Master's thesis

NTNU
Norwegian University of Science and Technology
Faculty of Social and Educational Sciences
Department of Psychology

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Longitudinal study of extra-stimulated, full-term control infants, and preterm infants: High-density EEG analysis of cortical activity in response to visual motion

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Supervisor: Audrey Van der Meer
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Abstract

Electroencephalogram (EEG) was used to investigate the effects of receiving extra motor stimulation and the effects of preterm birth during the first postnatal year on the development of visual motion perception. Infants receiving extra motor stimulation, a control group, and preterm infants were presented with an optic flow paradigm at pre-locomotor age and after they experienced several weeks of self-produced locomotion. EEG data were recorded with an array of 128-channel sensors. Visual evoked potentials (VEPs) and temporal spectral evolution (TSE, time-dependent amplitude changes) were analysed. VEP results showed extra-stimulated infants had significantly shorter latencies in response to visual motion than their full-term control peers and preterm infants during the course of the first year of life. Preterm infants did not significantly decrease their VEP latencies with age as a function of visual motion perception and did not discriminate between the motion conditions. Differences in induced activities were also observed with desynchronised theta-band activity in all three infant groups, with synchronised alpha-beta band activity observed only in extra-stimulated infants at the second session. Preterm infants showed more widespread desynchronised theta-band activities in the second testing session compared to the two other groups. It was concluded that the developmental progression in visual motion perception during the first year of life observed in the infants in the control group that had received a traditional Norwegian upbringing could be attributed to neural maturation and onset of self-produced locomotion. However, the greater improvement in extra-stimulated infants was attributed to their enriched stimulation. The poorer responses in the preterm infants could be related to impairment of the dorsal visual stream specialized in the processing of visual motion.

Sammendrag

Elektroencefalogram (EEG) ble brukt til å undersøke effekten av å motta ekstra motorstimulering og effekten av for tidlig fødsel i løpet av det første postnatalåret på utviklingen av visuell bevegelsesoppfatning. Spedbarn som fikk ekstra motorstimulering, en kontrollgruppe og premature spedbarn ble presentert for et optisk flytparadigme i før-lokomotorisk alder og etter at de opplevde flere uker med egenprodusert bevegelse. EEG-data ble registrert med en rekke 128-kanals sensorer. Visuelle fremkalte potensialer (VEP) og tidsmessig spektral evolusjon (TSE, tidsavhengige amplitudeendringer) ble analysert. VEP-resultatene viste at ekstra-stimulerte spedbarn hadde signifikant kortere ventetid som respons på visuell bevegelse enn deres jevnaldrende kontrollfamilier og premature spedbarn i løpet av det første leveåret. For tidlige spedbarn reduserte ikke VEP-latensene med alderen signifikant som en funksjon av visuell bevegelsesoppfatning og diskriminerte ikke bevegelsesforholdene. Forskjeller i induserte aktiviteter ble også observert med desynkronisert theta-båndaktivitet i alle tre spedbarnsgruppene, med synkronisert alfa-beta-båndaktivitet bare observert hos ekstra-stimulerte spedbarn ved den andre økten. Premature spedbarn viste mer utbredte desynkroniserte theta-båndaktiviteter i den andre testøkten sammenlignet med de to andre gruppene. Det ble konkludert med at utviklingsprogresjonen i visuell bevegelsesoppfatning i løpet av det første leveåret observert hos spedbarn i kontrollgruppen som hadde fått en tradisjonell norsk oppdragelse, kunne tilskrives nevral modning og utbrudd av egenprodusert bevegelse. Imidlertid ble den større forbedringen hos ekstra-stimulerte spedbarn tilskrevet deres ekstra stimulering. De dårligere responsene hos premature spedbarn kan være relatert til svekkelse av den dorsale visuelle strømmen som er spesialisert i prosessering av visuell bevegelse.

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Julie Borge Blystad

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Innhold

1 Introduction

When navigating through the dynamic environment, the gathering of perceptual information allows for controlling and guiding future actions so that accidents might be avoided, and goals reached. Visual motion perception is crucial for navigating the environment and provides essential information for self-motion, orientation, control of posture, and locomotion (Agyei, Holth, Van der Weel & Van der Meer, 2015; Vaina & Rushton, 2000). The perception of this information, termed optic flow, is the pattern of visual motion available to the eye when we are moving relative to our environment (J. J. Gibson, 1979). Considering the relevance of these abilities to everyday life, it is important to understand the developmental processes underlying how infants learn to make use of relevant visual information for perception (Agyei, Van der Weel, Van der Meer, 2016a).

The developmental changes that follow the onset of independent locomotion in the latter half of the infant's first year provides one of the best illustrations of the intimate connection between action and psychological processes (Anderson et al., 2013). The possibilities for exploration drastically increase as infants' transition from a state of being passively carried around to becoming active explorers of their surrounding world (Gilmore, Baker & Grobman, 2004). Developmental psychology has a long history of linking motor development to enhancement in cognitive and perceptual abilities. Piaget (1952) most famously proposed that infant motor behaviour is the launch point of cognitive development and that sensorimotor exploration is integral to the developmental process. E. J. Gibson (1988) stressed the importance of exploratory actions for revealing meaningful information about the world. Researchers have also begun to unravel the processes by which locomotion has its effects on psychological development, providing important insights into the mechanisms that underlie developmental change (e.g., Dahl et al., 2013). Both E. J. Gibson (1988) and Thelen (1995, 2000) suggested that motor development promotes and demands improvements in behavioural flexibility because new motor skills provide new opportunities for action and require new solutions.

There has been considerable progress in understanding the anatomy and electrophysiology of the parts of the visual system processing complex motion in monkeys and normal adults, yet little is known about the development and processing of this fundamental type of information in infants (Gilmore et al., 2004). Measurements of VEPs as a function of optic flow have demonstrated a progression towards more advanced processing of visual motion information during the first year of life (Vilhelmsen, Agyei, Van der Weel, & Van der Meer, 2019). As indexed by significantly shorter N2 latencies in response to visual motion with age, infants show rapid improvements in their optic flow processing between 3-4 and 11-12 months of age (Agyei et al., 2015). Moreover, EEG studies measuring VEPs have shown that normally developing infants at 11-12 months of age, similar to adults (Van der Meer et al., 2008), can differentiate between different types of visual motion and process forwards optic flow faster than they do reversed optic flow (Agyei et al., 2015). This is possibly because humans have more experience with forwards optic flow in their everyday lives (Van der Meer et al., 2008; Agyei, et al., 2015). The ability to perceive visual motion in infants seems to depend on an interaction between the experience of self-generated active locomotion and neurobiological development (Vilhelmsen et al., 2019). Self-generated active locomotion appears to improve and expedite the infant's development of visual motion perception (Agyei et al., 2016a; Higgins, Campos & Kermolan, 1996).

During visual perception tasks, EEG primarily records electrical activities of pyramidal neurons with high temporal resolution (in the millisecond scale) that permits the study of the neuronal basis of motion perception and the functional specializations of cortical structures. EEG studies measuring visual evoked responses have proven to be complementary techniques for the study of the neural basis of motion perception in the millisecond time scale (Rosander et al., 2007; Van der Meer, Fallet, & Van der Weel, 2008). In EEG recordings, visual evoked potentials (VEPs) reflect the activity of post-synaptic neurons in direct relation to a visual stimulus (Webb, Long, & Nelson, 2005), and are dominated by a motion sensitive N2 component thought to be generated in human hMT+/V5 (Ahlfors et al., 1999; Kuba, Kubová, Kremláček, & Langrová, 2007). Support is provided because motion perception is impaired by transcranial magnetic stimulation (TMS) when applied over MT+ at 130–150 ms after onset of the motion stimulus (Sack et al., 2006). VEP waveforms in EEG have been found to be dominated by a negativity (N2) with its origin assumed to be in area MT+ that occurs in adults at latencies around 130-150 ms (Heinrich, Renkl & Bach, 2005; Probst, Plendl, Paulus, Wist & Scherg, 1993) and in 8-month-old infants around 180–220 ms post-stimulus (Van der Meer et al., 2008). These latency differences are believed to imply changes in visual motion processing, with shorter values indicating faster processing (Agyei et al., 2015).

In addition to the use of VEPs in EEG studies, growing attention has been given to the time-frequency domain, which allows computing the temporal dynamics of EEG oscillations with a technique called temporal spectral evolution (TSE). Modulations in oscillatory activity may be observed as either increase (i.e., event-related synchronization, ERS) or a decrease (i.e., event-related desynchronization, ERD), indicating more or less synchrony in the rhythmic activity of the underlying neuronal populations (Pfurtscheller, 2001). Different classes of oscillations have been distinguished over the years: delta-band (1-4 Hz), theta-band (4-7 Hz), alpha-band (7-13 Hz), beta-band (13-30 Hz), and gamma-band (30-150 Hz), with each rhythm, assumed to reflect neurophysiological processes that manifest functionally different roles (Buzsaki & Draguhn, 2004, Engel & Fries, 2010, Ganzetti & Mantini, 2013, Saby & Marshall, 2012).

Studies using time-frequency analysis of the ongoing EEG in infants have found that brain activity in low-frequency oscillations, especially in the theta-alpha range, undergo systematic development from early childhood to adulthood (Stroganova & Orekhova, 2007; Stroganova et al., 1999). Recent infant studies had implicated low-amplitude desynchronized theta-band activities over visual areas when motion stimuli were compared with static stimuli (Agyei et al., 2015; Van der Meer et al., 2008), with further observation of high-amplitude activities, especially in alpha-band frequency observed in one-year-old infants (Agyei et al., 2015). Contrary to infants, optic flow studies in adults have found beta band ERS and beta band ERD activity in response to visual motion compared to a static control scene, respectively (Van der Meer et al., 2008; Vilhelmsen et al., 2019). This high-frequency activation in adults has been attributed to functional responses involving fewer but more specialised neuronal assemblies, reflecting a fully developed motion perception system (Agyei et al., 2015; Van der Meer et al., 2008; Vilhelmsen et al., 2019). The frequency differences between infants and adults from lower to higher frequencies is considered a sign of maturation in various psychophysiological studies (Hudspeth & Pribram, 1992; Stroganova et al., 1999).

The current and dominant view of the visual system is represented by the functional and anatomical dissociation between a ventral visual processing stream specialized for object form and recognition, and a dorsal stream that is essential in attention, decision making, motion perception, and movement planning (Milner & Goodale, 2006). The dorsal stream leads from the primary visual cortex to the medial temporal (MT) and medial superior temporal (MST) areas, together known as V5/MT+ (Morrone et al., 2000; Smith, Wall, Williams, & Singh, 2006), and on to the parietal lobe (Andersen, 1997). Considerable evidence from imaging and neurophysiological studies is emerging which points to human V5/MT+ and parietal areas of the dorsal visual stream of the cortex as areas that have neurons selectively activated by motion stimuli (Dupont, Orban, De Bruyn, Verbruggen & Mortelmans, 1994, Tootell et al., 1995). In particular, neurons within the medial superior temporal (MST) area of the dorsal visual stream are generally selective for moving visual stimuli and responding to rotating and expanding motion patterns. These characteristics suggest that these neurons are involved in optical flow processing (Duffy & Wurtz, 1991, Van der Meer et al., 2008; Vilhelmsen et al., 2019). Large neural networks such as the dorsal and ventral stream of the brain's visual processing system gradually develop with experience and age (Agyei et al., 2016a; Vilhelmsen et al., 2019).

The human brain is an organized dynamic network of interconnected neurons and associated synapses that work together such that dysfunctions within the network can have unfortunate effects on behavioural patterns (Agyei et al., 2016). Infants born preterm have been found to be more at risk of neurological deficits and developmental disorders. An infant is defined as preterm when he/she is born before 37 completed weeks of gestation. With increasing numbers of preterm infants surviving, the impact of preterm birth on later cognitive development has been given considerable attention over the years. Magnetic resonance imaging (MRI) studies have demonstrated that being born preterm causes differential brain development, leading to abnormalities in the microstructure of tissues and in cerebral morphology (Counsell & Boardman, 2005). Some of the dysfunctions of preterm birth have been related to cognitive and behavioural impairments (Aarnoudse-Moens et al., 2009; Bhutta et al., 2002; De Jong et al., 2012; Delobel-Ayoub et al., 2009; Johnson, 2007; Salt & Redshaw, 2006). Among the major functions affected by preterm birth, visual cognition is one (Atkinson & Braddick, 2007).

Studies on the perception of visual movement suggest that the cluster of deficits seen in children born prematurely may be related to networks involving the cortical dorsal stream and its connections to parietal, frontal, and hippocampal areas (Atkinson & Braddick, 2007). These findings suggest a possible vulnerability of the dorsal visual processing stream in preterm infants, contrary to findings in normally developing infants (Agyei et al.; 2016a; Braddick, Atkinson & Wattam-Bell, 2003). Differences in dorsal stream functions, but not in ventral stream functions, have been found between preterm and full-term infants (Hammarrenger et al., 2007; Tremblay et al., 2014). The dorsal visual stream is developed in the last weeks of fetal life, and premature birth can thus interfere with this development. Guezza et al. (2009) reported that preterm children appeared to perform worse than full-term controls in global motion (optic flow) perception, irrespective of the presence of brain damage. These findings suggest impairment of the dorsal stream during visual processing in preterm children with and without brain damage (Guezza et al., 2009). These findings are further supported by other studies where global motion, global form, and biological motion (combination of cues for form and motion) perception were compared in preterm children (e.g., Taylor et al., 2009). Further studies (e.g., Van Braeckel et al., 2010) that investigated the motor skills of preterm children at 7–11 years reported that they perform less accurately or slower in pointing tasks, implying less efficient elementary visuomotor processing and impaired functioning of the dorsal visual stream. Agyei, Van der Weel, and Van der Meer (2016a) studied the development of optic flow perception in both preterm and full-term infants using high-density EEG and found that preterm infants showed more insufficient responses to visual motion compared to full-term infants, with preterm infants not improving their latencies with age nor did show any synchronisations in alpha-beta frequency bands in response to the motion conditions, in contrast to their full-term peers. The poorer responses in the preterm infants could be related to impairment of the dorsal visual stream specialized in visual motion processing (Agyei et al., 2016a). Considering the importance of processing visual motion information in several everyday tasks, a dorsal stream vulnerability can have a number of implications for preterm infants' development.

An intriguing feature of the brain is its capacity for structural and functional modification in response to external stimuli. We can now identify an extensive range of neural changes associated with experience. These include increases in brain size, cortical thickness, neuron size, dendritic branching, spine density, synapses per neuron, and glial numbers (Kolb & Whishaw, 1998). This plasticity of the nervous system has been the focus of research efforts for decades (Mohammed et al., 2002). However, this research has long been limited to the adult nervous system. One cardinal principle in developmental psychology is that early experience profoundly affects human development (Fox & Rutter, 2010). A corollary to this principle is that there are certain periods in early development when experiences have a more significant effect than others, called critical or sensitive periods. These periods are often thought of as a window of opportunity where certain types of experience have a foundational effect on skills development (Greenough et al., 1987). The importance of early experience has been strengthened with advances in neuroscience. Greenough and colleagues (1987) introduced the term "experience-expectant plasticity" to refer to the role of experience in brain development during early sensitive periods. The developing brain depends on external stimuli to shape neural circuitry patterns via mechanisms of synaptic competition, in which the most effectively activated neural connections are selectively maintained and matured, and those less well-activated are eliminated (Greenough, Black, & Wallace, 2002). At birth, the human brain is equipped with 100 billion neurons, a few of which are connected. During the first years of life, millions of connections are made through an interplay of life experience and maturation, forming complex networks of neurons specialized in processing different kinds of information rapidly. Considering that optimal brain plasticity occurs in the first few months of life (Bonnier, 2008), it is reasonable to suggest infant stimulation can profoundly influence how the brain will develop and how the child will interact with the world throughout life.

Apart from the rapid maturation of the cortex, increased attention has been given to the link between locomotor experience and development in advancing psychological functions in infancy (Bertenthal & Campos, 1990; Gilmore et al., 2004; Higgins et al., 1996; James & Swain, 2011; Kermoian & Campos, 1988; Uchiyama et al., 2008; Ueno et al., 2018; Walle & Campos, 2014). In addition to EEG studies, several lines of evidence have demonstrated the onset of self-produced locomotion to bring about developmental change (e.g., Campos, 2000). One nearly universal experience is the acquisition of self-produced locomotion (Bertenthal & Campos, 1990). When infants acquire the first locomotor skill, typically crawling, it dramatically changes the relationship between the infant and the environment. Suddenly, the range expands, and the child can even move towards and touch things he or she has previously only looked at. The child is no longer dependent on an adult to move but has been given new and exciting freedom, and their opportunities to learn about objects and events in the world increases. This opens a sea of exploration opportunities for the infants, which provides new perspectives and experiences that can drive changes in a host of different psychological phenomena. The onset of independent locomotion marks a significant transition and heralds a broad set of changes in psychological functioning. However, infants need to have the opportunity to explore and interact with the environment independently to develop the competence of crawling. In contrast to the unidirectional traditional maturational view of brain development, more and more neurologically focused empirical work suggests that locomotion is not merely a maturational antecedent to these changes. Instead, the changes are a function of the specific experiences that accompany moving oneself through the environment (Anderson et al., 2013).

Motor development and psychological development are fundamentally related, even though they are often treated separately (Adolph & Hoch, 2019). Extra stimulation in the form of baby activities plays a central role in Asia and Africa. Infant stimulation includes activities that arouse or stimulate the infant's sense of sight, sound, touch, taste, or smell. In turn, such practices have been demonstrated to affect the timing of acquisition of motor skills (Hopkins

& Westra, 1988; Karasik, Tamis-LeMonda, Adolph & Bornstein, 2015; Super, 1976), with enriched stimulation being associated with an earlier onset of motor behaviours, and to have immediate as well as long-lasting developmental effects (Lee & Galloway, 2012; Lobo & Galloway, 2008; Zelazo, Zelazo, Cohen, & Zelazo, 1993). Regarding motor development, Western belief systems often proclaim infants to be fragile and should be handled with care, while some non-Western cultures consider rough handling and deliberate exercise necessary for healthy motor development (Adolph & Hoch, 2019). African and Caribbean people have a culture where caregivers encourage newborn upright stepping movements to train walking, and the result of these belief systems seems to be infants who sit and walk at younger ages than non-exercised infants (Hopkins & Westra 1988, 1990; Super 1976). This is also shown in true experiments with random assignment, where a brief daily exercise of walking and placing reflexes in infants leads to earlier onset of walking alone in Western infants (Zelazo, Zelazo & Kolb, 1972). Lobo and Galloway (2012) also found that a few weeks of daily postural training leads to faster improvements in prone and sitting skills and earlier onset of crawling and walking alone. These findings suggest broad and long-lasting changes can arise via brief periods of change in caregiver-infant interactions. It can thus be suggested that infants born into cultures where extra stimulation is considered important develop earlier than infants from cultures where this is not valued.

Experience with locomotion in a forward manner in everyday experience seems to be the reason both adults and normally developing infants process forwards optic flow faster than reversed optic flow (Van der Meer et al., 2008; Agyei, Holth, Van der Weel, & Van der Meer, 2014). Van der Meer et al. (2008) found that infants who have not yet started to walk process forwards optic flow slower and that processing time decreases with increased experience with flow due to self-produced locomotion through the environment (e.g., crawling). This finding was also confirmed in a later study by Agyei et al. (2014), showing that infants' processing time of optic flow decreased from 3-4 to 11-12 months of age. Normally-developing infants at 11-12 months of age are able to differentiate between different forms of visual motion, with faster processing of forwards optic flow than they do with reversed and random visual motion (Agyei et al., 2015). The better sensitivity to visual information specifying forwards motion has been indicated to come online following the onset of self-produced locomotion, suggesting that humans detect and process visual motion information faster when it is in agreement with what is typically experienced, i.e., forwards locomotion (Van der Meer et al., 2008).

The role of plasticity in correcting abnormal cognitive development is a crucial issue. Whether, and to what extent, plasticity can compensate for failure of cognitive functions to develop within the first few years of life has generated considerable attention (Bonnier, 2008). Interventions related to developmental disorders generally start later in life, despite being relatively late from the point of view of the brain's plasticity. The crucial significance of developmental processes in the first years of life has received support from data on the modulation of neuronal death, synaptic stabilization, axonal reorientation, axonal and dendritic budding, and recruitment of transient projections (Stanfield & O'Leary, 1982; Kolb & Whishaw, 1989; Huttenlocher & Bonnier, 1991), all of which depend on individual experience. In a systematic review of the effects of early interventions on motor development, it was found that interventions by using specific motor training programmes, such as training of locomotor movements in which intervention aims at stimulation of the infant's exploration of active motor behaviour, can exert a positive effect on motor development (Blauw-Hospers & Hadders-Algra, 2005).

The present study explores the effects of receiving extra stimulation in early infancy on the development of visual motion perception. Understanding the functional development of the brain and whether extra stimulation accelerates the development of visuo-cognitive systems is important to ensure early intervention in both physically healthy infants and at-risk infants such as preterm infants. Using EEG longitudinal data, the thesis investigated the development of visual motion perception by comparing three groups of infants, i.e., extra-stimulated infants, a control group of infants who received a traditional Western upbringing, and preterm infants, at the ages of 4-5 months and 9-12 months. VEP and time-frequency analyses were applied to investigate whether there are any significant differences in brain responses to visual motion between the three infant groups. Previous optic flow studies have shown N2 latencies to decrease with age and experience with self-produced locomotion during the first year of life, with the shortest latencies observed for forwards optic flow followed by reversed optic flow and the longest latencies observed for random visual motion. A developmental progression from induced activities at low frequencies to higher-frequency oscillations has further been reported during the first postnatal year. Given the association between experience and developmental advancements, it was expected for infants receiving extra stimulation to have had greater opportunities for actively engaging with their environment compared to their control and preterm peers, and therefore to show an accelerated development of visual motion perception. Thus, it was hypothesized that extra-stimulated infants would display overall shorter latencies of VEPs in addition to induced activities at higher frequencies than the other two groups. Based on research indicating impaired dorsal stream functioning, the preterm infants in this study were expected to show abnormal development of visual motion processing during the course of the first year of life compared to their peers.

2 Methods

2.1 Participants

A total of 30 infants, of which 10 had received extra stimulation, 10 belonged to a control group and 10 were born preterm, were recruited for this longitudinal study. The extra-stimulated group comprised full-term infants that had participated in baby swimming classes from an early age (mean weeks of swimming experience at first testing 10, *SD*=3.3), and one infant that had received baby massage twice a day from birth. The extra-stimulated infants had a mean gestational age of 39.7 weeks (*SD*=1.3, range=38.1-41.1), and mean birth weight of 3485 g (*SD*=628, range=2510-4565). All the infants in the control group were born full-term, with a mean gestational age of 40.1 weeks (*SD*=1.1, range=38.3-41.9), and mean birth weight of 3571 g (*SD*=425, range=3085-4400). The preterm infants (moderate to very preterm) were born at a mean gestational age of 31 weeks (*SD*=1.7, range=28-33 weeks). Their mean birth weight was 1570 g (*SD*=285, range=1000–2080). The preterm infants did not have any major neurological deficits including severe brain damage, retinopathy of prematurity (ROP), and other perinatal issues requiring serious medical interventions that may lead to abnormal development. All infants were born healthy without any neurological defects as determined by parental report.

Recruitment for the extra-stimulated infants (5 boys and 5 girls) entailed contacting parents directly at baby swimming classes held at Pirbadet in Trondheim, or by using a snowball technique. The control group (5 boys and 5 girls) were recruited by contacting parents following birth announcements in the local newspaper, or simply by word of mouth. The preterm infants (5 boys and 5 girls) were recruited through the Neonatal Intensive Care Unit at St. Olav's University Hospital in Trondheim.

Infants were tested at two time points in a longitudinal design. First, infants were tested at 4-5 months followed by a second testing when the infants had some crawling experience or at 9-12 months of age. The first test was always used, and the other tests were either at 9-10 months or 11-12 months of age, depending on the infant's crawling experience. The criterion for using the test at 8-9 months of age was that the infant should have been crawling for at least 9 weeks. The three groups of infants were matched according to sex, age, and experience with self-produced locomotion. Experience with self-produced locomotion was documented for both testing sessions, with self-produced locomotion being defined as crawling, walking, or in any other way achieving independent locomotion. For the first testing, the mean age of the extra-stimulated infants was 4 months and 19 days (*SD*=7.2 days). At the time of the first testing nine of the extra-stimulated infants had been attending baby swimming courses, and one of the infants had received baby massage twice a day for 18 weeks. None of the infants had experience with crawling at the first testing, but seven of the infants could roll over from back to stomach. At the time of the second testing five of the extra-stimulated infants had already started advanced swimming classes, and three were about to start soon. For the second testing the mean age was 9 months and 29 days (*SD*=53 days). For the second testing all infants could commando crawl and had been doing so for a minimum of 9 weeks (mean weeks of self-produced locomotion 13). In addition, one of the infants was walking with help, and four were walking independently at the second testing.

Infants in the control group were tested first at a mean age of 4 months and 10 days (*SD*=20 days) and then again at a mean age of 11 months and 10 days (*SD*=28 days). For this control group, four of the infants had some experience with rolling over from back to stomach at the first testing session, but no experience with self-produced locomotion. At the time of the second testing, all infants were crawling and had been able to do so for at least 7 weeks *(*mean weeks of self-produced locomotion 14). Three of the infants took some steps alone or with help from furniture, and three were walking independently at the second session.

In order to ensure valid matching, the preterm infants’ age was corrected for prematurity. For the first session, the mean age of the preterm infants was 4 months and 25 days (*SD*=7 days). At the second testing, the mean age of the preterm infants was 12 months (*SD*=12 days). At the first testing session, three of the preterm infants had some experience with rolling over from back to stomach, but no experience with crawling or other self-produced locomotion. At the second testing session, all of the infants were commando crawling and had been able to do so for a minimum of 6 weeks (mean weeks of self-produced locomotion 17). In addition, two of the infants had mastered independent walking and two could walk with help.

EEG recording is a non-invasive method that causes no known harm or physical pain to the participant. Parents gave their informed consent and had the right to withdraw from the testing at any time before or during the experiments. The Norwegian Regional Ethics Committee and the Norwegian Data Services for the Social Sciences approved the study.

2.2 Experimental stimuli

Stimuli were generated with the psychological software tool, E-prime, and mirror-projected onto a large screen (108 cm wide, 70.5 cm high), placed approximately 70 cm away in front of the infant. Three experimental conditions were employed, i.e. forwards optic flow, reversed optic flow and random motion, as well as a static non-flow control condition used in the time-frequency analysis. The stimulus consisted of 100 black circles on a white background, with the dots being 5 mm in virtual radius, and with the goal to simulate movement in space. Duration of presentation for each motion trial was 1500 ms, with the order randomly chosen. To reduce motion adaptation, each motion pattern was followed by a static trial occurring for 1500 ms. To simulate movement in space, 100 black dots were programmed to move on a white background, with the dots being 5 mm in virtual radius. The dots increased or decreased in size at a rate of 0.025 pixels per pixel with reference to the position of the fixation point such that the particles appeared small when far away from the eye in virtual space and large when closer. For forwards optic flow, the dots moved outwards from the centre of the screen, making the dots appear to move towards the infant. For reversed optic flow, dots coherently moved in the opposite direction to that of the forwards optic flow condition, with the dots moving towards the centre. For random motion, dots moved in random directions on the screen. Stimuli were presented as a uniform dot distribution to avoid accretion of dots at the centre or edges of the screen. Particles that moved outside the range of sight on the screen were automatically resized and repositioned on the screen where all particles in each motion condition had an equal probability of placement.

In the first testing session, extra-stimulated infants contributed on average 46 (*SD*=16) motion trials and 48 (*SD*=17) static control trials. The full-term infants in the control group contributed on average 60 (*SD*=15) motion trials and 61 (*SD*=16) static trials, and the premature infants contributed on average 54 (*SD*=18) motion trials and 53 (*SD*=20) static trials in the first testing. In the second session, mean trial contributions for extra-stimulated infants were 60 (*SD*=8) for motion, and 59 (*SD*=8) static trials. The control group contributed on average 54 (*SD*=21) motion trials and 54 (*SD*=22) static trials in the second testing, while mean trial contributions for premature infants were 61 (*SD*=19) and 60 (*SD*=19) for motion and static, respectively.

2.3 Data acquisition

EEG activity was recorded with a Geodesic Sensor Net 200 (GSN) consisting of an array of 128 sensors that were evenly distributed on the infant’s head. Amplified EEG signals were recorded with a sampling rate of 500 Hz with Net Station software on a Macintosh computer. To control the infant's visual attention, eye movements were recorded with a TobiiX50-eye tracking camera and processed with Clear View software on a HP computer. The infant's behaviour during the experiment was also recorded by two digital video cameras at different angles. Recorded data were subsequently stored for offline analyses in BESA 7.0.

2.4 Procedure

Parents arrived with their infant some time before the experiment so that the infant could get comfortable with the laboratory surroundings and the parents could sign the informed consent form. An assistant measured the circumference of the infant's head to determine the appropriate size of the EEG-net. The net was soaked in a saline electrolyte to ensure optimal electrical conductivity, and afterwards partially dried. The infant sat on the parent's lap and was distracted with soap bubbles and small toys as the net was placed on the head of the infant. After the net was in place, the parent carried the infant into a dimly lit experimental room, where the infant was placed in a baby car seat. The parent was seated right next to the infant during the whole experiment to reduce stress in the infant. Experimental assistants moved into the control room where they managed the data acquisition and stimulus presentation, while one assistant was present in the experimental room to monitor the experiment and help the baby concentrate. The net was connected to the amplifier, and impedance of the electrodes was checked while electrode contact was improved if necessary.

After the infant's eye movements were calibrated in virtual space to the eye tracker, the experimental session began. When the infant showed signs of boredom or loss of interest, the session was paused, and the assistant and the parent played with the infant for a short period to revive the level of interest. The experiment was ended if no further interest could be obtained or the infant showed considerable level of tiredness or frustration.

2.5 Brain data analysis

All data analyses were carried out in BESA (Brain Electrical Source Analysis) version 7.0. The procedure was the same for all three groups at both testing sessions. Initial pre-processing entailed segmenting and exporting the EEG recordings as raw files using Net

Station Software. All bad channels and artefact-contaminated channels resulting from head or body movements were visually inspected and either removed from further analyses or interpolated manually. In scanning for artefacts, threshold values for gradient and low signal were set at 75 μV and 0.1 μV, respectively, while maximum amplitude was set at 200–230 μV. Averaged window was from 200 ms to 800 ms at a baseline definition of -100 ms to 0 ms. The notch filter was set at 50 Hz to remove power line interference from recorded data. A low cut-off filter was set at 1.6 Hz to remove slow drift in the data, and a high cut-off filter was set at 60 Hz.

2.6 VEPs peak analysis

VEP peak analysis was carried out using individual averages. Individual EEG data from each infant were averaged and interpolated into standard 81-electrode configuration of the 10-10 international standard system after re-referencing to an artificial reference calculated from the average potentials over the scalp such that individual averages were obtained. Individual averages for infants in each of the two sessions were combined into a grand average for each session, allowing VEP peak analysis for approximate time intervals for the individual N2 components at selected electrode sites. The 3D spherical spline whole-head voltage maps of EEG scalp signal distributions were used in aid of visualizing N2 activity in occipital-parietal areas. Values for peak latencies and peak amplitudes of the individual averages were recorded, with peak latencies measured as the time from stimulus onset to the peak of each scalp N2 component. Peak amplitudes represented maximum amplitudes of the N2 component relative to the pre-stimulus baseline. The values were then subjected to further VEP analyses.

2.7 Time-frequency analysis in brain space

Time-frequency analysis was performed in brain space using pre-defined multiple source dipoles that modelled activities in the visual areas of the parietal and visual cortices. There is a wide distribution of focal brain activity at the scalp due to the smearing effect of the volume conduction in EEG and the nature of dipole fields. Since the resulting scalp waveforms have mixed contributions from underlying brain sources, source montages derived from a multiple source model were used to obtain optimal separation of focal activity (Scherg & Berg, 1991).

The analysis involved occipital and parietal areas, as these areas are found to be active during motion stimuli presentation (Probst et al., 1993; Zeki et al., 1991). The source montage consisted of 17 sources that modelled activities in the visual pathway and residual activities in other areas of the brain. Of these sources, visual cortex bilateral left (VCbL), visual cortex radial left (VCrL), the parietal midline (PM), and visual cortex radial right (VCrR) sources, that are believed to be active in the visual processing of motion stimuli (Probs et al., 1993, van der Weel & Van der Meer, 2009, Zeki et al., 1991) were further analysed (Figure 1). To analyse brain activities using these sources, a 4-shell ellipsoidal head model (Berg & Scherg, 1994; Hoechstetter et al., 2004; Scherg et al., 2002) with the source dipoles inserted was created for each infant where the artifact-corrected coordinate files were appended. Bone thickness was adjusted for infants at 3.0 mm and conductivity at 0.02σ as recommended for infants (Grieve et al., 2003; BESA information). Settings for epoch filters and average parameters were the same as in the VEP analyses.

The resulting time-frequency displays represented the change in amplitude over time (TSE, temporal spectral evolution) in the regional sources. Each displayed graph was a plot of spectral amplitude density of one montage channel over time and frequency-normalised to the baseline of each frequency. Comparisons between motion and static conditions were computed. Significance (α=0.05) was tested with a bootstrapping method in each TSE plot for each of the participants. TSE displays were set to frequency cut-off of 4–40 Hz at frequency and time sampling of 1 Hz, 50 ms.

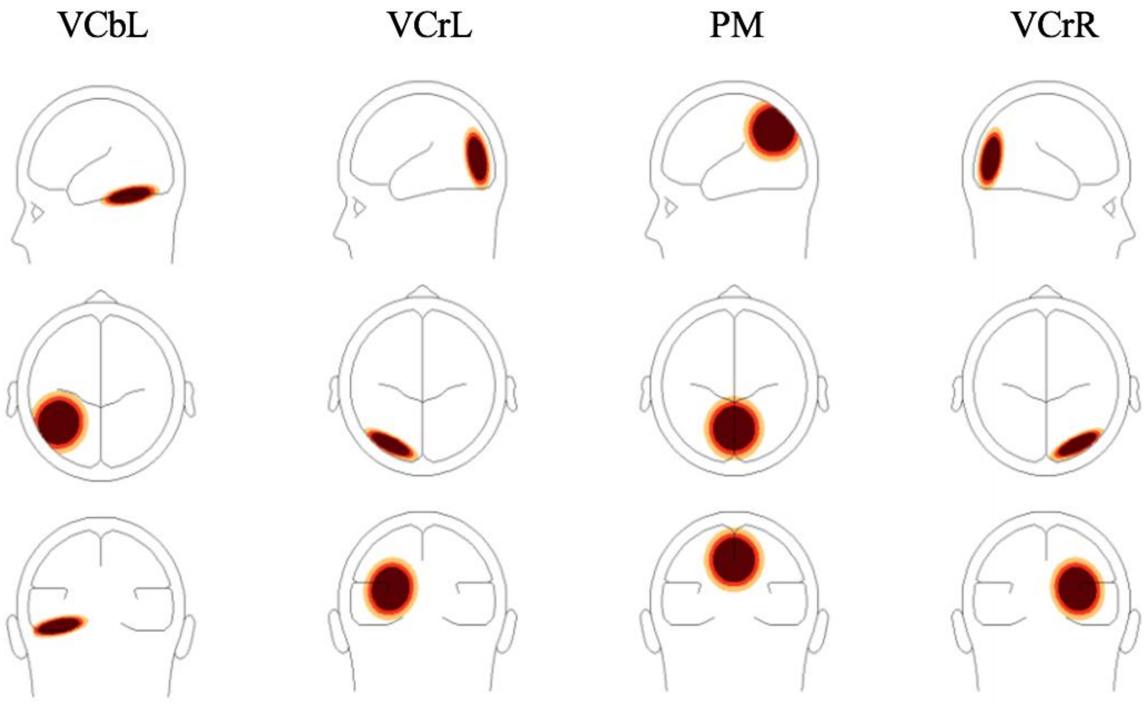

Figure 1 - *Head model with associated visual cortical areas, from left to right VCbL, VCrL, PM, VCrR. The signal magnitude reflects the estimated source activity in the related brain region if one brain region is active.*

Paired sample t-tests were carried out using BESA Statistics 2.0 (BESA, GmbH) to test for significance in amplitude values and frequency ranges between the TSEs of the motion conditions and the static condition for all infants in each testing session. The multiple comparisons problem was addressed using a combination of permutation testing and data clustering techniques (Maris & Oostenveld, 2007). Cluster alpha, which determines the significance level for building clusters in time and/or frequency, was set at 0.005. The comparisons allowed observations of significantly dominant oscillatory activities in the regional sources of interest.

3 Results

3.1 VEP responses

Four grand average channels were selected for each group and each experimental session based on having the highest mean N2 amplitudes for VEPs in the forwards optic flow condition. For infants receiving extra stimulation, the selected channels were POz, Pz, Oz, and O1 for the first testing session. For the control infants the corresponding electrodes were Pz, PO4, Oz, and O2, while electrodes for preterm infants at the first testing were PO4, PO8, Oz and O2 Electrodes at the second session for extra-stimulated infants were PO4, POz, Oz, O2. For the control group at the second testing the electrodes were PO4, Pz, POz, and Oz, and for the preterm infants they were P1, Pz, PO8, and POz. Latency values from the electrode with the highest N2 amplitude in the forwards optic flow condition were used in the ANOVA, with Bonferroni correction used to adjust for multiple comparisons. The chosen electrode varied across infants and testing sessions but was always one of the four stated above and was the same for the three motion conditions in each infant. Figure 2 displays the grand average VEPs for the three visual motion conditions for each group, and each testing session.

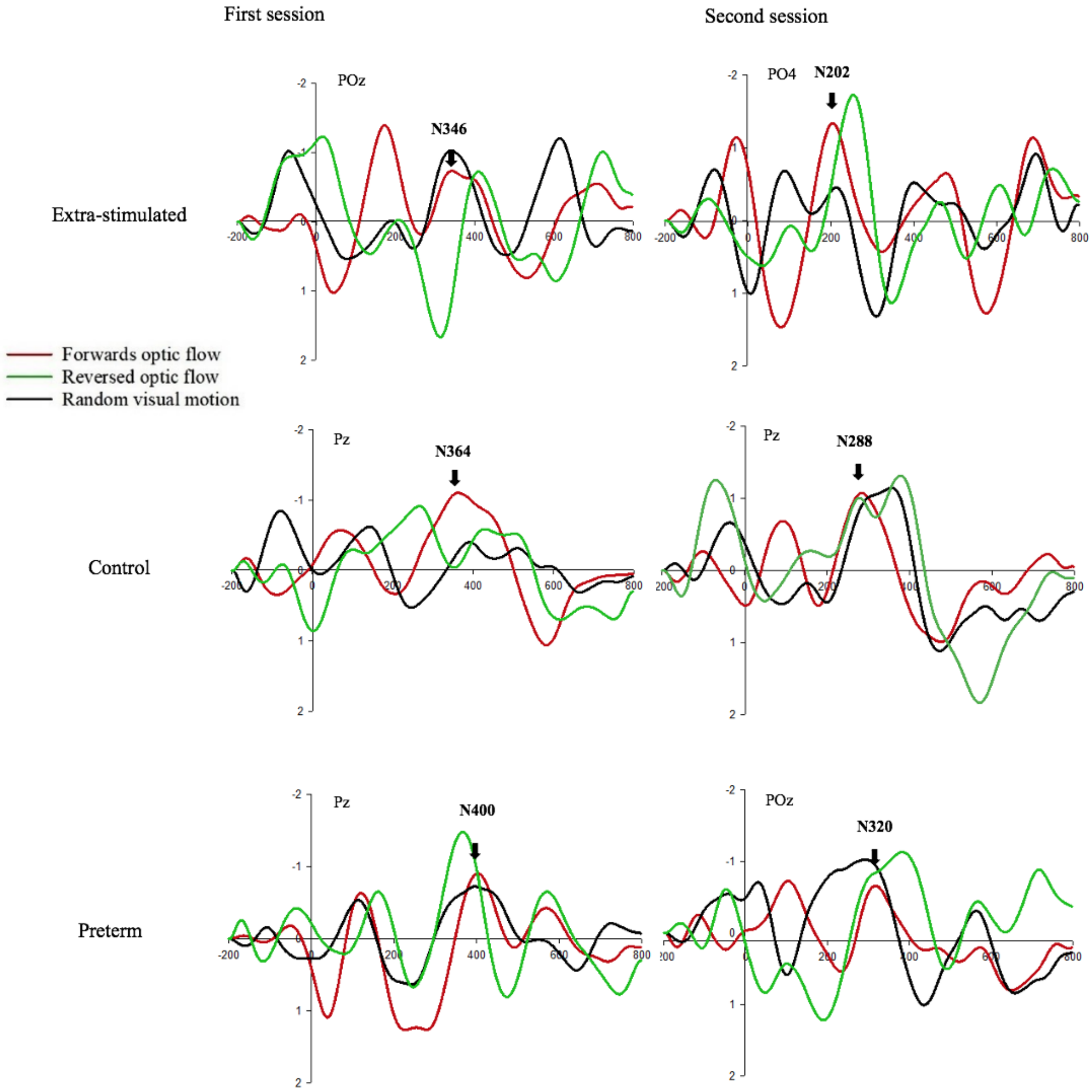

Figure 2 - *Grand average motion VEPs with epoch set from -200 to 800 ms. Amplitudes are on the y-axis and latencies on the x-axis. From left to right and top to bottom: the first and second session for infants receiving extra stimulation, control infants, and preterm infants, respectively. Motion conditions are illustrated with coloured waveforms and are as follows: forwards optic flow (red), reversed optic flow (green), and random visual motion (**black**). Vertical arrows indicate actual N2 latencies for forwards optic flow.*

3.2 VEP analysis

The mean N2 latency for extra-stimulated infants at the first session for the three visual motion conditions forwards optic flow, reversed optic flow, and random motion was 350 ms (*SD*=56), 351 ms (*SD*=59), and 380 ms (*SD*=49), respectively. The mean N2 peak latency for forwards optic flow for infants in the control group at first session was 382 ms (*SD*=54), with corresponding values for reversed optic flow and random motion at 425 ms (*SD*=73) and 434 ms (*SD*=73). For the preterm infants at first session corrected for prematurity, the mean N2 latency for the three motion conditions was 323 ms (*SD*=73), 362 ms (*SD*=70), and 374 ms (*SD*=78), respectively. The mean N2 latency for the three motion conditions for extra-stimulated infants at the second session was reduced to 188 ms (*SD*=36), 267 ms (*SD*=45), and 345 ms (*SD*=61), respectively. For the control group at the second testing, the mean latencies were 289 (*SD*=54), 348 (*SD*=53), and 430 ms (*SD*=80) for forwards optic flow, reversed optic flow and random visual motion, respectively. For the preterm infants at second session, the mean N2 latency for the corresponding motion conditions was 386 ms (*SD*=49), 388 ms (*SD*=51), and 414 ms (*SD*=93), respectively (Figure 3).

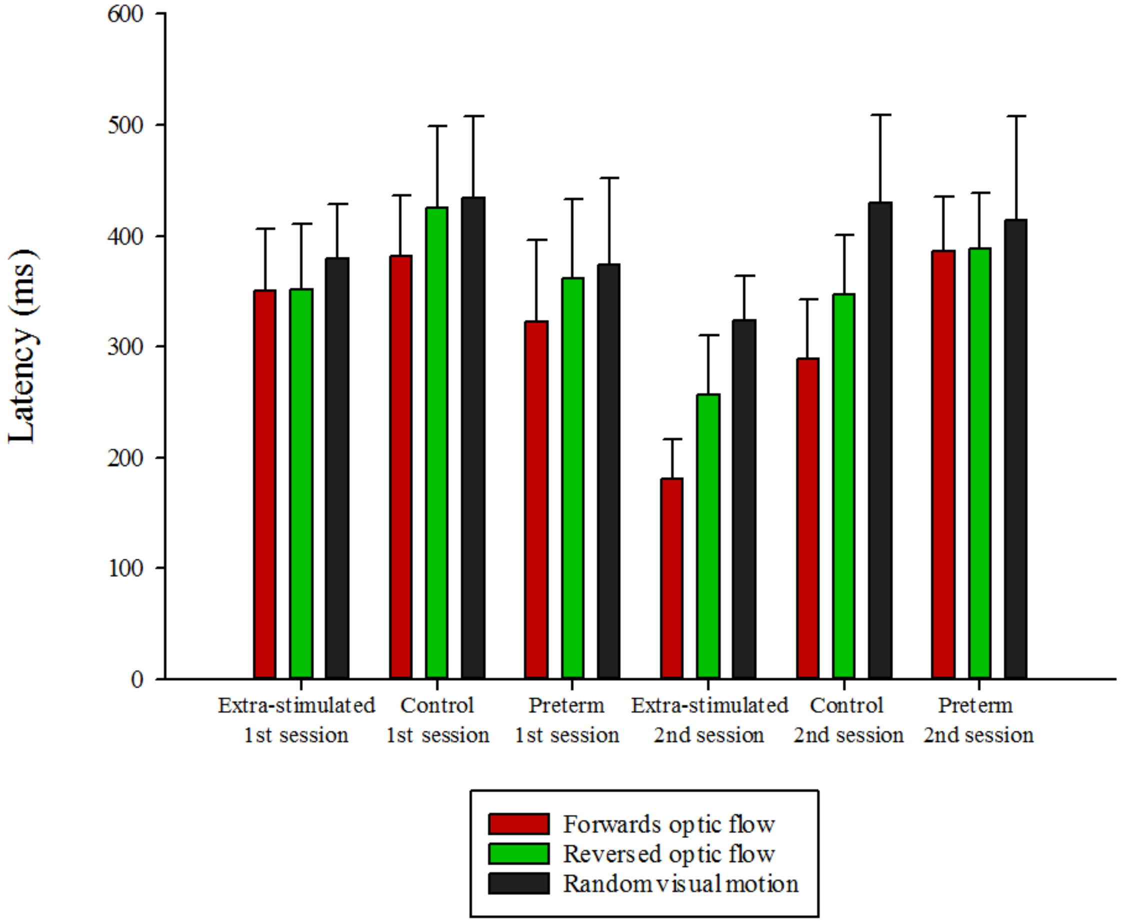

Figure 3 – *Illustration of group means with standard deviations of N2 peak latencies for forwards optic flow, reversed optic flow, and random visual motion for infants receiving extra*

stimulation, infants in the control group, and preterm infants at both testing sessions. In the first session, none of the groups were able to significantly discriminate between the three forms of visual motion, but extra-stimulated and preterm infants had significantly shorter overall latencies than the control group in the first session. Extra-stimulated infants and control infants had significantly improved their latencies from first to second testing, while the preterm infants did not show any improvement in latency. In the second session, only extra-stimulated infants and control infants were able to differentiate between the three forms of visual motion with the shortest latencies for forwards optic flow, followed by reversed optic flow, and the longest for random visual motion. Overall mean latencies were significantly shorter for extra-stimulated infants than the other groups in the second session, indicating faster processing of visual motion for extra-stimulated infants compared to the control infants and the preterm infants. Preterm infants did not decrease their latencies for visual motion during the course of the first year, and they did not show any evidence of being able to differentiate between forwards and reversed optic flow, and random visual motion.

Latencies and amplitudes of the VEPs were analysed separately using repeated-measures ANOVAs. The within-group factor was motion condition (forwards optic flow, reversed optic flow, random visual motion) and testing session (pre-locomotor, self-produced locomotor experience), while between-groups factor was infant group (extra-stimulated, control group, preterm).

For latency, a significant two-way interaction, $F(2, 24)=14.03$, $p<0.001$ between group and session was found, indicating that overall latencies were significantly shorter for infants receiving extra stimulation than for the control group and preterm infants in the second session. Overall latencies for forwards optic flow in the second session for the extra-stimulated infants were approximately 100 ms shorter than for the control group, and 200 ms shorter than for the preterm infants. None of the groups could significantly differentiate between the three motion conditions at the time of the first testing. However, extra-stimulated and preterm infants had significantly shorter latencies than the control group ($p<0.05$) across visual motion conditions in the first session.

Further, a significant three-way interaction was found, $F(4, 54)=2.63$, $p<0.05$, showing that only extra-stimulated infants and infants in the control group were able to significantly differentiate between the three visual motion conditions at the second testing session, with shortest latencies for forwards optic flow, followed by reversed optic flow, and longest latencies for random motion with approximately 70 ms between each visual motion condition. Post hoc analyses confirmed that in the second session, extra-stimulated infants had significantly shorter latencies across motion conditions than both control ($p<0.05$) and preterm infants ($p<0.05$), and that preterm infants had significantly longer overall latencies than infants in the control group ($p<0.05$) and extra-stimulated infants ($p<0.05$). Preterm infants were not able to differentiate between visual motion conditions at the second session, and they did not decrease their latencies during the course of the first year.

3.3 TSE Analysis

A time-frequency analysis was carried out for all infants separately for the three visual motion conditions and the static control condition. Subsequent statistical comparisons showed no significant differences between the motion conditions when they were individually compared with one another. The motion conditions were therefore combined into a single motion condition for further analysis.

Figure 4 shows the results of the permutation test displaying the average for infants in each testing session when TSEs of the combined motion condition were compared with the static condition. The permutation test showed significant negative clusters (suggesting significantly smaller values in the motion condition than the static condition) in at least one of the visual areas of interest in all three groups. For each group and in each session, significant negative clusters were found in at least one of the four regional sources of interest. The results of the permutation test for the comparison of the combined motion condition and static condition showed negative clusters in the visual areas of interest that appeared to be dominated by activity within the theta-band range in all the three groups at both sessions. This prevalent theta-band activity occurred over relatively longer periods of time when infants were younger (Figure 4A, C and E) compared to shorter periods of time when infants in each respective group were older (Figure 4B, D and F). In addition, the results showed that theta-band activity was more prevalent and widespread in the first session for the control infants (Figure 4B) compared to a shorter period for the extra-stimulated and the preterm infants (Figure 4A and C). However, preterm infants showed more widespread theta-activity (Figure 4F) compared to extra-stimulated (Figure 4D) and control infants (Figure 4E) in the second session.

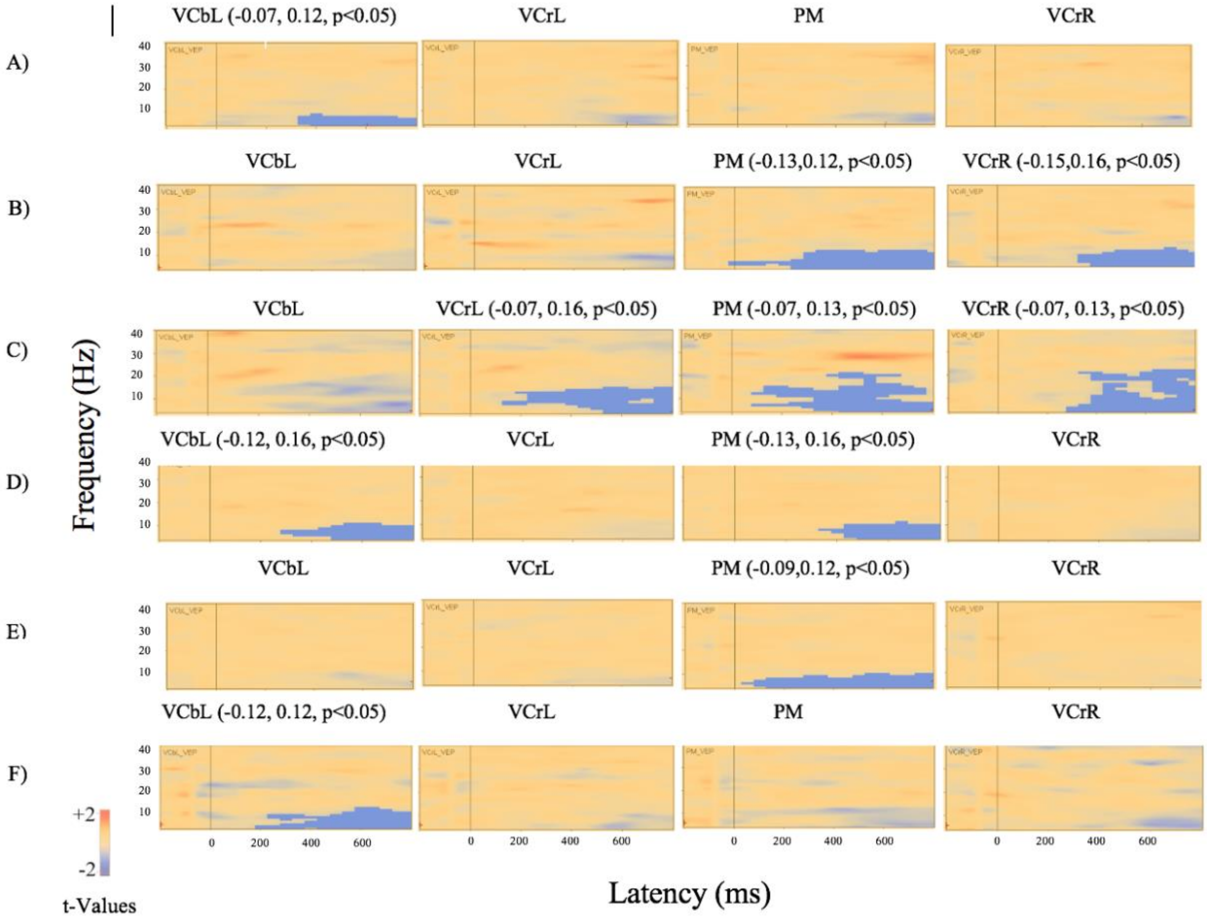

Figure 4 - *Average visualisation of significant data clusters in the visual sources of interest when the combined motion condition was compared with the static condition in extra-stimulated infants at first (A) and second session (B), control infants at first (C) and second session (D) and preterm infants at first (E) and second session (F). Light blue colours represent negative clusters (i.e., combined motion condition had smaller t-values than static control condition) and positive clusters are marked with light red colours (i.e., motion condition had larger t-values than static condition). Significant negative clusters in the visual areas of interest (VCbL, VCrL, PM, VCrR) are marked with light blue voxel marks. A vertical line marks stimulus onset, and epoch is from -200 to 800 ms. Each visual area is dominated by activity in the theta-band but over longer periods of time and more prevalent when infants*

in all groups were younger. The results showed that theta-band activity was more prevalent and widespread in the first session for control infants compared to a shorter period for extra-stimulated and preterm infants. However, preterm infants showed more widespread theta-activity compared to extra-stimulated and control infants in the second session.

The prevalent theta-band activity appeared as desynchronized oscillatory activity in the TSEs of all the groups of infants in both testing sessions when the combined motion condition was compared with the static condition (Figure 5). Further, frequencies of extra-stimulated infants and control infants had increased to include expression of desynchronized beta band frequencies (Figure 5D and 5E), while preterm infants still showed desynchronized oscillatory activities in the theta and alpha range (Figure 5F). Synchronization in the beta-band frequency, however, was observed in extra-stimulated infants at both first (Figure 5A) and second session (Figure 5D).

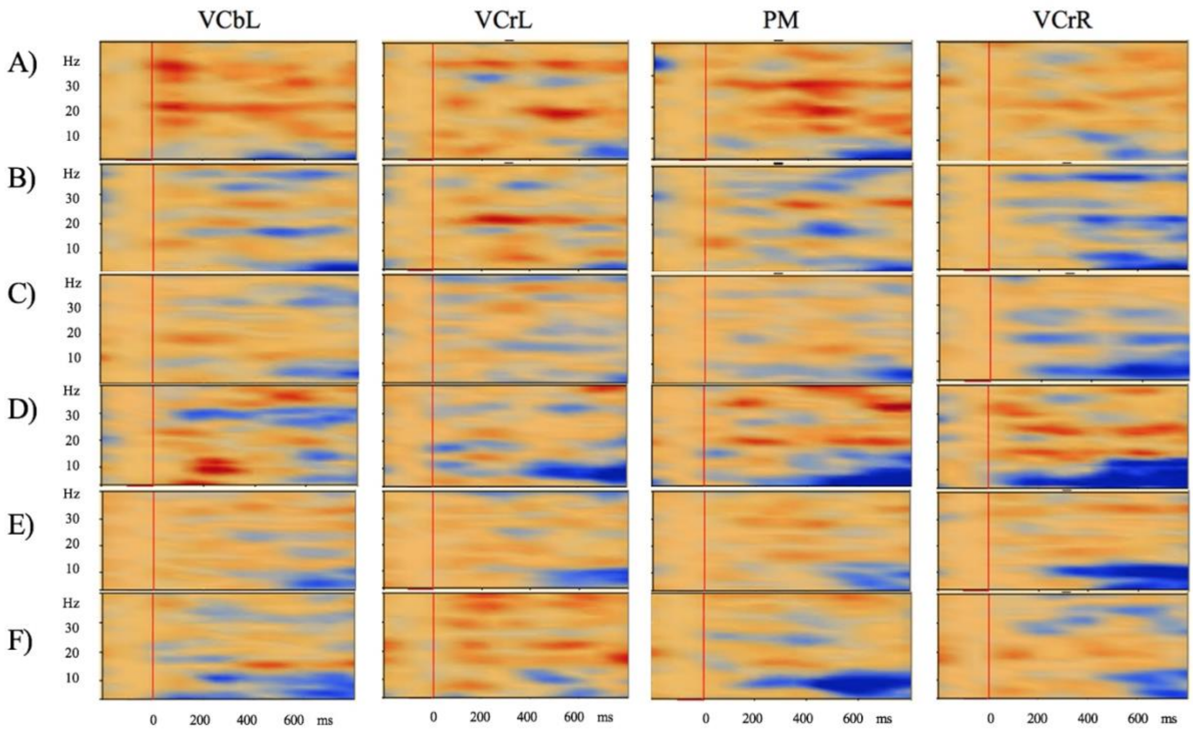

Figure 5 - *TSE plots across brain regions (VCbL, VCrL, PM, VCrR) when the combined motion condition was compared with the static condition for a typical infant in the extra-*

stimulated group (A), in control group (B) and in the preterm group (C) at first session, and for the same infant in the extra-stimulated group (D), control group (E) and in the preterm group (F) in second session. Epoch length is -200 to 800 ms, with a baseline of -100 to 0 ms. A red line indicates stimulus onset at 0 ms. In the TSE plots, induced synchronised and desynchronised activities are shown in red and blue contours, respectively. Induced theta-band desynchronized activities were observed in all visual areas of interest at both first (A, C, E) and second (B,D,F) testing sessions. Synchronization in the beta-band frequency, however, was observed in extra-stimulated infants at both first (A) and second session (D).

4 Discussion

The present longitudinal study aimed to examine the effects of receiving extra stimulation on the development of functional cortical responses to visual motion in the first year of life. Infants receiving extra stimulation, infants receiving a traditional Western upbringing, and preterm infants were presented with visual motion on a large screen simulating forwards optic flow, reversed optic flow, and random visual motion. VEP and TSE analyses were applied on infants' evoked and induced electrical brain responses, respectively, to investigate whether extra stimulation was associated with enhanced development of visual motion perception in early infancy, and whether preterm infants showed an abnormal development of visual motion perception compared to their full-term peers, indicating a possible dorsal stream vulnerability.

The VEP analysis revealed that during the course of the first postnatal year, developmental improvements in visual motion perception were only observed in infants receiving extra stimulation and infants in the control group. This is in line with previous longitudinal studies, which have demonstrated normally developing infants to have faster responses to visual motion stimuli towards the end of the first postnatal year (Agyei et al., 2015; Vilhelmsen et al., 2019). The ongoing maturation of neuroanatomical structures (Agyei et al., 2015) could partly lead to the relatively faster processing of visual motion and to the shorter latencies found in older infants in the extra-stimulated and control group. However, infants receiving extra stimulation showed a greater improvement in visual motion perception during the first year than infants in the control group. Thus, brain maturation is not likely the only factor in the development of visual motion perception, suggesting a close link between self-generated actions and improved optic flow processing (Agyei et al., 2016a, Agyei, Van der Weel & Van der Meer, 2016b; James & Swain, 2011).

Despite genetic factors known to mediate these developmental processes, external influences have been suggested to greatly affect the developing neocortical architecture of the brain (Baroncelli et al., 2010; Berardi, Sale, & Maffei, 2015; Dubois, Hertz-Pannier, Dehaene-Lambertz, Cointepas, & Le Bihan, 2006; Johnson, 2001; Paus et al., 2001). A large number of experiments have shown how rodents raised in stimulating environments show an increase in cortical thickness (Bennett, Krech, & Rosenzweig, 1964; Forgays & Forgays, 1952; Sirevaag, Black, Shafron, & Greenough, 1988). Several studies on experience-dependent changes in the cortex have been using animals like cats and monkeys as well, and in general, these studies have found similar results (e.g., Beaulieu & Colonnier 1987, Floeter & Greenough 1979, Stell & Riesen 1987). Among other things, the increase in cortical thickness has been attributed to an enhanced rate of synaptogenesis and myelination of white matter fibres (Markham & Greenough, 2004; Rampon et al., 2000; Sirevaag et al., 1988; Sirevaag & Greenough, 1987), increased complexity in synapse morphology (Sirevaag & Greenough, 1987), and an increase in non-neuronal metabolic components (Oliet, Piet, & Poulain, 2001), all of which advance neuronal functions and connectivity. The magnitude of these changes should not be underestimated.

Even though the literature on similar effects in humans remains relatively scarce (Jacobs, Schall, & Scheibel, 1993), enriched stimulation in early infancy has proven beneficial for facilitating brain development and, in particular, visual development in preterm infants (Guzzetta et al., 2009). The VEP analysis revealed that developmental improvement in visual motion perception appeared to be greater in extra-stimulated infants during the first postnatal year than in control and preterm infants. Extra-stimulated infants showed significantly shorter N2 latencies for visual motion than both control and preterm infants in the second testing session at 9-12 months, with latencies approximately 100 ms shorter than the control group and 200 ms shorter than the preterm infants. This major difference in brain responses to visual motion indicates that receiving stimulation in the water or through baby massage during early infancy, may accelerate brain development of dorsal stream functions. Interestingly, these results were found despite extra-stimulated infants being significantly younger than their control peers when tested for the second time. These results reflect the findings of Lobo and Galloway (2012), who found that infants receiving enhanced handling and positioning had a richer perceptual-motor history than traditionally-raised infants. Enriched stimulation has been associated with less time spent in a stationary position (Adolph & Hoch, 2019), and an accelerated onset of motor behaviours such as crawling, standing, independent walking, and improved postural control (Adolph & Hoch, 2019; Karasik et al., 2015; Lobo & Galloway, 2012; Zelazo, Zelazo, & Kolb, 1972). In turn, such behaviours give rise to greater amounts of self-generated optic flow, which is argued by Gilmore and Rettke (2003) to provide the foundation from which perceptual information becomes functionalized. The current results may therefore suggest that extra-stimulated infants were more experienced in processing different patterns of flow than their peers, likely due to having received more opportunities to interact with their surroundings, through enhanced handling and activities, for example, baby swimming or baby massage. These activities are "enhanced" because they involve behaviours that are not typical of daily life for young infants born into Western cultures, where infants spend considerable time being placed in supine positions by caregivers (Guezetta et al., 2009). Descriptive studies have linked greater experience in multiple positions in the first months after birth with better development in the first year for healthy infants and infants born preterm and at risk for delays in development (Fetters & Huang, 2007). Considering that optimal brain plasticity occurs in the first few months of life (Bonnier, 2008), the considerably faster brain responses to visual motion in extra-stimulated infants may therefore indicate that receiving stimulation in an upright position during early infancy may increase processing speed by enhancing brain development of dorsal stream functions.

Previous studies have noted the vital role of visuomotor experiences in favouring certain visual stimuli (Anderson et al., 2013; Bell & Fox, 1996; Gilmore, Hou, Pettet, & Norcia, 2007). VEP analysis also showed that extra-stimulated and control infants could significantly differentiate between visual motion conditions at the second session, with the shortest latencies for forwards optic flow, followed by reversed optic flow and longest latencies for random visual motion with approximately 70 ms between each condition. These results corroborate earlier findings (Giaschi, Zwicker, Young & Bjornson, 2007; Gilmore, Hou, Pettet & Norcia, 2007; Imura et al., 2008; Shirai, Kanazawa & Yamaguchi, 2004; Takeuchi, 1997) that found preferential sensitivities to expanding as against contracting stimuli in infants, which could be attributed to infants experience with locomotion since humans typically move in a forwards manner (Agyei et al., 2015; Shirai et al., 2009; Van der Meer et al., 2008). In addition to maturation, optic flow studies have suggested the ability to differentiate between different forms of visual motion to be related to the onset of self-produced locomotion (Agyei et al., 2015, Vilhelmsen et al., 2019). Infants start to passively explore the environment soon after birth, either in a stroller or when carried by their caregivers, until they begin crawling or walking (Raudies et al., 2012). As infants become more and more independently mobile during the first year of life, they depend to a greater extent on the correct pick-up of visual information to efficiently manoeuvre and actively explore their surroundings through self-produced movement (Agyei et al., 2014). Infants receiving extra stimulation showed mean latencies for the N2 peak of forwards optic flow at just 188 ms after stimulus onset. Considering previous studies reported N2 latencies to occur at around 130-150 ms after stimulus onset in adults (Probst, Plendl, Paulus, Van der Meer et a., 2008, Wist, & Scherg, 1993), the short latencies observed in extra-stimulated infants suggests a progression towards almost adult-like responses to optic flow. Further, the faster processing (shorter latencies) of forwards optic flow in extra-stimulated infants compared to control and preterm infants supports the proposition of enriched stimulation acting to accelerate brain development through providing infants with active visuomotor experiences. The faster detection of optic flow than random visual motion could further reflect the general importance of optic flow for effective self-navigation during infancy (c.f., Warren, Kay, Zosh, Duchon & Sahuc, 2001).

Interestingly, preterm infants showed significantly shorter latencies at the first session regardless of visual motion condition compared to control infants at the first session at 4-5 months of age. The faster perceptual response can be explained by the fact that preterm infants were tested corrected for prematurity, and therefore had up to 3 months longer exposure and experience to real-world visual flow than their full-term peers. The current results may therefore suggest that by the time of the first testing session, extra-stimulated infants and preterm infants were more experienced in processing different patterns of flow than full-term infants in the control group. For extra-stimulated infants, it is likely due to being given more opportunities to interact with their surroundings (e.g., baby swimming classes), while for preterm infants, it is likely to be related to longer experience outside the womb. Both explanations give, in turn, support to the notion of how experience can impact the development of visual motion perception during the first year of life.

Even though preterm infants had, in fact, more self-produced locomotion experience than their extra-stimulated and full-term control peers at the time of the second testing, they did not differentiate between the three motion conditions nor did their latencies decrease as they got older. Studies have noted that preterm infants at corrected age of 2-3 months are delayed several weeks compared to full-term infants when differentiating between changes of direction (Birtles et al., 2007, Braddick et al., 2005). One could expect that, when age is corrected for prematurity, preterm infants would follow a developmental path similar to that of full-term infants. However, in line with earlier findings, preterm infants in the current study did not show a similar development regarding visual motion processing as seen in their full-term peers. These findings could indicate a lack of specialization in, and development of, the dorsal visual processing stream. The developmental period of the dorsal stream is believed to be concentrated around the third trimester of pregnancy (Hammarrenger et al., 2007, Klaver et al., 2011), and the cells of the dorsal pathways need high levels of polyunsaturated fatty acids for optimal functioning of physiological processes (Sabel et al., 2009, Stein, 2001), and is, therefore, more prone to be disrupted by the effects of preterm birth. Thus, it is possible that the unimproved latencies observed in preterm infants at the end of the first year corrected for prematurity, indicate a dorsal stream deficit. However, it is also possible that the unimproved latencies and the inability to differentiate between different forms of visual motion in preterm infants at the second session, indicate a normal delay related to premature birth that may be recovered at a later age (Agyei et al., 2016a). A follow-up study to monitor the developmental progress into school age of the preterm group could help ascertain the validity of this presumption.

Induced responses when perceiving visual motion were further examined in the present research. When comparing the TSEs of the combined visual motion condition with the TSEs of the static control condition, induced expressions of theta band desynchronisation were seen in all three infant groups. The finding corroborates earlier studies showing infant EEG to be dominated by low-frequency activity with larger amplitudes during processing of visual motion (Agyei et al., 2015; Başar, Başar-Eroglu, Karakaş, & Schürmann, 2001; Klimesch, 1999; Van der Meer et al., 2008). Such low-frequency rhythms typically appear as widespread patterns of cortical activity across the scalp, suggesting greater compositions of neurons to be implicated in slower- compared to faster-oscillating cell assemblies (Orekhova, Stroganova, Posikera, & Elam, 2006). In light of this, Agyei et al. (2016a) suggest that low frequency activation in infants is likely to reflect the employment of larger and less specialised cortical networks and cells when perceiving visual motion. The widespread theta activities observed in the present study may therefore be interpreted as a general sign of immaturity.

Further, more prevalent and widespread desynchronised theta-band activities occurred when infants were young compared to when they were older in each group. A previous study used the same stimulus with forwards optic flow, reversed optic flow, and random visual motion, and found that infants at both 4-5 and 8-11 months displayed theta- and alpha-band oscillations in response to visual motion (Agyei et al., 2016a). The present study corroborates these findings, where extra-stimulated and control group infants showed low-frequency oscillatory brain activity in response to visual motion with an increase from theta- to alpha-band activity as they got older. Alpha- and beta-band oscillations have been suggested to be important for cross-network functional connectivity (Ganzetti & Mantini, 2013). Moreover, enhancement in beta rhythm synchronisation is suggested to serve as an integrative agent for long-range communication between neuronal populations residing in different cortical regions (Pfurtscheller et al., 1997). This progression may become more evident as infants become adults since studies have observed increased gamma-band power in the visual cortex during motion processing in adults (Hoogenboom et al., 2006, Krishnan et al., 2005).

Surprisingly, induced responses also indicated that extra-stimulated and preterm infants showed a less widespread theta-activity compared to the control group at the time of the first testing. As such, the less widespread theta activities observed in extra-stimulated and preterm infants compared to control group infants at the first testing could indicate that fewer yet more specialised neurons were employed during visual motion processing in extra-stimulated infants and preterm infants. This can be explained by infants receiving extra stimulation and preterm infants having more experience with visual motion processing. The extra-stimulated infants received this through enhanced experience with the environment and the preterm infants by having longer experience in the real world due to the age being corrected for prematurity. This is in line with the VEP analysis from the first testing session, showing extra-stimulated and preterm infants to have significantly shorter latencies across motion conditions compared to the control group. These findings further support the idea of enhanced stimulation and experience in early infancy to act as a facilitating agent in advancing development.

In addition to induced alpha desynchronisation, synchronised activities in the beta-band frequency could be seen in the TSE maps for extra-stimulated infants when comparing the combined visual motion condition with static control in the second session. The finding is in accordance with earlier observations by Agyei et al. (2016a), showing beta band synchronisation in response to visual motion towards the end of the first year of life. Compared to alpha-band frequency, beta-band rhythms are implied to involve fewer but more specialised neurons (Pfurtscheller, Stancak Jr, & Edlinger, 1997). As these activities have been reported in response to optic flow stimuli in adults (Van der Meer et al., 2008), expressions of synchronised beta oscillations in extra-stimulated infants, and the absence of these in the control and preterm infants, suggest that induced responses were developmentally advanced in extra-stimulated infants. Observation of beta-band oscillations in the extra-stimulated infants at the second session could further explain the significantly shorter latencies for VEPs displayed by extra-stimulated infants in the same session.

Preterm infants at the second session showed no synchronised oscillatory activities in the alpha-beta range, but more widespread theta-band desynchronisation when the TSEs of the combined motion condition were compared with the static control pattern. The absence of high-frequency activity observed in preterm infants at the second session, combined with the longer VEP latencies, indicates that preterm infants have not yet developed sufficiently specialized networks for rapid processing of visual motion information. These findings reflect previous studies, which have found that preterm infants have less myelinated cortical white matter (Hüppi et al., 1998; Mewes et al., 2006), and demonstrate slower cortical growth (Kapellou et al., 2006) than their full-term peers. This may be due to the probably disrupted dorsal visual stream development that may occur when being born preterm (Hammarrenger et al., 2007), as stated earlier.

Combined, the present study adds to the body of literature demonstrating that visual experience and brain maturation together work to advance the development of visual motion perception in infancy (Agyei et al., 2015; Agyei et al., 2016a; Orekhova et al., 2006; Vilhelmsen et al., 2019). The current findings support the relevance of visuomotor experience during the first year of life. Enriched stimulation during the first year of life constituted an important factor in facilitating enhanced visual motion perception in extra-stimulated infants. The present results support previous findings demonstrating enriched stimulation to promote developmental behavioural advancements (Adolph & Hoch, 2019; Karasik et al., 2010, Lobo & Galloway, 2008) by examining this link from a neurodevelopmental perspective. However, the preterm infants did not show a similar progression when it comes to visual motion processing with age as their peers.

Existing interventions aimed at minimizing disabilities and to improve capabilities in children with - or at risk for - neurodevelopmental disorders have been suggested to be most effective when focusing on enhancing caregiver-infant interactions and advancing general motor development (Blauw-Hospers & Hadders-Algra, 2005; Dusing, Lobo, Lee, & Galloway, 2013; Heathcock, Lobo, & Galloway, 2008). In support of such findings, cultural and theoretical studies have reported handling and interaction patterns between caregivers and their infants to significantly affect developmental outcomes (Karasik et al., 2010; Karasik et al., 2015; Lobo & Galloway, 2012). In light of this, it is reasonable for the current results to have occurred not only because of the specific enriched activities received by extra-stimulated infants, but also because of the overall handling patterns of their caregivers. It is reasonable to assume extra-stimulated infants had a broader handling flexibility than control infants, which probably had a more traditional upbringing, where infants are viewed as in need of gentle handling and spend 90% of their waking time in a supine position. Hence, the present research offers a further affirmation of the key role played by caregivers in the developmental trajectories of their infants.

The present longitudinal study demonstrated an association between receiving extra stimulation in infancy and accelerated developmental improvements of visual motion perception as observed in VEPs and TSE. The study confirmed that both extra-stimulated infants and control infants show a developmental trajectory in which their sensitivities to optic flow increase and in which they become faster in detecting structured optic flow than random visual motion during their first year. Time-frequency analyses showed that both extra-stimulated and control infants showed a progression from low-frequency desynchronisation in theta-band frequencies to higher frequency desynchronisation in alpha-band frequencies with age. Preterm infants did not show a similar developmental trajectory when it comes to visual motion processing. Preterm infants did not significantly decrease their VEP latencies for visual motion from first to second test session and they did not discriminate between the motion conditions. Unlike in the extra-stimulated and control infants, however, no such high-frequency activities were generally observed in the preterm infants as they got older.

The findings revealed that infants receiving extra stimulation showed an overall greater sensitivity to visual motion than their traditionally-raised peers and preterm infants during the first year as reflected by their shorter latencies in response to visual motion, and oscillatory activities at higher frequencies in the alpha-beta frequency ranges. The greater improvement in extra-stimulated infants than their traditionally-raised peers was attributed to their caregivers' overall handling patterns, including enriched activities. The poorer responses in the preterm infants were associated with impairment of the dorsal visual stream specialized in the processing of visual motion. Consequently, the results may prove beneficial for future attempts to improve infants capabilities at risk for abnormal visuomotor and neurological development. Future studies, as well as follow-up studies of the extra-stimulated enrolled in the present study at school age, may reveal whether the accelerated developmental improvements of visual motion perception in extra-stimulated children are still present and what potential effects this may have on the children's everyday lives, especially as potential interventions to advance development in infants born with risk factors.

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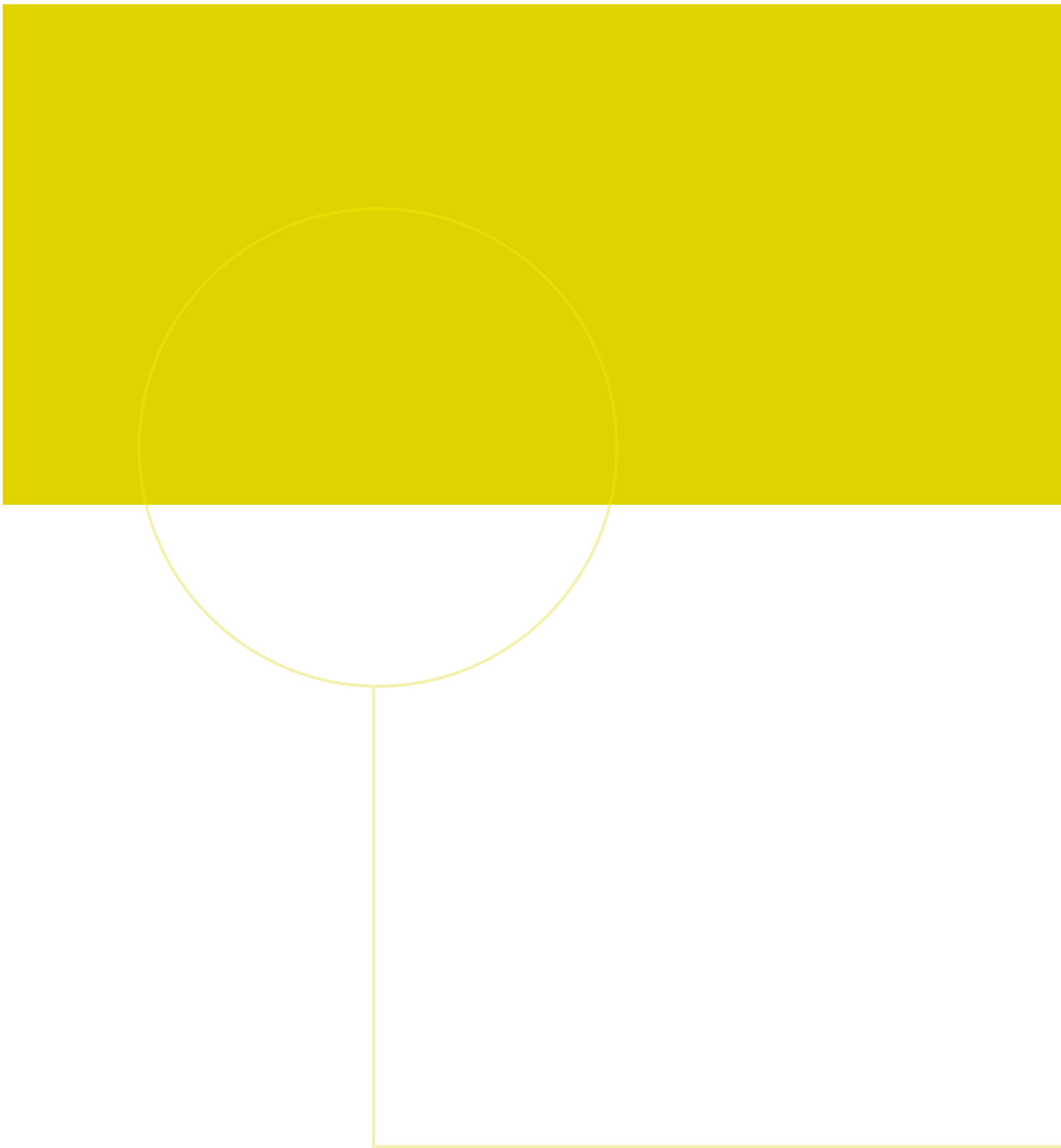

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