly dominant oscillatory activities across the visual area of interest for each participant in each testing session. Bonferroni procedure and permutation test, as described by Simes (1986) and Auranen (2002), were used and applied to correct for multiple testing. TSE displays for infants and children were limited between frequency cut-offs of 4-40 Hz, while frequency and time sampling were set at 1 Hz and 50 ms.

BESA statistics 2.0 (BESA, GmbH) was used to test the probability of significance in frequency ranges and amplitude values between the TSEs of the motion conditions and the static non-flow condition for all the infants and children in each testing session. Statistical comparisons between the TSEs of the three visual motion conditions, as well as between the combined motion conditions and the static condition were carried out. An average of TSE statistics for infants and children in each testing session was produced. Significant time-frequency ranges could thus be used as a guide when finding patterns of maximum oscillatory activities in each individual TSE. A combination of permutation testing and data clustering was used to address the multiple comparisons problem. Cluster alpha (the level of significance for building clusters in time and/or frequency) was set at 0.005, number of permutations was set at 512, and frequency cut-offs and amplitude were set at the same as stated above.

2.5.4 Movement ABC. The Movement Assessment Battery for Children (M-ABC) (Henderson & Sugden, 1992) was performed on the full-term and preterm 6-year-old children to measure motor skills at this age in relation to their individual analysis of the VEPs. The M-ABC consisted of two parts: a performance test where the children performed eight different motor tasks in a standard way, and a checklist designed to be completed by a family member of the child’s day-to-day motor functions. The test is designed for children between 4 and 12 years of age, and consists of 32 items that are subdivided into 4 age bands (age band 4-6 years and 7-8 years was used in the present study). The motor tasks are grouped under three different categories: manual dexterity, ball skills, and static and dynamic balance. For each of these domains there are multiple subsets. The M-ABC manual has different requirements for the different motor tasks, and specifies faults of procedure that can result in a child “failing” a task (Henderson & Sugden, 1992). The design is developed to capture both the qualitative and quantitative aspects of the child’s motor performance, as well as the emotional and behavioural factors that might influence the child’s test performance.

The overall test took 20-40 minutes for each child. The child’s quantitative performance on each physical test item was scored from 0 (best) to 5 (worst), where high scores indicate poor performance. Individual scores were summed to produce a total score, ranging from 0-40. The total score could then be compared to a standardized age group score from Europe for 4- to 12-year-old children. Total score from 13.5 or higher, places the child in the category of “clumsiness” (categorized as having general perceptual-motor problems) and among the 5% worst for their age group. A total score between 10 and 13, places the child in a border area (requires monitoring) and among the 15% of the worst for their age group (Henderson & Sugden, 1992).

3.0 Results

3.1 VEP responses

The four posterior electrodes that showed the highest N2 amplitude values in the forwards optic flow condition of the grand average VEPs were chosen from each group and each testing session for further analysis. Figure 3 displays the grand average VEPs for the three visual motion conditions for full-term and preterm infants and children at each age and testing session (see Appendix A and B for all electrodes). The four grand average channels for full-term infants at 4-5 months were Oz, O2, O1 and POz, at 11-12 months they were PO3, PO4, POz and O2, and for full-term children at 6 years of age the grand average channels were POz, PO4, Oz and O2. The corresponding electrodes for preterm infants at 4-5 months were POz, PO4, PO3 and Oz, at 11-12 months they were POz, Oz, O1 and O2, and for preterm children at 6 years of age they were POz, PO4, Oz and O2. The selected electrodes are shown in Figure 2.

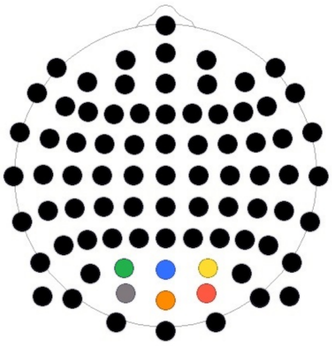

Figure 2. *Head drawing (nose up) showing the scalp positions of the standard 81 electrodes. The six electrodes of interest are indicated with colour-filled circles (from top to bottom, left to right): PO3 (green), POz (blue), PO4 (yellow), O1 (grey), Oz (orange) and O2 (red).*

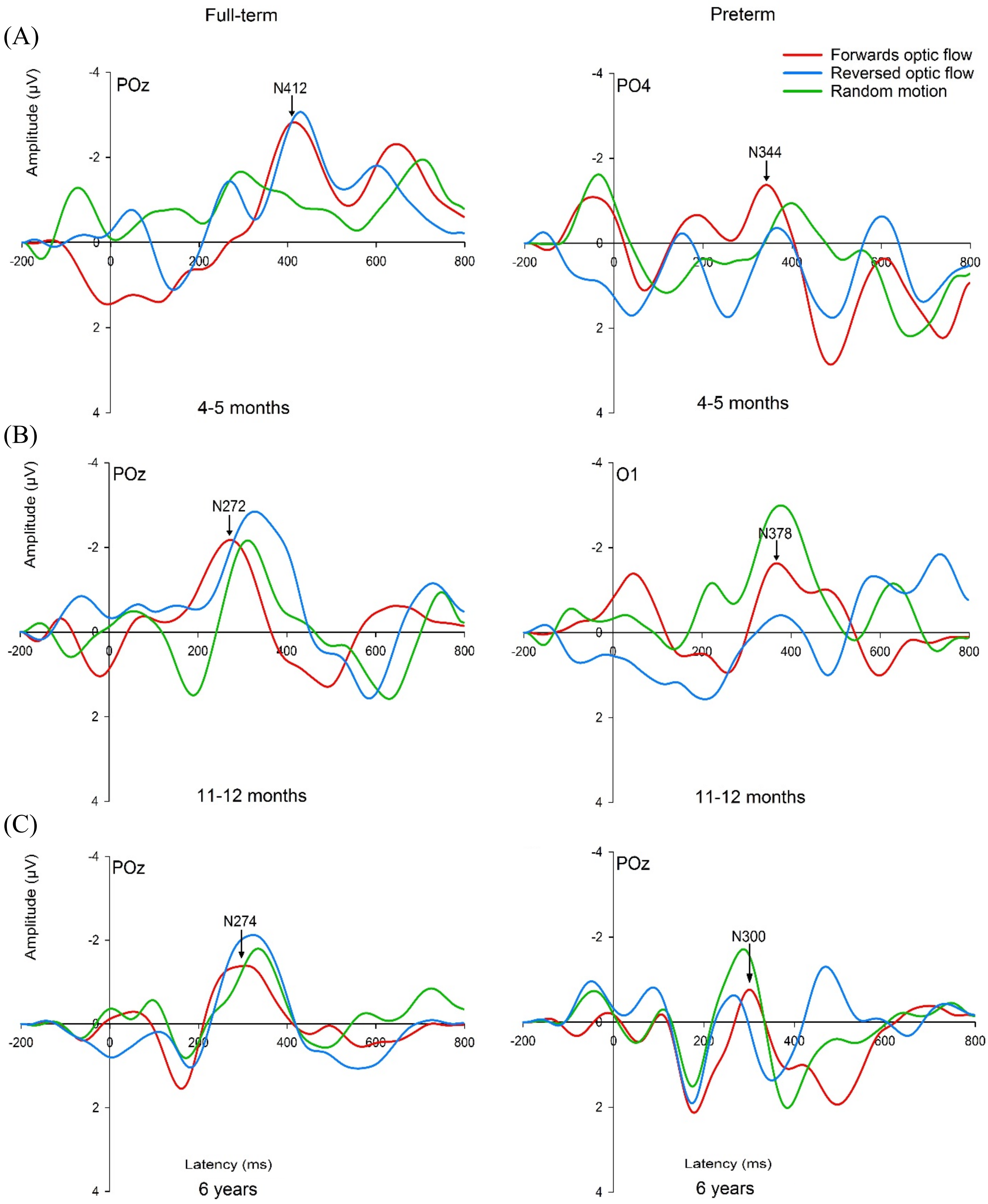

Figure 3. *Grand average motion VEPs in full-term (left) and preterm (right) infants and children at 4-5 months (A), 11-12 months (B), and 6 years of age (C). Latencies are on the x-axis and amplitudes are on the y-axis. The N2 peak for forwards optic flow is indicated with actual latency at each electrode for each testing session. The latency is from -200 to 800 ms.*

3.2 Latency analyses of VEPs

Latencies of the VEPs were analysed using mixed model analysis of variance, in a 2 (group: full-term and preterm) x 3 (age: 4-5 months, 11-12 months, and 6 years) x 3 (visual motion conditions: forwards optic flow, reversed optic flow, and random visual motion) design. Bonferroni correction was used to adjust for multiple comparisons. The electrode that showed the highest amplitude value of the four electrodes selected for the different testing sessions in the forwards optic flow condition for each infant, was used in the analysis. Consequently, the electrode used varied across participants and testing sessions, but would always be one of the four posterior electrodes stated above and would always be the same for the three motion conditions in each participant.

The mean N2 peak latency for full-term infants at 4-5 months for the three motion conditions for forwards optic flow, reversed optic flow and random motion was 408 ms (SD = 46), 413 ms (SD = 36), and 436 ms (SD = 54), respectively. Corresponding latencies at 11-12 months were 260 ms (SD = 38), 335 ms (SD = 33), and 381 ms (SD = 53), respectively. Further, at the age of 6 years the mean latency was 271 ms (SD = 27), 317 ms (SD = 29), and 338 ms (SD = 23), respectively. Matching N2 mean peak latencies for preterm infants for the three motion conditions at 4-5 months were 342 ms (SD = 71), 357 ms (SD = 55), and 385 ms (SD = 67), respectively. Further, at 11-12 months latencies were 384 ms (SD = 47), 367 ms (SD = 81), and 383 ms (SD = 52), respectively. At the age of 6 years the mean latency was 246 ms (SD = 28), 276 ms (SD = 33), and 286 ms (SD = 48), respectively.

A significant three-way interaction of condition, age and group was found, F (4, 162) = 2.94, $p < .05$, indicating that significant latency differences between the motion conditions were found, but only for the full-term infants at 11-12 months and at 6 years of age. The results showed that for the full-term infants at 11-12 months, latency significantly increased from forwards optic flow to reversed optic flow to random visual motion. And that the same results were found for the full-term children at 6 years of age, where the forwards optic flow condition was significantly shorter than the other two motion conditions (see Figure 4). The preterm participants did not differentiate between the three visual motion conditions, neither at 4-5 months, 11-12 months, nor at 6 years of age. Further, the analysis revealed a significant two-way interaction of age and group, F (2, 162) = 22.6, $p < .001$, indicating significant decrease in latency for the full-term infants from 4-5 months to 11-12 months, and for the preterm children from 11-12 months to 6 years of age. In addition, the two-way interaction of age and group indicates that at 4-5 months and at 6 years of age, preterm participants showed a significantly shorter N2 latency than the full-term participants did, irrespective of visual motion condition.

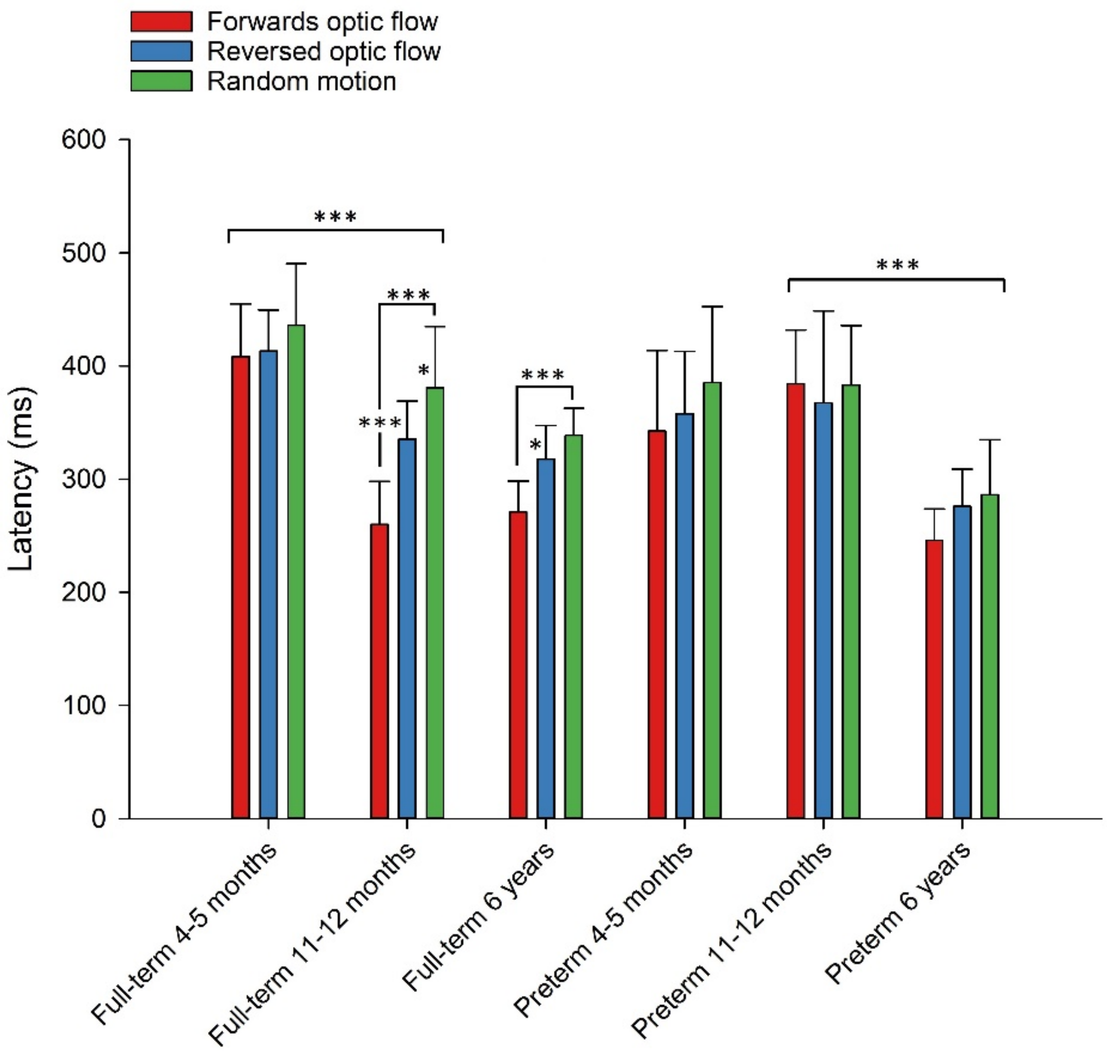

Figure 4. *Group means (and SD) of N2 latency peaks for three motion conditions in full-term and preterm infants and children at 4-5 months, 11-12 months, and 6 years of age. Latencies decreased significantly with age for the full-term infants from 4-5 months to 11-12 months and for the preterm children from 11-12 months to 6 years of age. In addition, significant differences in N2 peak latencies for the three different visual motion conditions were found only in full-term participants at 11-12 months and at 6 years of age, where latencies significantly increased from forwards optic flow to reversed optic flow to random visual motion at 11-12 months, and significantly increased from forwards optic flow to reversed optic flow, and from forwards optic flow to random visual motion at 6 years of age. The preterm group did not differentiate between the motion conditions, neither at 4-5 months, 11-12 months, nor at 6 years of age, even though at this age a trend could be seen. In addition, at 4-5 months and at 6 years of age, the preterm participants had a significantly shorter N2 latency than the full-term participants irrespective of visual motion condition. *Significant at $p < .05$, ***Significant at $p < .001$.*

3.3 Individual analyses of VEPs and M-ABC

VEP latency data for the full-term and preterm participants at 11-12 months and at 6 years of age were further investigated, considering that only full-term participants at 11-12 months and at 6 years of age could significantly differentiate between the three motion conditions, with no such differentiation observed for the preterm participants at any of the ages tested. The individual analyses explored whether some preterm participants were especially delayed in their responses to optic flow compared to the other full-term and preterm participants at these ages. An outlier value was defined as a larger value than the mean + SD*2.5, as formulated by Field (2013). Mean + SD*2.5 was calculated separately for the three visual motion conditions in the full-term infants at 12 months and full-term children at 6 years, as the reference for comparison. The results showed that all except two preterm infants at 11-12 months had latency values higher than the mean + SD*2.5 of the average VEP latencies in the full-term infants at 11-12 months, but only for the forwards optic flow condition (see Table 1). In addition, two of the preterm infants, MS and TU, stood out with longer latencies for both forwards and reversed optic flow. Interestingly, when looking at the mean latency for the different visual motion conditions, the full-term infants were a staggering 124 ms faster in detecting forwards optic flow than the preterm infants at 11-12 months, whereas the latencies for random visual motion were equally high for both groups (see Table 1). At 6 years of age, neither the full-term nor the preterm children had latency values higher than the criterion (see Table 2.) Moreover, by looking closer at the VEP latencies for the preterm group, the individual analyses reveal that five out of seven preterm children show the tendency towards differentiating between the three motion conditions, with shortest latency for forwards optic flow, followed by reversed optic flow, and longest latency for random visual motion, and most importantly all of them showed shortest latency for forwards optic flow.

Further, M-ABC was performed on the 6-year-old children to see if there were any differences in motor function between full-term and preterm children at this age, and if the same preterm children that scored high on the M-ABC-test, also had a longer latency value at 11-12 months or at 6 years of age. The M-ABC test showed no differences in the average score between the full-term and the preterm children. The M-ABC revealed that two preterm and three full-term children had a score above 10 points, and thereby end up within the 15% of the weakest in their age group, suggesting that these children need monitoring. Among these children, only one preterm, but also one full-term child had a score above 13.5, suggesting they belong within the 5% of the weakest in their age group, where preterm child

DT had the highest score of 21 points. Preterm child DT was overall the only child that both showed delayed responses to optic flow at 11-12 months, and poor scores on the M-ABC-test at 6 years of age (see Table 1 and 2).

Table 1. *VEP latencies (ms) of the three visual motion conditions (forwards optic flow, reversed optic flow, and random visual motion) for 12-month-old full-term and preterm infants. The highlighted numbers indicate the preterm infants who showed latency values larger than mean + SD*2.5 of the average latency values of the full-term group. Preterm infants MS and TU stood out with their long latencies for both optic flow conditions. In addition, six more preterm infants showed larger latencies than mean + SD*2.5 in forwards optic flow, where AT and DT had the largest latencies.*

Full-term	**For**	**Rev**	**Ran**	**Preterm**	**For**	**Rev**	**Ran**
BK	294	338	370	**AT**	**492**	410	478
BE	240	356	314	**DK**	**358**	366	360
GE	234	378	410	**DT**	**406**	354	336
JY	260	344	392	**EL**	308	288	328
LS	320	376	492	**MS**	**380**	**466**	466
ME	208	350	330	**MA**	350	224	330
ST	206	332	420	**SK**	**396**	352	384
SE	269	304	362	**TA**	**368**	400	392
SN	276	272	322	**TU**	**398**	**498**	392
VE	294	306	398	**WM**	**388**	316	366
Mean	260	335	381		384	367	383
SD	38	33	53		47	81	52
Mean+SD*2.5	**355**	**418**	**514**				

Table 2. *VEP latencies (ms) of the three visual motion conditions (forwards optic flow, reversed optic flow, and random motion) for 6-year-old full-term and preterm children. None of the preterm children had latency values higher than mean + SD*2.5 of the average latency values of the full-term group. Moreover, five out of seven show the tendency to differentiate between the three different motion conditions, with shortest latency for forwards optic flow, followed by reversed optic flow and random visual motion, whereas all of them showed shortest latency for forwards optic flow. In addition, M-ABC scores for full-term and preterm children at 6 years of age are shown. The highlighted scores show the two preterm and three full-term children that had scores above 10, and fall within the 15% of the worst for their age group, indicating these children being on a border area of having perceptual-motor problems. Among these children, only one preterm and one full-term child had a score above 13.5, and fall within the 5% of the worst for their age group, where preterm DT had the highest score of 21.*

Full-term	**For**	**Rev**	**Ran**	**M-ABC**	**Preterm**	**For**	**Rev**	**Ran**	**M-ABC**
BE	256	266	336	6	**AT**	266	274	282	5.5
GE	262	364	334	0	**DT**	298	300	304	21
JY	306	314	318	5	**EL**	240	336	270	13
LS	268	332	338	10	**MS**	216	240	250	2
ST	312	328	388	8	**SK**	224	276	230	4
SN	240	310	316	12	**TA**	244	250	382	4
VE	254	310	342	14	**WM**	243	256	286	3.5
Mean	271	317	338			246	276	286	
SD	27	29	23			28	33	48	
Mean+SD*2.5	**339**	**390**	**396**						

3.4 TSE analyses

TSEs for the full-term infants at 4-5 months showed desynchronized oscillatory activity in the theta-band range for the motion conditions, while appearing as synchronized activity in the same frequency band in the TSEs of the static non-flow condition (see Figure 5A and B for a typical infant). Figure 5C is showing the comparisons between the motion conditions and the static condition, revealing the largest difference in activity observed in the theta-band range. The average frequency of the maximum induced ERD for the VClL, PM and VClR was 5.8 Hz (SD = 0.9), with mean latency of 654 ms (SD = 12.0). The results of the bootstrapping procedure for full-term infant BK is presented in Figure 5D where the TSE of the motion conditions was compared to the TSE of the static non-flow condition. Figure 5D shows theta-band induced activity in the regional sources VClL, PM and VClR that was significantly different in the motion conditions compared to the static non-flow condition (also see Appendix C for another example).

TSEs for preterm infants at 4-5 months of age showed similar results of desynchronized oscillatory activity in the theta-band range in the motion conditions, which occurred as synchronized activity in the same frequency band in the static non-flow condition (see Figure 6A and B for a typical preterm infant). TSE map 6C is showing the comparisons between the motion conditions and the static non-flow condition, where the largest differences in oscillations can be observed in the theta-band range. Average frequency of the maximum induced ERD for the regional sources VClL, PM and VClR was 5.0 Hz (SD = 0.5), with mean latency of 680 ms (SD = 82.0). TSE of the bootstrapped procedure for preterm infant SK when the motion conditions were compared to the static non-flow condition shows theta-band induced activity in the regional sources of interest as significantly different in the motion conditions compared to the static condition (Figure 6D, also see Appendix D).

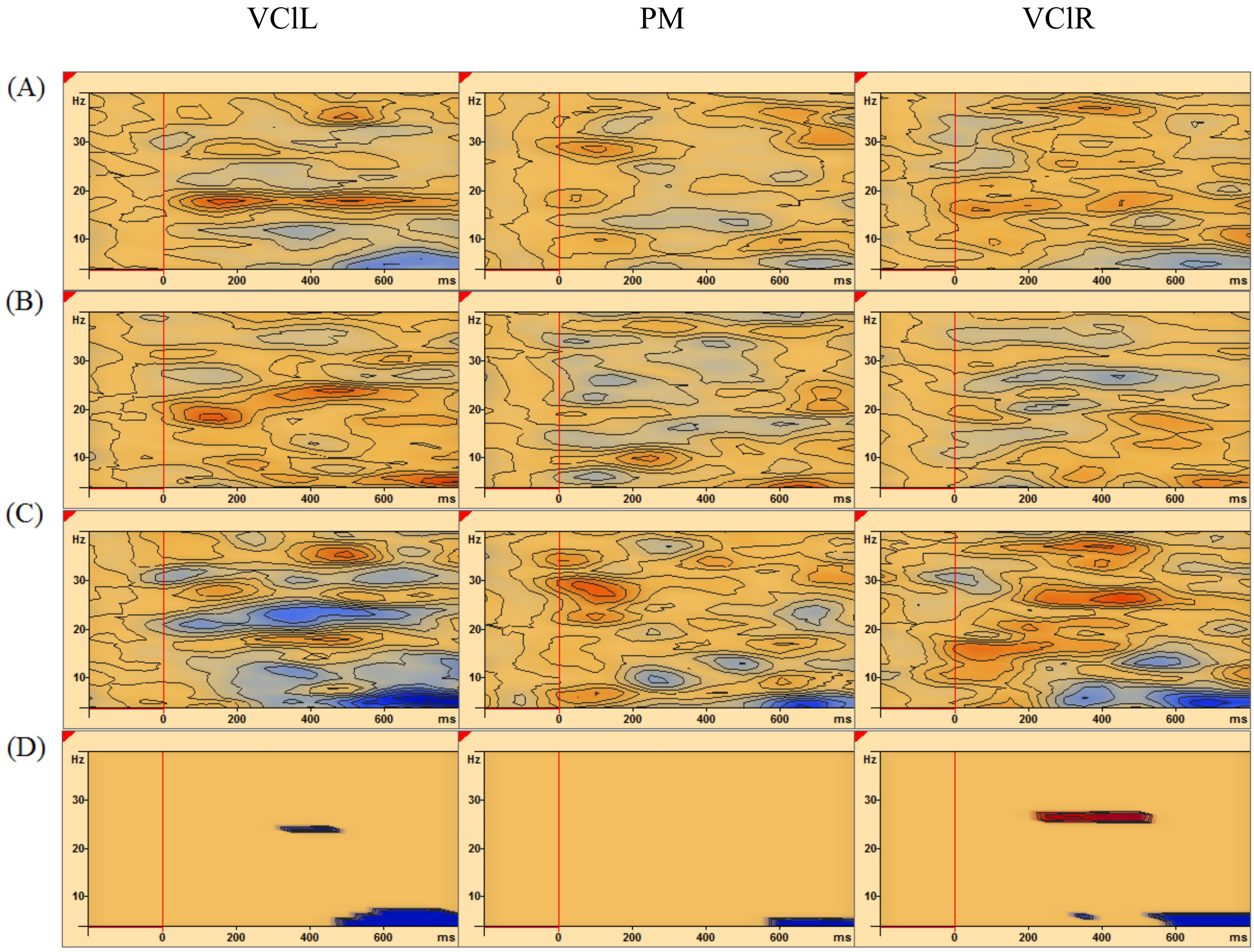

Figure 5. *TSE plots across brain regions of interest (VClL, PM, VClR) in full-term infant BK at 4-5 months of age. Epoch is from -200 to 800 ms, and stimulus onset at 0 ms is marked with a red vertical line. For the TSE plots, blue areas represent decreased spectral amplitude (induced desynchronized activity), while red areas represent increased spectral amplitude (induced synchronized activity). TSE of the motion condition (A) shows desynchronized activity in the theta-band range, while appearing as synchronized activity in the TSE of the static non-flow condition (B). TSE plot (C) shows the comparison between the motion conditions and the static non-flow condition. Figure (C) shows desynchronized activity (blue colour) in the theta-band frequency around 450 ms after stimulus onset, representing the largest change in activity. Note that the same area showed up as significant in the statistical analysis (D). Results of bootstrapping procedure (D) when comparing the motion conditions to the static condition. Significant decreased activity is indicated with blue colour, while significant increased activity is represented by red colour in the TSE. Bootstrapping procedure (D) showed significant induced desynchronization in the theta-band range.*

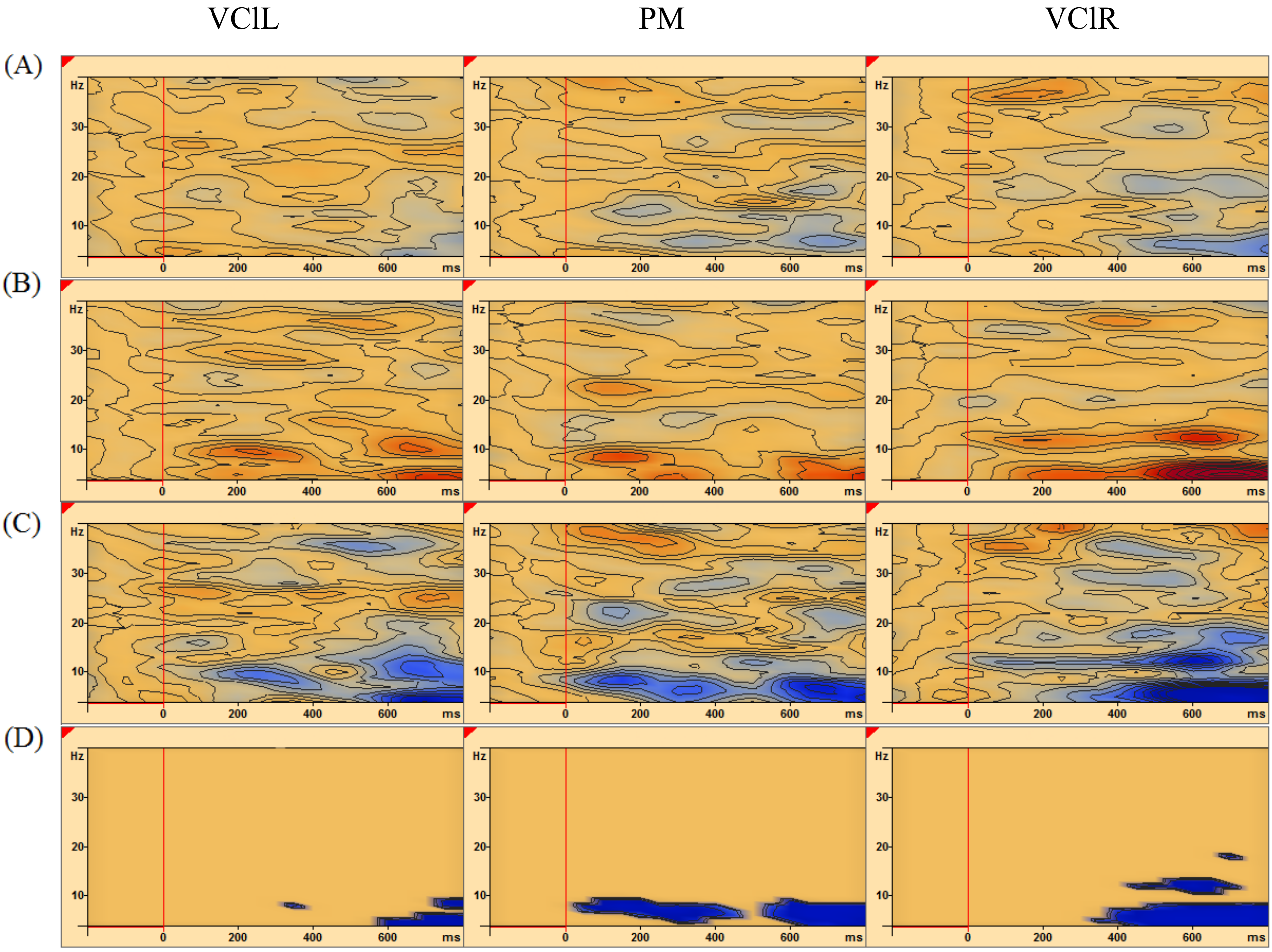

Figure 6. *TSE maps with epoch from -200 to 800 ms for preterm infant SK at 4-5 months of age. Stimulus onset is indicated at 0 ms with a red vertical line. TSE plots of VClL, PM and VClR represent the visual areas of interest. Blue areas represent decreased spectral amplitude (induced desynchronized activity), while red areas represent increased spectral amplitude (induced synchronized activity). Desynchronized activity in the theta-range can be observed in the TSE plot of the motion condition (A), while synchronized activity in the theta-band range can be observed in the TSE plot of the static non-flow condition (B). TSE map of the comparisons between the motion conditions and the static non-flow condition in infant SK can be seen in (C), showing desynchronized activity in the theta-band range around 200-400 ms from stimulus onset, representing the areas with largest changes in activity. The same theta-band desynchronization showed up as significant in the statistical analysis (D) when the motion conditions were compared to the static non-flow condition. No significant synchronized activity was observed.*

TSEs for 11-12-month-old full-term infants showed desynchronized activity within the theta-band range for the motion condition. Further, some higher synchronized activity especially within the late alpha and early beta ranges was observed, peaking at different latencies from start to around 250 ms after stimulus onset, and to around 695 ms to the end of stimulus (see Figure 7A for a typical infant). Synchronized activity in the motion conditions occurred as desynchronized activity in the same frequency band in the TSE of the static non-flow condition (see Figure 7B, also see Appendix C). This can be observed in the TSE map of the comparison between the motion conditions and the static non-flow condition (see Figure 7C). For the three visual sources of interest, average frequency of the maximum induced ERS was 13.4 Hz (SD = 5.4), with mean latency of 422 ms (SD = 259). The results of the bootstrapped procedure for the comparison between the motion conditions with the static condition can be seen in Figure 7D for full-term infant JY. The TSEs show induced synchronized activity in late alpha and early beta-band and desynchronized theta-band activity as significantly different in the motion condition compared to the static non-flow pattern (see Figure 7D).

TSEs for preterm infants at 11-12 months showed desynchronized activity in the theta-band range for the motion condition, similar to what was observed when the preterm infants were 4-5 months of age. For the tree visual sources of interest VClL, PM and VClR, average frequency of the maximum induced ERD was 6.6 Hz (SD = 0.9), with mean latency of 627 (SD = 133). Unlike the full-term infants at 11-12 months, no high-frequency activities were generally observed for the preterm infants at this age (see Figure 8D for å typical preterm infant). Even so, two preterm infants at 11-12 months showed some significant synchronized high-frequency activity in the late alpha, early beta-band ranges (see Appendix D for an example), but less prominent than in the full-term infants TSEs, and most of the preterm infants did not show similar activity at all. Figure 8A displays the TSE for preterm infant AL at 11-12 months of age, where desynchronized activity in the motion condition occurred as synchronized activity in the static condition in the same frequency band (see Figure 8B). Figure 8C displays the TSE of the comparisons between the motion conditions and the static non-flow condition, showing only desynchronized activity peaking around 200-450 ms after stimulus onset. The results of the bootstrapping procedure (Figure 8D) between the motion conditions and the static condition confirms that there are no significant differences in synchronized activity for preterm infant AL at this age. Similar results were observed in the other preterm infants at this age.

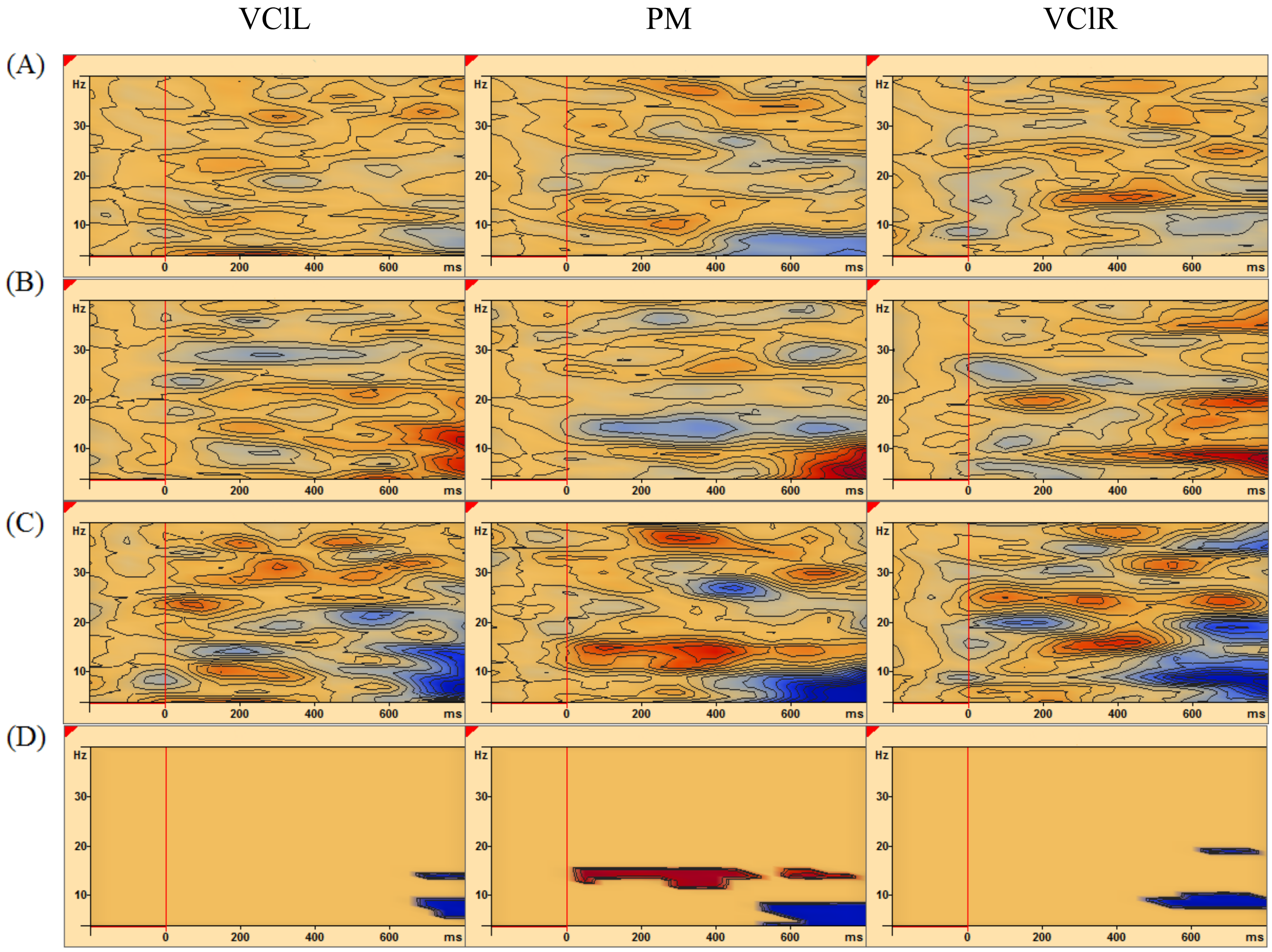

Figure 7. *TSE maps with epoch from -200 to 800 ms for full-term infant JY at 11-12 months of age. Stimulus onset is marked with a red vertical line at 0 ms. TSE plots of VClL, PM and VClR represents the visual areas of interest. Blue contours indicate induced desynchronized activity, while red contours indicate induced synchronized activity. TSE maps of the motion condition (A) show some synchronized activity in the alpha-beta band frequency in addition to lower frequency of desynchronized theta-band activity. Corresponding TSE plots of the static condition (B) show desynchronized activity in the same alpha-beta band ranges as in the TSEs of the motion condition (A). TSE maps of the motion conditions when compared to the static condition showed high amplitudes within the alpha-beta frequency band (C). The red colour for the synchronized alpha-beta band activity around 200-300 ms after stimulus onset represents the areas with the largest changes in activity. The same frequency bands occurred as significant in the bootstrapping procedure (D) when the motion conditions were compared to the static non-flow pattern. The significant decreased areas are represented by blue colour, while the significant increased areas are represented by red colour in the TSE maps. Significant induced desynchronization in the TSE can be observed in the theta-band*

frequencies, while significant induced synchronization in the TSE can be observed in the alpha-beta band frequencies (D).

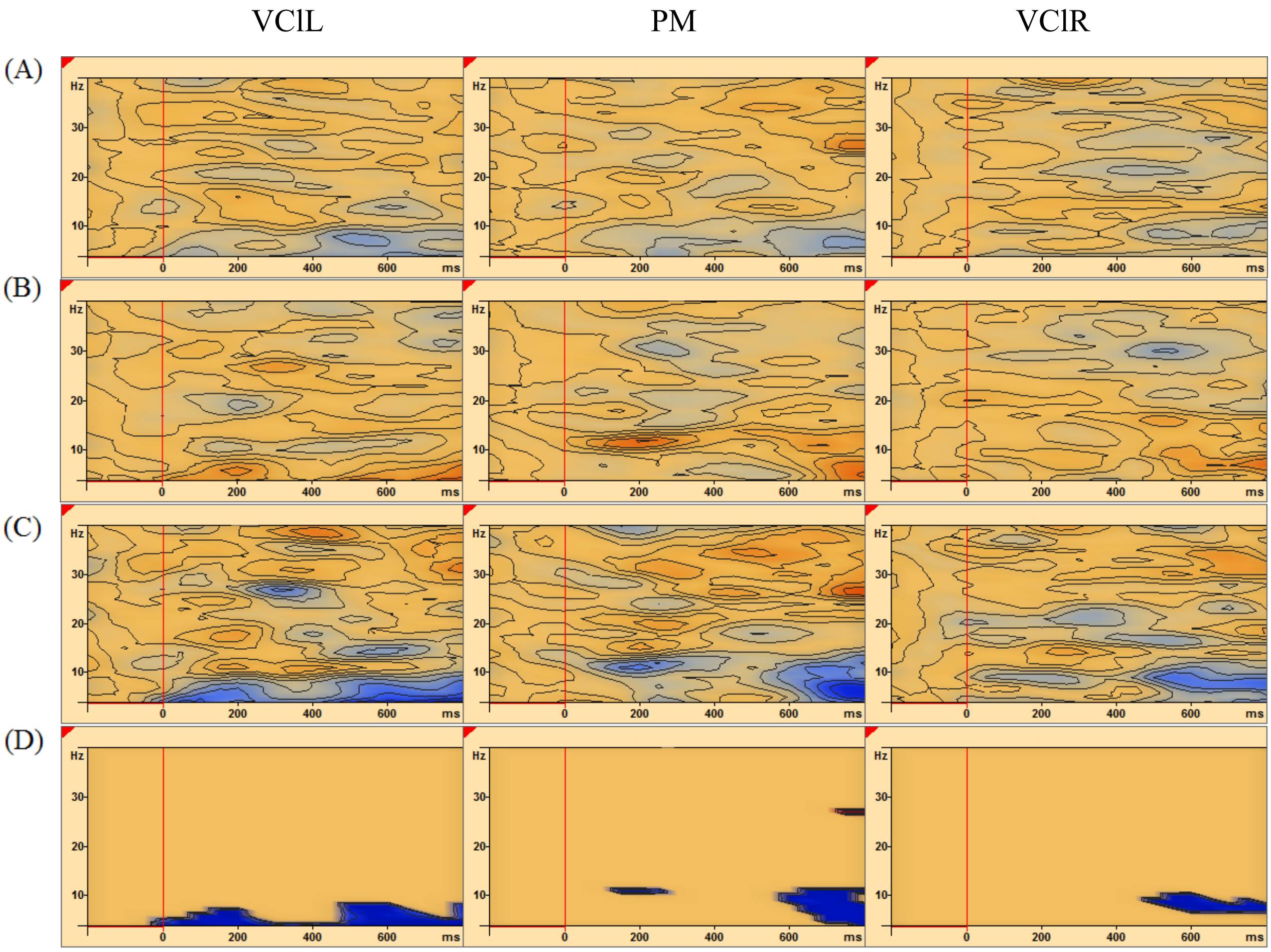

Figure 8. *TSE maps with epoch from -200 to 800 ms for preterm infant AT at 11-12 months of age. Stimulus onset is marked at 0 ms with a red vertical line. TSE plots of VClL, PM and VClR represent the visual areas of interest. Blue coloured contours indicate induced desynchronized activity, while red coloured contours indicate induced synchronized activity. TSE maps of the motion condition (A), show desynchronized activity in the theta-band range, appearing as synchronized activity in the same frequency band in the static condition (B). TSE maps when the motion conditions were compared to the static non-flow condition for preterm infant AT, can be observed as desynchronized activity in the theta-band range between 200-600 ms after stimulus onset, and represent the areas with largest change in activity (C). The same areas are significant in the results from the bootstrapped procedure (D) when the motion conditions where compared to the static non-flow condition, indicating significant decrease in the TSE.*

For 6-year-old full-term children, the TSEs of the motion condition showed desynchronized activity in the late alpha-, early beta-frequency range. In addition, higher synchronized frequencies especially within the late alpha- and early beta-band ranges were observed for the full-term 6-year-old children, where three of them also showed gamma-band frequencies (see Figure 9A for a typical child at this age). This was especially evident in the TSE of the comparisons between the motion conditions to the static non-flow condition (see Figure 9C). Unlike full-term infants at 11-12 months, less or no theta-band frequencies were observed for full-term children at 6 years of age (see Figure 9C, also see Appendix C). For the three visual sources of interest, average frequency of maximum induced ERS was 14.5 Hz (SD = 4.0), with mean latency of 239 ms (SD = 137). Figure 9D displays the results of the bootstrapping procedure for full-term participant SN at 6 years of age when the TSE of the motion conditions was compared to the TSE of the static non-flow condition. The result showed induced desynchronized and synchronized activity within the late alpha-, early beta-band frequencies, in addition to some synchronized gamma-band frequencies as significant different in the motion conditions compared to the static non-flow condition for full-term child SN (see Figure 9D).

For preterm children at 6 years of age, the TSEs of the motion condition showed desynchronized activity in late alpha-, early beta-band ranges (see Figure 10A for a typical child at this age). Similar to what was observed in the full-term childrens' TSEs, less or no desynchronized theta-band activity was observed. This is especially evident in Figure 10C where the TSE of the comparison between the motion conditions and the static non-flow condition only show desynchronized activity in the late alpha-, early beta-band ranges for child EL (also see Appendix D). Unlike the full-term children, only two premature children showed some higher-frequency activities in the alpha-band ranges at this age. For the three visual sources of interest VClL, PM and VClR, average frequency of maximum induced ERD was 9.5 Hz (SD = 1.1), with mean latency of 530 ms (SD = 12.0). Figure 10D displays the results of the bootstrapping procedure for preterm child EL when the motion conditions were compared to the static non-flow condition. The TSE of the regional sources VClL, PM and VClR shows that the late alpha-, early-beta band induced activity was significantly different in the motion conditions compared to the static non-flow condition. In the TSEs of each infant and child and in each testing session, no significant induced activities were observed in any other frequency bands, when frequency cut-off was analysed above 40 hz or below 4hz.

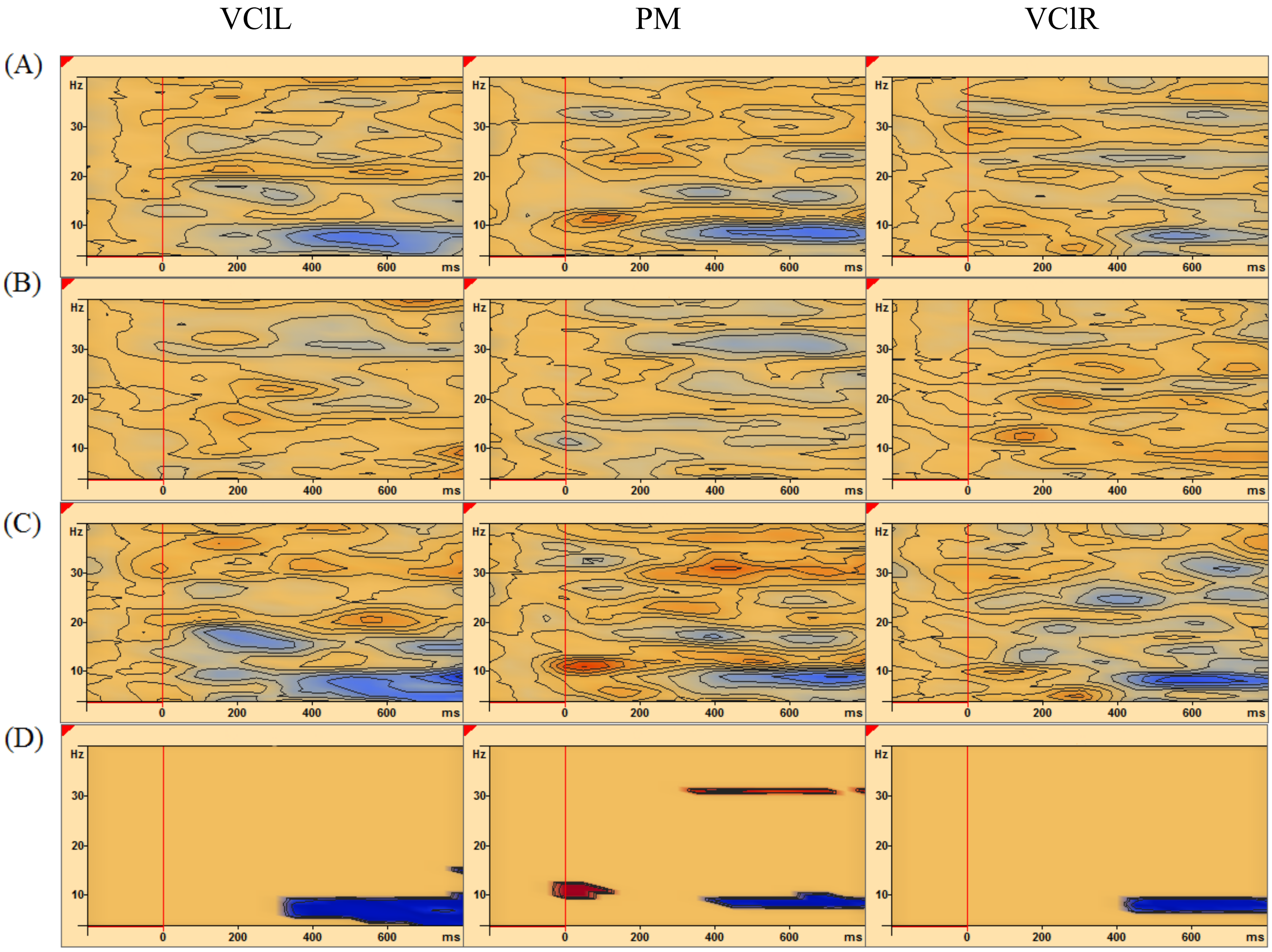

Figure 9. *TSE maps with epoch from -200 to 800 ms for full-term child SN at 6 years of age. Stimulus onset is indicated at 0 with a red vertical line. TSE plots of VClL, PM and VClR represent the visual areas of interest. Blue coloured areas represent decreased spectral amplitude (induced desynchronized activity), while red coloured areas represent increased spectral amplitude (induced synchronized activity). Desynchronization within the late alpha-, early beta-band ranges was observed in the TSE of the motion condition (A), while some synchronization in the same frequency ranges was observed in the TSE of the static non-flow pattern (B). In addition, some higher frequency oscillations in the alpha-beta-gamma-band ranges can be observed in the TSE of the motion condition (A), and especially evident in the comparisons between the motion conditions and the static non-flow condition (C). The strong blue coloured contours in the alpha band frequency around 400 ms, the strong red coloured contours in the alpha-beta-band frequencies around 100-300 ms, and the strong red coloured contours in the gamma-band frequencies around 400-600 ms represent the areas with the largest changes in activity. Further, the same areas showed up as significant in the statistical analysis (D). Results of the bootstrapping procedure for child SN at 6 years of age when*

comparing the motion conditions to the static condition in figure (D). The blue areas represent significant decrease in TSE, while red represents significant increased areas in TSE. Both significant induced desynchronization (decrease in TSE) and significant synchronization (increase in TSE) can be observed at alpha-beta-band frequencies in addition to some synchronized gamma-band frequencies.

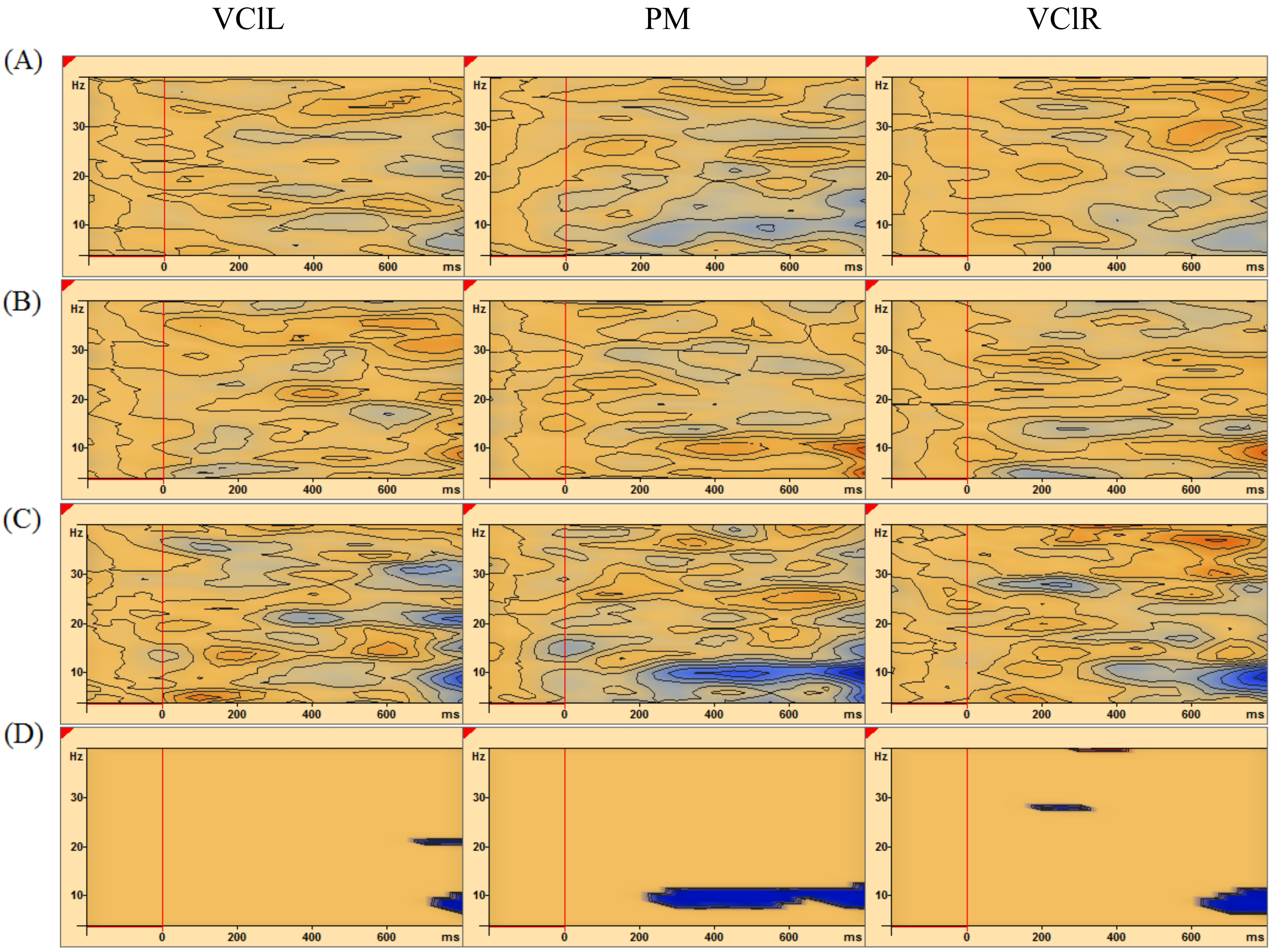

Figure 10. *TSE maps with epoch from -200 to 800 ms for preterm child EL at 6 years of age. Stimulus onset is marked at 0 ms with a red vertical line. TSE plots of VClL, PM and VClR represent the visual areas of interest. Blue coloured areas indicate induced desynchronized activity, while red coloured areas indicate induced synchronized activity. Desynchronization in the alpha-beta-band ranges can be observed in the TSE of the motion condition (A), while synchronized activity of the same frequency bands can be observed in the TSE of the static non-flow condition (B). (C) TSE plots of the comparisons between the motion conditions and the static non-flow condition for preterm EL at 6 years of age. The strong blue areas in the late alpha-, early beta-band ranges around 200-600 ms represent the areas with largest change in activity at this age. The same frequency-bands showed up as significant in the bootstrapping procedure (D) when comparing the motion conditions to the static non-flow condition. This indicates areas which are significantly decreased in the TSE.*

Figure 11 displays the results of the permutation test for the average visualization of significant clusters when TSE of the motion conditions were compared to TSE of the static non-flow condition for full-term infants and children at 4-5 months (A), 11-12 months (B) and at 6 years of age (C), and for preterm infants and children at 4-5 months (D), 11-12 months (E) and 6 years of age (F). The permutation test showed significant negative clusters in the regional sources of interest (VClL, PM and VClR) when the motion conditions were compared to the static condition, indicating that motion had significantly smaller amplitude values than the static non-flow condition. The significant clusters seemed to be more prevalent and widespread in full-term infants at 4-5 months (Figure 11A) than full-term infants at 11-12 months (Figure 11B). No significant positive clusters in the higher frequency ranges were seen in the permutation tests, mostly due to individual differences in frequency and latency. There were no significant differences observed when separate TSEs of the three different motion conditions (forwards optic flow, reversed optic flow and random motion) were compared with each other.

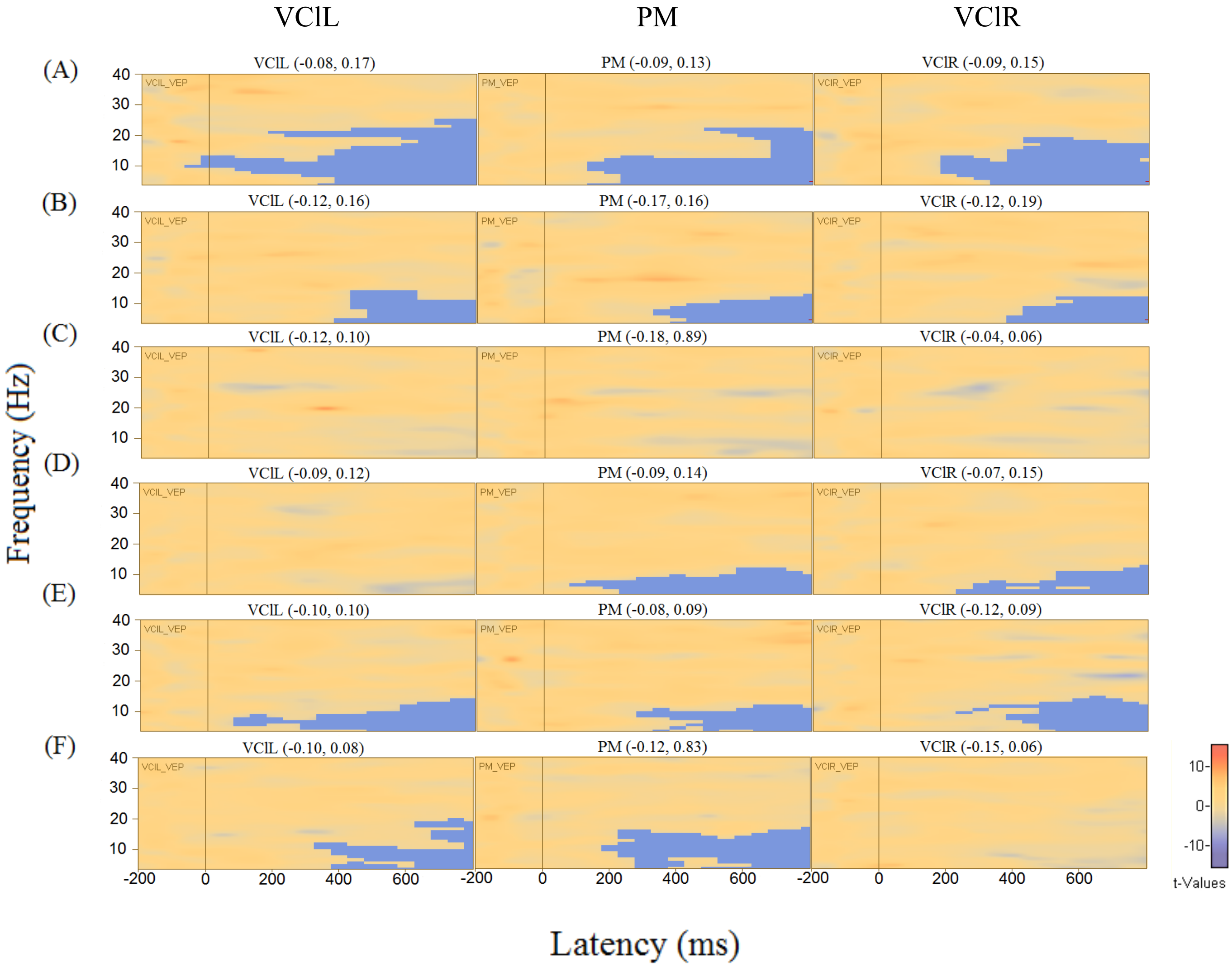

Figure 11. *Average visualization of significant data clusters in the visual regional sources of interest when the motion conditions were compared to the static non-flow condition in full-term participants at 4-5 months (A), 11-12 months (B) and 6 years (C), and preterm participants at 4-5 months (D), 11-12 months (E) and 6 years (F). Blue colours indicate negative clusters (i.e., combined motion conditions had smaller t-values than the static condition), while red colours indicate positive clusters (i.e., motion conditions had larger t-values than the static condition). Black vertical line indicates stimulus onset at 0 ms. Latency is from -200 ms to 800 ms. Cluster means for the combined motion conditions and the static non-flow condition are presented in the parentheses, in respective order. All the significant clusters had a significant level of p< .05.*

4.0 Discussion

In the present longitudinal study, high-density EEG was used to investigate brain electrical activity as a function of perception of visual motion in full-term and preterm infants and children at 4-5 months, 11-12 months and 6 years of age. The optic flow experiment consisted of three visual motion conditions, simulating forwards and reversed optic flow and random visual motion, in addition to a static non-flow pattern used as a control condition. The study investigated whether there were any differences in visual motion perception between normally developing term-born and preterm born infants and children at three different time points in their development.

Both VEP and TSE analyses were used to investigate possible differences in evoked and induced brain electrical activity between the groups when perceiving different structured radial motion, i.e. forwards optic flow and reversed optic flow, and non-structured random visual motion. In addition, individual analyses of brain responses and motor functions were carried out. The purpose was to investigate in a longitudinal design whether preterm infants and/or children suffer from developmental abnormalities of visual motion perception compared to their term-born peers, possibly indicating a dorsal stream vulnerability related to preterm birth.

The VEP analyses of optic flow revealed that during the course of development, only full-term infants significantly decreased their VEP latencies for all the visual motion conditions from 4-5 to 11-12 months of age. This corresponds with and supports earlier findings from a longitudinal study of Agyei et al. (2015) reporting that brain electrical activities related to visual motion perception change during the first year of life, showing that full-term infants become more sensitive to structured optic flow with faster processing time.

In the present study, the long latencies observed in the full-term and preterm infants at 4-5 months of age, may reflect a lack of specialized neuronal networks in the brain and a larger amount of coherently activated neurons to process visual stimuli (Dubois et al., 2006; Johnson, 2000). The significant decrease in the latency of the N2 component of the VEP waveforms observed in the full-term infants at 11-12 months can be attributed to the rapidly ongoing neurobiological specialization in the brain during the first year of life. Studies have reported rapid cortical synapse formation and overproduction in most of the cortical areas through the first two years of life (Casey, Giedd & Thomas, 2000). This overproduction of synapses is important for adaptation and plasticity of the brain during maturation (Chugani, Müller & Chugani, 1996; Tierney & Nelson, 2009). Studies have shown that fibre volume of white matter increases from early infancy until adulthood because of the ongoing axonal myelination, which results in increasing speed of neural communication. Further, neuronal networks and pathways become selective and processing speed increases along with individual experience (Agyei et al., 2015; Dubois et al., 2006; Mukherjee et al., 2002; Paus et al., 2001). This maturation may explain why important visual information shows faster processing time by the end of the first year of life. This is confirmed by earlier studies on development, showing that VEP latencies decrease with increasing age and become more mature and adult-like during the first year of life (Agyei et al., 2015, 2016; Blom, Barth & Visser, 1980; Fielder et al., 1983; Hammarrenger et al., 2007), indicating brain plasticity and efficient specialization of neuronal networks (Dubois et al., 2006; Mukherjee et al., 2002; Paus et al., 2001). In addition to overproduction of synapses, studies have also reported maturation of local glucose metabolic rate during the same period, particularly in the posterior temporal and parietal lobes (Chugani et al., 1996). The increase of glucose metabolic rates would allow more neuronal energy for effective motion processing (Grieve et al., 2003). The combination of increase in glucose metabolic and neuronal myelination of connecting fibres may explain the faster processing of visual motion in the full-term infants at 11-12 months compared to 4-5 months.

VEP analyses revealed that at 11-12 months and at 6 years of age, the full-terms significantly differentiated between the three visual motion conditions, as opposed to when they were younger. At 11-12 months of age, the full-term infants had significantly decreased their latency from forwards optic flow to reversed optic flow to random visual motion, and at 6 years of age the latency in forwards optic flow was significantly shorter than in the other two motion conditions. This is in accordance with Agyei et al. (2015, 2016), reporting that the N2 latency becomes shorter with age as a result of the infants becoming more mobile and experiencing self-produced optic flow. The significant discrimination between the motion conditions observed both at 11-12 months and at 6 years of age as opposed to at 4-5 months of age, could thus be attributed to the increase of self-produced locomotion and neuronal specialization (Gilmore & Rettke, 2003; Gilmore et al., 2004). Given that infants at 4-5 months have limited to no experience with self-produced locomotion, their brains have not formed any specialized networks for differentiating between different visual motions, and consequently they do not have the ability to respond appropriately to the different flow patterns. Sensitivity to optic flow has proved to increase significantly in infants when they start crawling (Anderson et al., 2001), and the functional detection of optic flow has thus been proposed to develop hand in hand with self-produced locomotion (Van der Meer et al., 2008) This is supported by James and Swain (2011) reporting that only self-generated interaction of body and environment will lead to a stronger connection between perception and action in the developing brain. In the present study, infants at 4-5 months, who had only had passive experience of motion from being carried around by adults, were not able to distinguish between the different patterns of the radial motions until the age of 11-12 months, when they had gained experience with self-produced movements through crawling. The present study corresponds with the previous findings by showing that only after experience with active locomotion through self-movement, infants display faster processing and activation of neural networks for motion recognition. Thus, the low latencies at 11-12 months and at 6 years of age show fast detection of direction of travel, which demonstrates the importance of optic flow for self-navigating in infancy and childhood, allowing them to move their bodies more correctly according to the constant incoming information from the surroundings.

The fast detection of optic flow observed for full-term children at 6-years of age, where latencies in forwards optic flow were significantly shorter than in the two other motion conditions, confirms a further maturation towards a more adult-like sensitivity, especially for forward motion. One reasonable explanation for the shorter latency in forwards optic flow observed in the full-term participants, is most likely connected to the fact that humans normally move in a forward direction to perform everyday tasks. Thus, our most common experience is the environment flowing towards us, rather than away. It is therefore logical to assume that the human brain will be more adjusted to, and respond more rapidly to, the more familiar visual motion such as forwards optic flow, rather than reversed optic flow, simulating backwards motion, or random visual motion, an unstructured motion pattern hardly ever experienced by humans. This is in accordance with the notion that forwards optic flow activates both visual and nonvisual cortical areas to a greater extent than reversed optic flow (Ptito et al., 2001). Supporting findings were made in a EEG study by Gilmore et al. (2016), reporting that children at 4-8-years of age showed similar evoked patterns of neural activity to changing optic flow patterns (translation, rotation, and radial expansion/contraction) as adults. In their study, children showed evoked responses to global and local motion similar to what was observed in adults, but with some specific differences probably reflecting immaturity in motion processing systems. This suggests that motion processing networks undergo substantial changes from infancy to early childhood and continue developing into early adolescence. The short processing time, especially for forwards optic flow, of around 240-312 ms observed in the full-term children, is more adult-like, but not as short as 130-200 ms, which is found in adults (Van der Meer et al., 2008). Other studies also report that the visual system for processing motion is not fully developed in school-aged children, but that maturation occurs well into childhood (Giaschi & Regan, 1997; Gunn et al., 2002; Parrish et al., 2005). This illustrates that from infancy to childhood, children have a better, but not fully developed, ability to differentiate between directions. The more mature processing system at 6 years probably reflects improved functional specialization of neurons in the dorsal stream in combination with increased locomotor experience of more complex forms like walking and running, making children more capable to detect and respond to visual information in the environment (Anderson et al., 2001; Gilmore et al., 2016).

As for the preterm participants, on the other hand, the VEP analyses revealed that none of them were able to discriminate between the three different motion conditions, neither at 4-5 months, or at 11-12 months, and not even at 6 years of age. Even though the preterm children are likely to have had the same amount of experience with locomotion such as walking and running as the full-term children by 6 years of age, they were not as capable as the full-term children in differentiating between the three motion conditions. This is corresponding with the study by Taylor et al. (2009) reporting that premature children fall short when it comes to perception of global motion, global form, and biological motion. Furthermore, Atkinson and Braddick (2007) have shown that premature children exhibit marked deficits in their ability to detect coherent global motion, a skill that is thought to depend on the functional integrity of the MT complex (Newsone & Pare, 1988; Schenk & Zihl, 1997). The lack of discrimination between the different motion conditions could be caused by less specialized networks for processing visual motion in the premature participants. This finding supports the notion that visual functions associated with the dorsal stream, such as perception of different structured radial motion, may be impaired by premature birth, reflecting that these forms of visual motion processing develop at different rates, and may be vulnerable to atypical neurodevelopment (e.g., Atkinson and Braddick, 2007; Guzzetta et al., 2009; Taylor et al., 2009).

However, the VEP analyses showed that the premature children did significantly reduce their VEP latency for all of the visual motion conditions from 11-12 months to 6 years of age. This improvement was observed in the full-terms already at 11-12 months of age. Several studies agree on that white matter organizations are still affected in late childhood by preterm birth (Skranes et al., 2007; Vangberg et al., 2006), and that myelination deficits are affecting the structural and functional connectivity leading to slower signalling in the brain (Hollund et al., 2018). The abnormalities of the reduced unmyelinated and myelinated white matter reported in preterm individuals (Mewes et al., 2006), may partly account for the delayed improvement of latencies observed in the preterm participants.

Another contributing factor is a delayed or abnormal pruning program caused by premature birth (Nosarti et al., 2008; Padilla et al., 2014). In the late second to early third trimester of gestation, the development of the infant brain is characterized by axonal ingrowth and elaboration of synaptic connections (Dubois et al., 2006; Volpe, 2009). Premature birth will therefore remove the development of the visual system from the nurturing environment in the womb during a period of rapid maturation. The visual cortex is argued to be especially vulnerable to alterations from environmental influences where abnormal visual experience is disrupting the normal maturation (Wiesel, 1982; Bourgeois, Jastreboff & Rakic, 1989; Frégnac & Imbert, 1984). The brain of a prematurely born infant will therefore grow and develop in a different way than it would in the womb. It is possible that exposure of the immature visual system to early visual stimulation caused by premature birth, affects the maturational process and the wiring of the brain (Lubsen et al., 2011). This altered connectivity of a developing brain can also be a contributing factor to the delayed development of processing visual motion observed in the preterm participants.

Interestingly, when compared to the full-term participants, preterm infants at 4-5 months and preterm children at 6 years of age showed significantly shorter latencies regardless of visual motion condition. Considering that the preterm group in this study was corrected for prematurity, this may possibly explain the faster perceptual response at 4-5 months of age, as the preterm infants have had up to 3-months longer exposure to visual flow experience outside the womb. Given that the 6-year-old premature children do catch up with the full-term peers in terms of N2 latencies, and to such a great extent, it could be expected to find a corresponding improvement in the ability to discriminate between the motion conditions. The present study indicates that, by the age of 6, preterm children show no processing deficit for visual motion, but still a perceptual problem to distinguish between different visual motion information, reflecting a dorsal stream abnormality or delay. Since premature children do show improvements in VEP latencies overall, and a tendency towards differentiation, it is possible that, if tested at a later age, they may also be able to differentiate between different radial motions.

A possible deficit in neuronal network for rapid motion processing can be discovered by investigating individual N2 latencies. The individual analyses of the VEP data revealed that two of the preterm infants at 11-12 months of age showed extremely long latencies for both forwards and reversed optic flow, whereas all except two preterm infants showed extremely long latencies for forwards optic flow only. However, the individual VEP analyses revealed that at 6 years of age, all the premature children had normal latencies in response to structured optic flow compared to the full-term children, and they inclined towards differentiation between the visual motion conditions with shortest latency for forwards optic flow. It is likely that the long latencies observed at 11-12 months represent a delayed development related to premature birth for processing optic flow that recovers with age, as seen in the 6-year-old premature children.

In comparison, M-ABC revealed that the full-term and the preterm group showed equal motor functions at 6 years of age. Individual scores showed that only one preterm, but also one full-term child had a total score above 13.5 suggesting that these two children may have perceptual-motor problems defined as "clumsiness". The full-term child that scored 14 points was one out of two that had just turned 7 years of age, and therefore completed another age band (7-8 years) with other motor tasks at a higher difficulty than the other full-term and preterm children. This may explain why the full-term child scored above the normal range. In addition, two other full-terms and one preterm had a score above 10 points, defined as borderline or a risk of having movement difficulties (i.e., monitoring required). It is important to note that during testing, circumstances within and outside the child, such as concentration, cooperativeness, time of the day, comfort and familiarity with the different motor tasks, have an impact on how the child will perform. An interesting finding is that four out of five of the premature children who scored within the normal range, had earlier been treated with physiotherapy, which may possibly explain why there were no noteworthy differences between the two groups, and why the majority of the preterm children had low test scores. Overall, preterm child DT was the only child who scored high on the individual VEP latency analysis at 11-12 months, and also showed the highest score of 21 points on the M-ABC at 6 years of age. By looking closer at preterm child DT's performance, the M-ABC revealed that the high score was mainly due to poor manual dexterity, which suggests that the child primarily struggles with fine perceptual motor skills, commonly reported among preterm children in M-ABC (Bos, Van Braeckel, Hitzert, Tanis & Roze, 2013). The individual VEP analyses in combination with the M-ABC suggest that the neuronal abnormalities observed in the premature participants do not resolve in major motor problems at 6 years of age. However, the disadvantage of a standard neuropsychological test such as the M-ABC, is the wide age range (loss of specificity), and a large proportion of different motor tests in a very limited time (8 items/20-40 min). Moreover, the test is based on a total test score of motor tasks that may have a low correlation, and is therefore probably not telling much about the child's overall motor development, but rather particular motor-task related difficulties. Since the M-ABC measures both fine and gross motor skills, but then combines the results to a total score and compares this score to a normative group, important information is possibly lost. A standard neuropsychological test like M-ABC may therefore be too coarse to pick up smaller perceptual and motor problems experienced by these children. Thus, the test should not be used to rule out the possibility that the remaining six premature children may have some sort of motor impairments, but it may contribute to point out individuals who are in need of closer attention.

Investigating the differences in induced activities in the TSE analyses revealed that when the TSEs of the combined motion conditions (forwards and reversed optic flow, and random visual motion) were compared to the static non-flow condition, both full-term and preterm infants at 4-5 and 11-12 months showed low-amplitude values in the theta-band ranges over the visual areas of interest observed as desynchronized activity in the TSE plots. Pfurtscheller et al. (1994), along with other studies, have reported EEG in infants to be dominated by a low-frequency of large amplitudes, an observation that is in general attributed to a sign of immaturity in infancy (Carmeli, Knyazeva, Innocenti & De Feo, 2005; Orekhova et al., 2006; Thierry, 2005). Low frequency activity is typically associated with higher amplitudes and an increase in the number of coherently activated neuronal networks. The observed dominance of induced change in theta-band frequency in the TSEs of the motion conditions is therefore not surprising. The prevalent desynchronized theta-band activity may suggest a broader and less specialized activity, meaning that the activity involves larger neural networks, or more cell assemblies, to interpolate the information of radial motion, a finding that is corroborated by previous studies (Agyei et al., 2015, 2016; Pfurtscheller & Lopes da Silva, 1999).

While induced theta-band desynchronization was observed in the TSEs for the motion conditions, induced theta-band synchronization was observed in the TSEs for the static non-flow condition. This shows that neuronal cell assemblies fire in synchrony during perception of the static condition, but the synchronized activity is supressed during perception of radial motion. Desynchronization during perception of radial motion is thought to be an oscillatory mechanism for communication between underlying cortical networks in infancy (Agyei et al., 2015), as enhanced theta-band desynchronization has been suggested to indicate increased task complexity (Pfurtscheller et al., 1994).

Further, the TSE analyses revealed that the full-term group showed higher frequencies with increasing age for processing visual motion. At 11-12 months, the full-term infants showed a smaller area of theta-band activity and, in addition, faster oscillating alpha-beta-band frequencies were observed, indicating that at this age the infants use a smaller number of neural networks and cell assemblies to process visual motion information. The increase of higher-frequency synchronized activity at 11-12 months confirms earlier research (Agyei et al., 2015), demonstrating that older infants show induced activity as a function of visual motion more similar to what is observed in adults (Van der Meer et al., 2008).

Amplitude of oscillation is reported to be proportional to the quantity of neurons firing in synchrony. Slowly oscillating cell assemblies would therefore generally comprise more neurons than fast oscillating cell assemblies (Elul, 1972; Pfurtscheller & Klimesch, 1992; Pfurtscheller & Lopes da Silva, 1999; Singer 1993). The slower oscillating theta-band frequency found in the infants at 4-5 months against the faster oscillating alpha-beta-band frequencies found only when the full-terms were older, at 11-12 months and at 6 years of age, indicates a developmental maturation. This could suggest a progression from larger oscillatory cell assemblies that are more immature and less specialized, to a more adult-like mature pattern of specialization in processing visual motion, where cell assemblies have fewer, but more specialized neurons. The appearance of synchronized activity in older full-terms is probably a shift in cortical coupling, where the lower frequency communication network is gradually replaced by more effective cortical couplings to process visual motion stimuli, as proposed by Agyei et al. (2015).

By the age of 6, all the full-term children showed less or no desynchronized theta-band activity, but desynchronized and synchronized alpha-beta-band frequencies were observed, in addition to some synchronized gamma-band activity in the visual areas of interest in response to visual motion. An increase in amplitude is argued to reflect a more efficient performance for processing visual motion and suggests active information processing (Pfurtscheller & Lopes da Silva, 1999). Alpha and beta rhythms are suggested to be important for cross-network connectivity (Ganzetti & Mantini, 2013) and may operate to connect actions across wide areas of the brain (De Pasquale et al., 2010, 2012). The faster gamma-band oscillations are supposed to be more effective in establishing rapid couplings between cell assemblies with more specific and locally confined information processing. (Fries, 2005; Fries, Scheeringa & Oostenveld, 2008; Singer, 1993). The shift from low-to high-amplitude frequencies observed in the full-term children confirms a further maturation towards a more adult-like specialized functional neuronal network within the visual areas for processing motion (Van der Meer et al., 2008; Pfurtscheller et al., 1994). These synchronized activities at higher frequencies may also suggest that subsets of cortical areas and higher cortical structures are activated for processing the radial motion at this age (Agyei et al., 2015, 2016; Carmeli et al., 2005; Pfurtscheller & Lopes da Silva, 1999; Pfurtscheller et al., 1996; Van der

Meer et al., 2008), implying that from the end of the first year of life and through childhood higher cortical structures are activated in perception of visual motion.

The observed synchronized activity at higher frequencies in the TSEs for the full-term infants and children, is corresponding with the observed significant decrease and differentiation in VEP latencies in the analysis of evoked activity. This confirms that full-terms, from early infancy through childhood, develop specialized neuronal networks for processing visual motion more efficiently due to maturation of synaptic connections and increased experience with self-initiated locomotion in the environment (Held & Hein, 1963; James and Swain, 2011).

As for the preterm groups, little or no synchronization in higher frequency bands was observed in the TSEs at any age. In the TSEs of the combined motion conditions, only two premature infants showed some synchronization in the alpha-beta-band ranges at 11-12 months and at 6 years of age. This was also confirmed by the bootstrapping procedure when the motion conditions were compared to the static condition, where only a few preterm infants and children showed significant differences in high-frequency synchronization. TSEs for the preterm group at 11-12 months were still dominated by theta-band frequencies, showing a persisting immature neuronal network. However, by 6 years of age, less or no theta-band activity was observed for the preterm children, but rather desynchronized alpha-beta band activity, which was also observed for the full-term children at 6 years. This corresponds with the decreased VEP latencies observed at 6 years of age, suggesting that at this age premature children show some progression towards a more functionalized neuronal network within the visual areas for processing visual information. On the other hand, the lack of observed higher frequencies in the preterm group and the longer VEP latencies observed at 11-12 months, together with absence of latency differences between the visual motion conditions at all testing sessions, indicate that preterm children still have an immature or altered network for processing visual motion information at the age of 6. The results are in conjunction with earlier studies reporting that preterm individuals show abnormal brain development of less myelinated cortical white matter and a slower cortical growth (Agyei et al., 2016; Hüppi et al., 1998; Kapellou et al., 2006; Mewes et al., 2006), supporting the notion of a delayed development of different abilities linked to the dorsal stream.

A dorsal stream impairment leading to poorer visual motion processing can have a number of implications for preterm infants' development. Preterm children are reported to have a higher prevalence of perceptual-motor problems by school age, often referred to as "clumsiness", when compared to their full-term classmates (Jongmans et al., 1997; Losse et al., 1991). Some of the reported problems are motor deficits in balance, coordination, gross and fine motor control and visual motor integration (Edwards et al., 2011; Williams, Lee & Anderson, 2010). Children described as “clumsy” have in the recent years been put in the diagnostic category of developmental coordination disorder (DCD) which is reported to be more prevalent among preterm born individuals (Davis, Ford, Anderson & Doyle, 2007; Goyen & Lui, 2009; Holsti, Grunau & Whitfield, 2002). DCD is characterized by impaired motor performance that is not due to any other psychiatric disorders or medical conditions such as cerebral palsy, hemiplegia, or muscular dystrophy (Holsti et al., 2002; Polatajko et al., 1995). Children with DCD have problems with daily activities that require motor coordination and these impairments are shown to have negative effects reaching beyond the motor domain, with deficits commonly reported in behavioural, educational, and social domains (Dewey, Kaplan, Crawford & Wilson, 2002; Geuze & Börger, 1993; Losse et al., 1991; Piek, Dworcan, Barrett & Coleman, 2000; Schoemaker & Kalverboer, 1994; Shaw, Levine & Belfer, 1982). A better understanding and system for distinguishing the range of motor impairments observed in preterm children, including mild motor impairment and DCD from other neurological impairments, are important for implementing early interventions and helping caregivers and schools facilitate these problems to minimize the effects caused by premature birth.

The less efficient motion perception observed in premature individuals even in the absence of brain damage, can be explained by a dorsal stream vulnerability (Guzzetta et al., 2009). The visual ventral and dorsal pathways have been widely studied by using visual evoked potentials, revealing differences in their maturation rates. VEP latencies are proven to be suitable to indicate brain development as a function of synaptic maturation and specialization (Agyei et al., 2015, 2016; Van der Meer et al., 2008). As mentioned, visual evoked potentials are expected to change in terms of shorter latency with increasing age for healthy full-term infants (Agyei et al., 2015, 2016; Van der Meer et al., 2008), indicating brain maturation and specialization of neuronal networks (Dubois et al., 2006; Mukherjee et al., 2002; Paus et al., 2001). However, the same maturational process is not found in premature infants (Agyei et al., 2016), and most studies regarding development of the visual pathways in infants and children born preterm, agree that preterm birth is associated with poorer visual and visual-cognitive outcomes (Agyei et al., 2016; Back et al., 2007; Back & Rivkees, 2004; Guzzeta et al., 2009; Peterson et al., 2003 Tremblay et al., 2014). Studies show that preterm infants have a normal development of the ventral pathway, but a delayed or abnormal development of the dorsal pathway (Hammarrenger et al., 2007; Tremblay et al., 2014). The dorsal stream (M-pathway) is thought to develop at an earlier stage and mature more rapidly than the ventral stream (P-pathway). The dorsal stream is therefore more vulnerable to preterm birth as the development occurs in the intrauterine environment during the third trimester before birth, as opposed to the ventral stream, which is thought to develop weeks after birth (Hammarenger et al., 2003). This early development of the dorsal stream is thus disrupted by premature birth, which may explain why the M-pathway is more negatively affected than the P-pathway (Hammarenger et al., 2007). Bosworth and Dobkins (2009, 2013) also suggest that the P-pathway may even have some positive effects of the earlier visual experience from preterm birth, as additional visual experience rather accelerates the maturation of the P-pathway, whereas the early visual experience rather disrupts the development of synaptic production and maturation in the M-pathway.

When age is corrected for prematurity, one could expect that preterm infants and children would follow a similar development as their full-term peers. In conjunction with earlier findings, the present study found that preterm born individuals show a different development of visual motion processing than full-term individuals. Despite the dorsal stream vulnerability, preterm children do catch up with their full-term peers in visual motion processing, indicating an adequate myelination of neurons in the dorsal stream. But as this was evident first by the age of 6 years, this confirms a delayed or altered development of the visual system. However, at the same age, preterm children are still not capable of detecting structured optic flow more efficiently than random visual motion, a capability which was observed in the full-term infants already at the age of 11-12 months. This is a concern as it confirms a less specialized neuronal network in the dorsal stream for processing visual motion at 6 years of age in the preterm children. It is possible that the registration of the motion happening, and the interpreting of the information in the visual motion, mature at different rates in the brain during normal development, so that each ability may be differently affected by premature birth. It is noteworthy that even in full-term children, development of visual motion perception is found to have a slow progress. There are studies reporting on children gradually improving their discrimination for motion direction, reaching a mature level for visual motion perception first at 14 years of age (Bogfjellmo et al., 2014). Furthermore, Joshi and Falkenberg (2015) found that sensitivity to radial optic flow is still immature at 16 years of age, indicating that higher cortical areas, including MST, are not yet fully matured even in adolescence. Given these findings along with the results of the present study, there is a reason to expect that the preterm children, with time, will show adequate visual perceptual functioning for processing different radial motions.

In conclusion, the present study found that from infancy and up to primary school age, full-term born individuals follow a development where they increase their sensitivity to optic flow and become capable of detecting structured optic flow more efficiently than random visual motion as they grow older. These improvements have been attributed to neural maturation accompanied with increased self-produced locomotion experiences. Frequency analyses revealed that with increasing age, full-terms showed a progression from low-frequency desynchronization to high-frequency synchronization of induced brain activity. This indicates a progression towards a more adult-like processing of visual motion due to increased specialization and myelination in the developing brain. On the other hand, preterm infants and children follow a different developmental path, increasing their sensitivity to optic flow first at 6 years of age. In addition, they were not capable of detecting structured optic flow more efficiently than random visual motion at any of the ages studied. Frequency analyses revealed that preterm infants and children show less high-frequency synchronization at 11-12 months and at 6 years of age compared to their full-term peers, and that most of them did not show any high-frequency synchronization at all. Moreover, most of the preterm children seemed to do well in perceptual-motor tasks related to the visual dorsal stream. These results show that from 4-5 months up to 6 years of age, preterm born individuals show a delayed development of visual motion processing compared to full-term infants and children. The differences in functional visual motion perception support earlier research of a dorsal stream impairment caused by premature birth. Although the premature children do seem to have caught up on some areas for visual motion perception by the time they start school, only further studies can determine whether the observed dorsal stream impairments are just a sign of developmental delay or will follow them into young adolescence and even adulthood.

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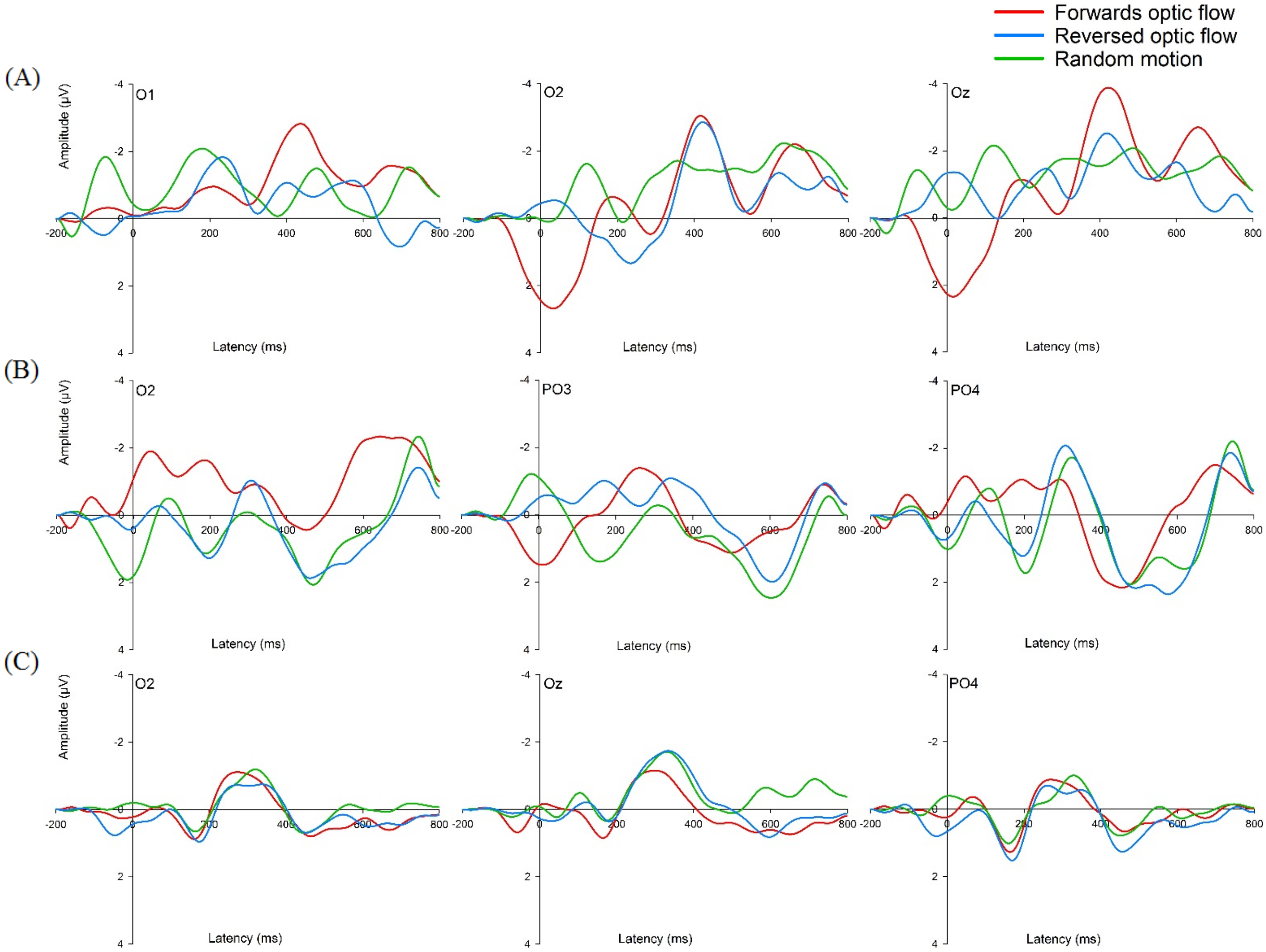
Appendices

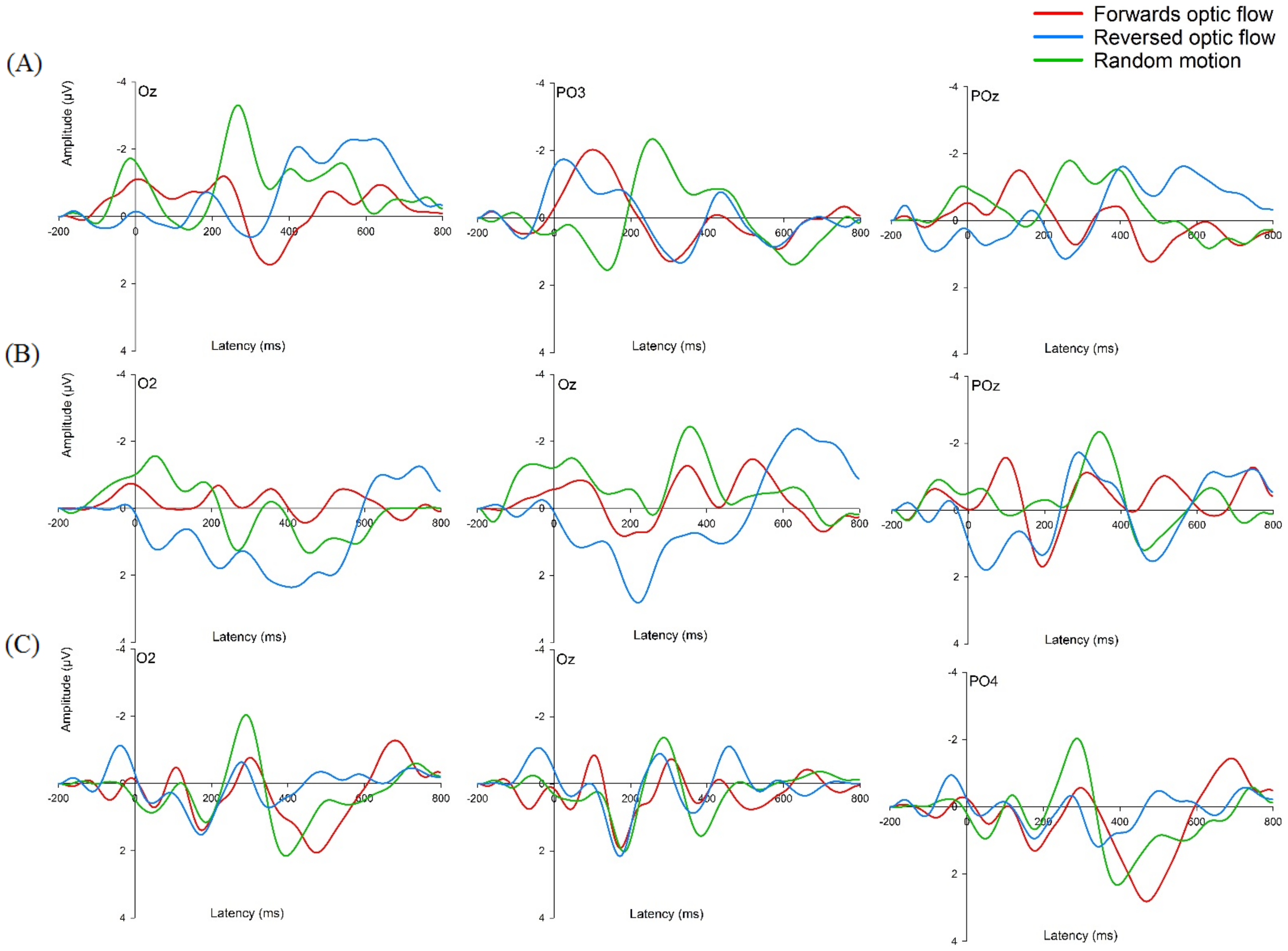
Appendix A

Grand average channels of motion VEPS for full-term infants at 4-5 months (A), 11-12 months (B), and full-term children at 6 years of age (C). Epoch is from -200 to 800 ms. Amplitude is on the y-axis and latencies on the x-axis.



Appendix B

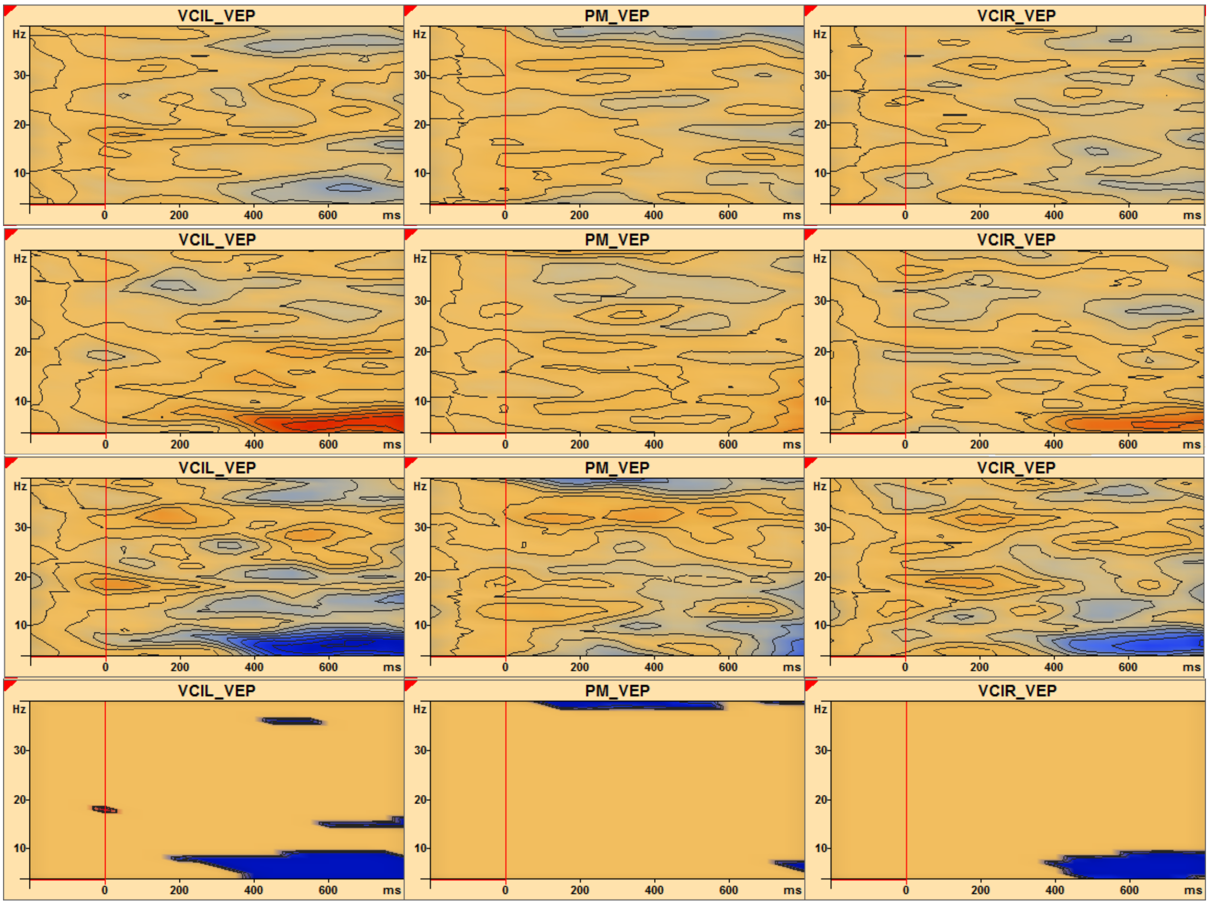
Grand average channels of motion VEPS for preterm infants at 4-5 months (A), 11-12 months (B), and preterm children at 6 years of age (C). Epoch is from -200 to 800 ms. Amplitude is on the y-axis and latencies on the x-axis.



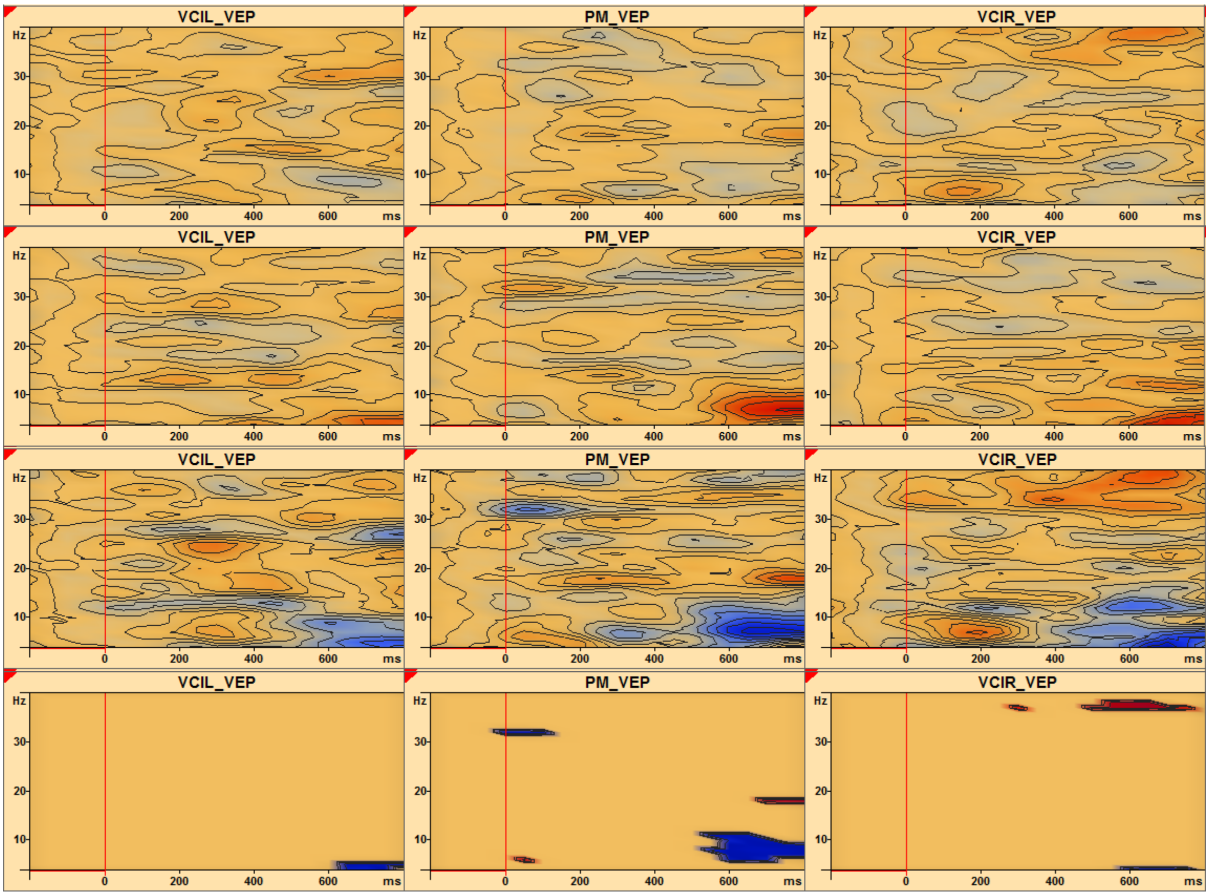
Appendix C

TSE maps for the brain regions of interest (VClL, PM, VClR) for full-term infant SN at 4-5 months of age, full-term infant VE at 11-12 months of age and full-term child JY at 6 years of age, respectively. TSE maps show the motion condition (A), the static non-flow condition (B), when the combined motion conditions were compared to the static non-flow condition (C), and the bootstrapping procedure when the motion conditions were compared to the static non-flow condition (D). Epoch is from -200 to 800 ms, and stimulus onset at 0 ms is marked with a red line. Blue areas represent decreased spectral amplitude (Induced desynchronized activity), while red areas represent increased spectral amplitude (induced synchronized activity).

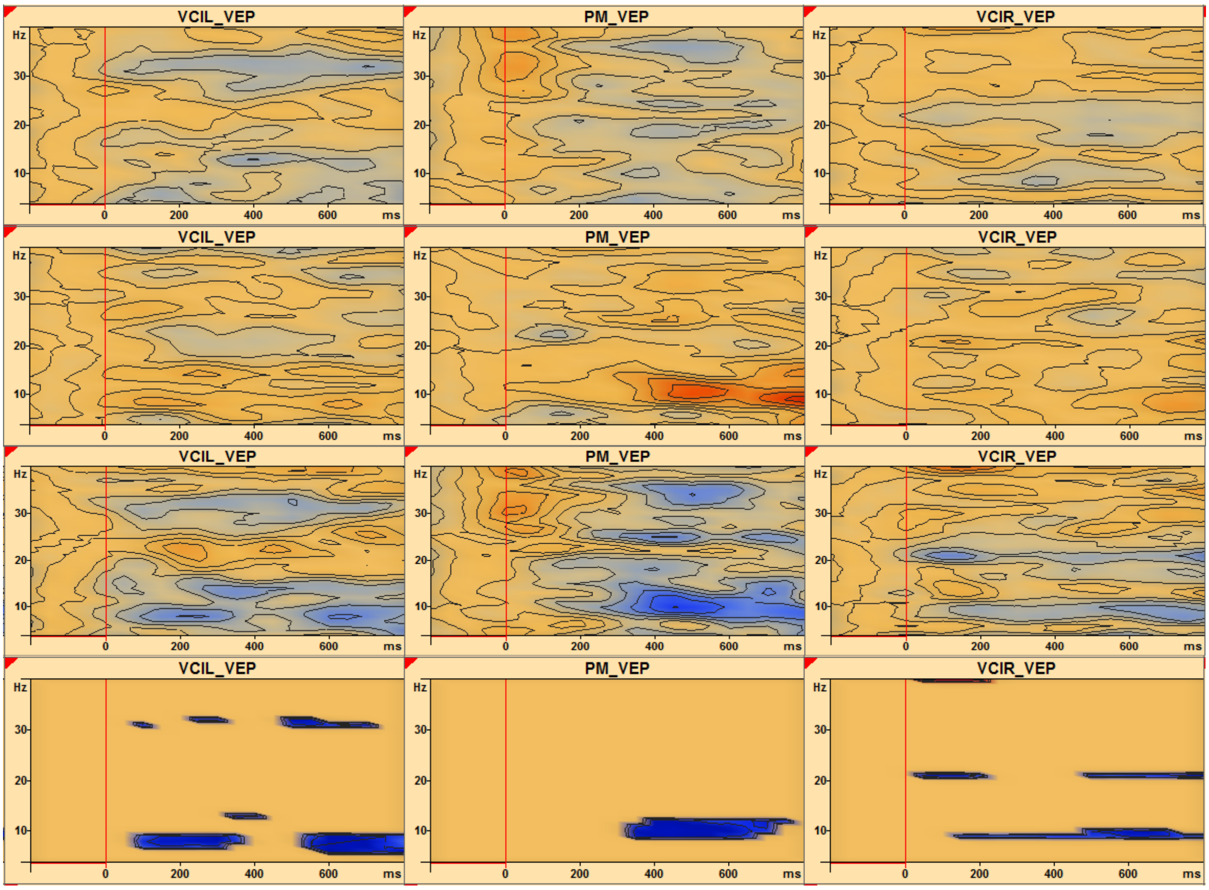
SN



VE


VCIL_VEP
PM_VEP
VCIR_VEP
VCIL_VEP
PM_VEP
VCIR_VEP
VCIL_VEP
PM_VEP
VCIR_VEP
VCIL_VEP
PM_VEP
VCIR_VEP
Hz
30
20
10
0
200
400
600
ms

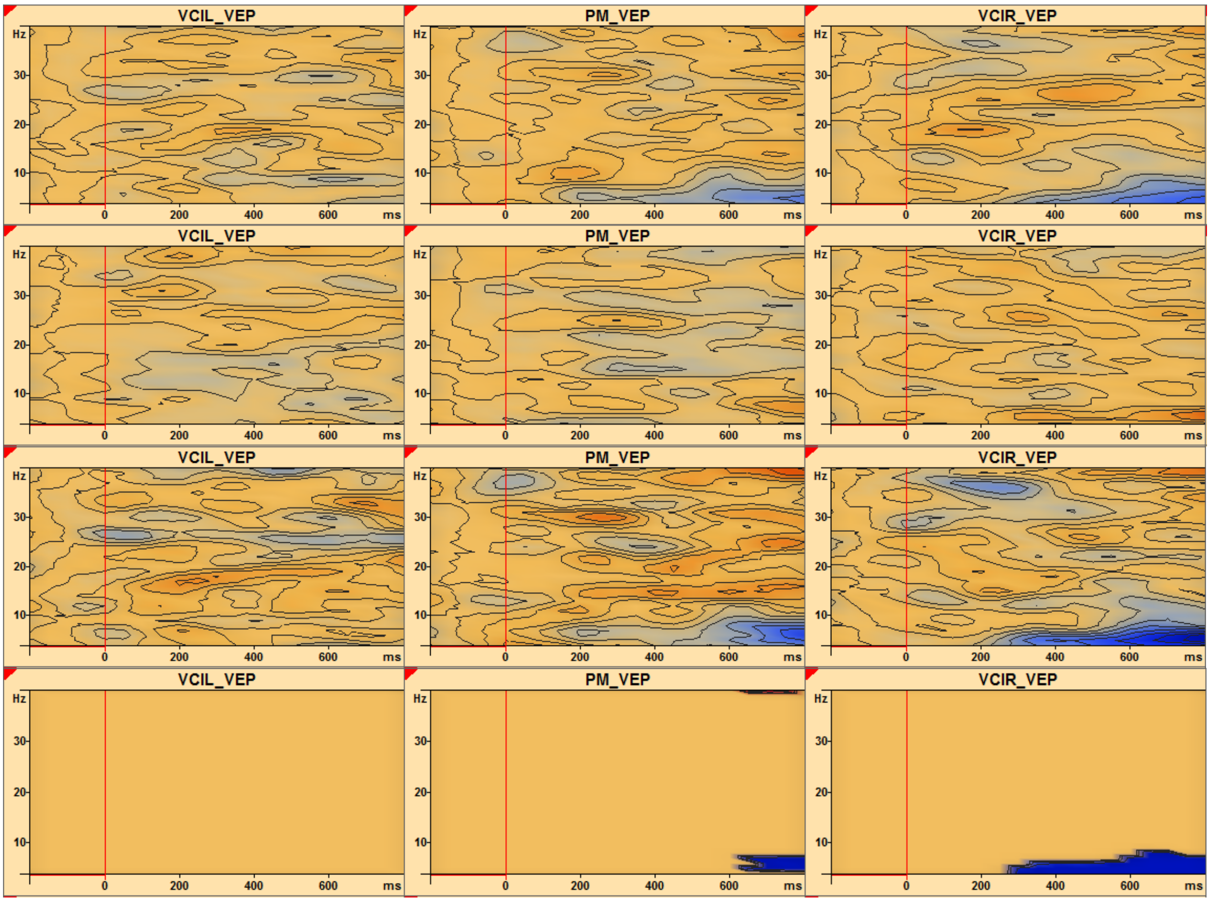
JY


VCIL_VEP
PM_VEP
VCIR_VEP
VCIL_VEP
PM_VEP
VCIR_VEP
VCIL_VEP
PM_VEP
VCIR_VEP
VCIL_VEP
PM_VEP
VCIR_VEP
Hz
30
20
10
0
200
400
600
ms

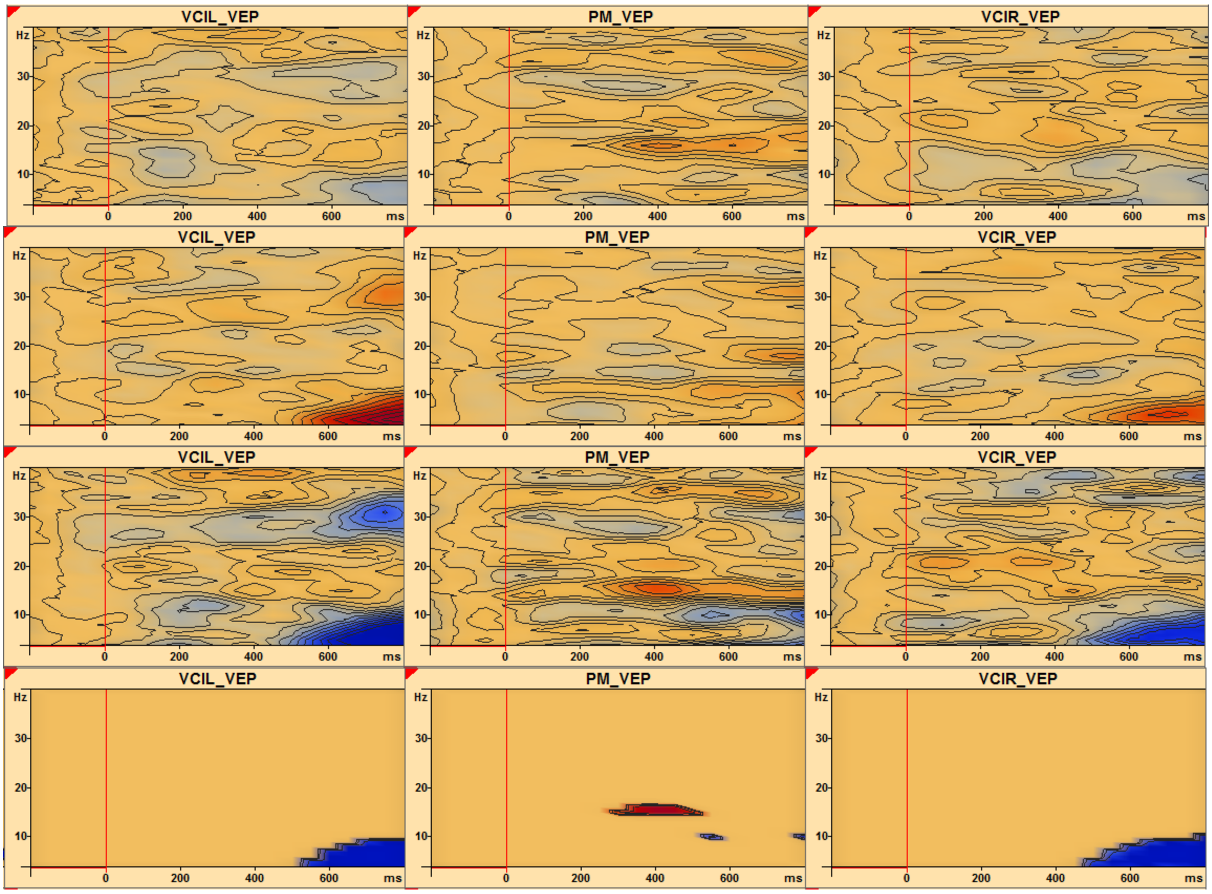
Appendix D

TSE maps for the brain regions of interest (VClL, PM, VClR) for preterm infant AT at 4-5 months of age, preterm infant DK at 11-12 months of age and preterm child TA at 6 years of age, respectively. TSE maps show the motion condition (A), the static non-flow condition (B), when the combined motion conditions were compared to the static non-flow condition (C), and the bootstrapping procedure when the motion conditions were compared to the static non-flow condition (D). Epoch is from -200 to 800 ms, and stimulus onset at 0 ms is marked with a red line. Blue areas represent decreased spectral amplitude (Induced desynchronized activity), while red areas represent increased spectral amplitude (induced synchronized activity).

AT



DK


VCIL_VEP
PM_VEP
VCIR_VEP
VCIL_VEP
PM_VEP
VCIR_VEP
VCIL_VEP
PM_VEP
VCIR_VEP
VCIL_VEP
PM_VEP
VCIR_VEP
Hz
30
20
10
0
200
400
600
ms

TA