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Longitudinal study on receiving extra motor stimulation in early infancy: High-density EEG analysis of cortical responses to visual motion

Master's thesis in Psychology
Supervisor: Audrey van der Meer
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Abstract

Electroencephalogram (EEG) was used to investigate brain electrical activity as a functional response mechanism to visual motion stimuli in infants receiving extra motor stimulation and infants receiving a traditional Western upbringing. In this longitudinal study, infants were presented with an optic flow pattern simulating forwards and reversed self-motion, and unstructured random visual motion twice during the first year of life. Infants were pre-locomotor at the first session at 4-5 months and had at least 7 weeks of crawling experience at the second session at 8-12 months. Analyses of visual evoked potentials (VEP), temporal spectral evolution (TSE), and EEG coherence connectivity were performed. VEP results showed overall N2 latencies for motion to be significantly shorter for extrastimulated infants than for control infants in both sessions. Further, both infant groups showed a significant improvement in latencies with age and significantly shorter latencies for forwards optic flow as to reversed optic flow and random visual motion at 8-12 months. TSE results indicated a progression from desynchronised low-frequency theta-band activity to desynchronised high-frequency alpha-band activity observed at the end of the first postnatal year. However, extrastimulated infants also showed expressions of more mature beta-band activity at 8-12 months. EEG coherence connectivity analysis showed few significant connections when infants were 4-5 months, while increased connectivity was prominent in the extrastimulated infants at 8-12 months but not in the control group. It was concluded that the overall advanced performance of extrastimulated infants was attributed to their enriched motor stimulation. The substantial improvement in visual motion perception during the first year of life was interpreted as increased experience with self-produced locomotion and neurobiological development. Finally, the poorer responses in traditionally-raised control infants are probably related to immaturity of visual pathways involved in motion processing as observed in longer latencies and low-frequency oscillatory activity.

Sammendrag

Elektroencefalografi (EEG) ble brukt for å undersøke hjerneaktivitet som funksjonell responsmekanisme til visuell bevegelsesstimuli hos spedbarn som mottar ekstra motorisk stimuli og spedbarn som mottar en tradisjonell vestlig oppdragelse det første leveåret. I denne longitudinelle studien ble spedbarna presentert optisk strømningsmønster som simulerer forover og bakover selv-bevegelse og ustrukturert tilfeldig visuell bevegelse to ganger innen det første leveåret. Ved første test, 4-5 måneder, hadde spedbarna ingen erfaring med egenprodusert bevegelse, mens ved andre testing, 8-12 måneder, hadde spedbarna minst syv uker krabbeerfaring. «Visual evoked potentials»- (VEP), «temporal spectral evolution»- (TSE) og «coherence connectivity» analyse ble gjennomført for å undersøke forskjeller i hjerneaktivitet i respons til visuell bevegelsesstimuli. VEP-analysen viste betydelige kortere latenser for bevegelse sammenliknet med kontrollbarna ved begge testingene. Betydelig kortere N2-latenser for bevegelse ble også observert med alder i tillegg til betydelig kortere N2-latenser for forover bevegelse sammenliknet med bakover og tilfeldig bevegelse da spedbarna da 8-12 måneder. TSE-resultatene viste en progresjon fra desynkronisert lavfrekvent theta-aktivitet til desynkronisert høyfrekvent alfa-aktivitet som respons på bevegelse i løpet av det første leveåret. Ekstrastimulerte spedbarn viste også uttrykk av beta-bånd aktivitet ved 8-12 måneder. Coherence connectivity analysen viste et lite antall koblinger mellom hjerneområder ved første testing, men et økt antall koblinger ble observert kun hos de ekstrastimulerte spedbarna ved andre testing. Det ble konkludert med at den mer avanserte prosesseringen av visuell bevegelse hos ekstrastimulerte spedbarn ble attribuert til deres berikede motoriske stimulering. Den generelle forbedringen av visuell bevegelsespersepsjon det første leveåret ble relatert til en kombinasjon av erfaring med egenprodusert bevegelse og nevrobiologisk utvikling. Svakere responser hos kontrollspedbarna ble relatert til umodne visuelle baner involvert i bevegelsesprosessering som ble observert i tregere responstider og lavere oscillatoriske frekvenser.

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1. Introduction

1.1. Visual motion perception and optic flow

Daily activities such as social interactions and cognitive skills, object categorization, and navigating through the environment depend on perception and correct interpretation of visual information. Considering the relevance of these abilities to everyday life, it is crucial to understand the developmental processes underlying how infants learn to use relevant perceptual information.

When moving around in the environment, we change course to reach our destination and avoid obstacles in our path (van der Meer et al., 2008; Wilkie & Wann, 2003). The pattern of visual motion resulting from the observer's own motion is referred to as optic flow (Gibson, 1979/2015) and gives valuable information about the relative motion of objects to the observer (Rasulo et al., 2021). The role of optic flow perception for action has often been studied in various activities. Evidence shows that optic flow information is crucial for heading direction (Bruggeman et al., 2007), stabilizing posture (Warren et al., 2001), and estimating the time-to-collision of an approaching object (Kayed & van der Meer, 2009). Optic flow also plays a significant role in controlling driving speed and direction (Vilhelmsen et al., 2019).

In response to visual motion stimuli, adults can distinguish between different forms of motion, such as expansion/contraction, rotational, and horizontal/vertical (Gilmore et al., 2007). Infants, on the other hand, are not as efficient as adults in detecting motion (Gilmore et al., 2004; Gilmore et al., 2007; van der Meer et al., 2008). However, from three days of age, infants respond to optic flow information by leaning their heads backwards when presented with optic flow stimuli moving towards them (Barbu-Roth et al., 2009; Jouen et al., 2000). A rudimentary coupling between optic flow information and locomotion at birth suggests a precocious capacity in the newborn to perceive and utilize visual information specifying self-motion (Barbu-Roth et al., 2009). Furthermore, findings indicate that infants perceive three-dimensional object shapes from optic flow at eight weeks of age (Arterberry & Yonas, 2000). Between 5 to 18 weeks of age, cortical responses to changes in head direction increase in magnitude (Braddick et al., 2003). Studies using electroencephalogram (EEG) have shown that infants at 4-5 months do not differentiate between visual motion speeds and directions, while infants at 8-12 months have been shown to differentiate between forwards and reversed optic flow and random visual motion, with the shortest latencies for forwards optic flow (Borge Blystad & van der Meer, 2022; Vilhelmsen et al., 2019). This perceptual development

suggests a rapid improvement in processing optic flow information during the first postnatal year (Agyei et al., 2015; van der Meer et al., 2008; Vilhelmsen et al., 2019).

1.2. EEG for understanding the cortical responses to visual motion stimuli

Various brain studies in humans and other primates have investigated the specialised cortical areas for processing visual information (van der Meer et al., 2008). Evidence is emerging that the dorsal visual stream specialises in motion processing (Creem & Proffitt, 2001; Perry & Fallah, 2014). The dorsal visual stream processes the complex motion of objects within the environment around us, either as we are stationary or moving through the environment (Perry & Fallah, 2014). Physiological evidence shows that neurons within the human medial temporal/visual area 5 (hMT/V5) are involved in processing radial motion. Global motion elicits activity in visual area 3a (V3a) and parietal areas. Moreover, the dorsal medial superior temporal (dMST) area is found to be specifically involved in optic flow processing (Creem & Proffitt, 2001; Duffy, 1998; Duffy & Wurtz, 1997; Perry & Fallah, 2014).

The understanding of the anatomy and the electrophysiology of the visual system's complex processing has made considerable progress in monkeys and normal adults (van der Meer et al., 2008), yet little is known about the development and processing of this fundamental type of information in infants (Gilmore et al., 2004). EEG primarily records the electrical activities of pyramidal neurons with a high temporal resolution during visual perception tasks (Agyei et al., 2015; Tucker, 1993). EEG allows us to investigate changes in the state of underlying neuronal networks and continuously reveal task-specific spatial activation patterns (Pfurtscheller, 1992). Visual evoked potentials are found to be dominated by a motion-sensitive negativity (N2) that is thought to originate in MT/V5 (Agyei et al., 2015; Ahlfors et al., 1999; Kuba et al., 2007; Vilhelmsen et al., 2019). In adults, N2 is found approximately 130-150 ms after stimulus onset (Heinrich et al., 2005; Probst et al., 1993; Sack et al., 2006), while in infants N2 is found around 180-220 ms post-stimulus (Vilhelmsen et al., 2019). Previous studies have reported the N2 visual component to be longer in latency and higher in amplitude in infants than in adults. Furthermore, studies have found N2 latency to decrease with age (Agyei et al., 2015; van der Meer et al., 2008; Vilhelmsen et al., 2019). Other studies of early visual N1, P1, and P2 components have shown similar results where latencies were observed to decrease as children became older (Fielder et al., 2009; Hammarrenger et al., 2007).

In conjunction with VEPs, growing attention has been given to EEG studies in the time-frequency domain (Temporal spectral evolution, TSE) (Agyei et al., 2015). Neuronal processes are highly dynamic, yet little is known about how the different brain systems work together (Lopes da Silva, 1991; Singer, 1993). TSE-analysis allows the study of cognitive and perceptual functions through the observations of the natural frequencies in the EEG (Agyei et al., 2016a). Frequency changes are observed as event-related synchronisations or desynchronisations, representing a decrease or increase in amplitudes within a specific frequency band (Elul, 1972; Pfurtscheller & Lopes da Silva, 1999). Oscillations are, in general, interactions between different areas in the brain and the complex interactions and the following distinctive frequencies are, in short, reflecting different cognitive processes (Pfurtscheller & Lopes da Silva, 1999). Over the years, classes of oscillations within specific frequencies have been distinguished: 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). These rhythms reflect neurophysiological processes that exhibit functionally different roles (Agyei et al., 2015; Buzsaki & Draguhn, 2004; Ganzetti & Mantini, 2013; Saby & Marshall, 2012). For instance, signal detection and decision making are thought to be included in the delta-band (Başar et al., 2001), and theta-frequencies are essential for neuronal plasticity and coding of perceptual information (Hanslmayr et al., 2013). Further, the control of inhibition and cortical processing is thought to occur in the alpha-band (Klimesch et al., 2007), involvement in multisensory stimulation and the shifting of neuronal systems to state of attention in the beta-band (Khader et al., 2010; Pfurtscheller et al., 1997), while memory matching of information for perception is thought to be found in the gamma frequency (Herrmann et al., 2010). Low-frequency rhythms have typically been reported in young infants at 4-5 months in response to visual motion and have been attributed to signs of immaturity. However, low-frequency oscillations in the theta-alpha range undergo systematic development from early childhood to adulthood (Stroganova et al., 1999). Accordingly, infants at 8-12 months of age have been shown to include higher-frequency oscillations in response to visual motion (Agyei et al., 2016b; Borge Blystad & van der Meer, 2022; van der Meer et al., 2008; Vilhelmsen et al., 2019). The progression from lower to higher frequencies during development is considered a sign of maturation in various psychophysiological studies (Hudspeth & Pribram, 1992; Stroganova et al., 1999).

1.3. The plasticity of the brain

An intriguing feature of the brain is its capacity for structural and functional modification in response to external stimuli (Mohammed et al., 2002). Plasticity refers to the brain's ability to change structure and function, and experience is found to have a foundational effect on the development of skills (Fox & Rutter, 2010; Kolb & Whishaw, 1998; Merzenich et al., 1996). For instance, anatomical changes, including increasing dendritic length, spine density, synapse formation, glial activity, and altered metabolic activity, are thought to occur with experience-dependent changes (Kolb & Whishaw, 1998; Oldham & Fornito, 2019). One cardinal principle in developmental psychology is that early experience profoundly affects human development (Borge Blystad & van der Meer, 2022; Fox & Rutter, 2010; Giaschi et al., 2007; Shirai et al., 2009). Greenough et al. (1987) introduced the term “experience-expectant plasticity”, which refers to the role of experience in brain development during early sensitive periods. External stimuli shape neuronal circuitry patterns in the developing brain (Bullmore & Sporns, 2012; Engel et al., 2001; Tononi, 2004), where the most effectively activated neural connections are selectively maintained and matured, while the less well-activated neural connections are eliminated (Greenough et al., 1987). Based on a series of classical animal studies, there is knowledge that cortical representations are dynamic and continuously modified by experience, which studies in humans support and complement (Fox & Rutter, 2010; Pantev et al., 2003).

At birth, the human brain is equipped with 100 billion neurons, a few of which are connected (Kolb & Whishaw, 1998). During the first year of life, millions of connections are made through an interplay of life experience and maturation, forming complex networks of neurons specialized in rapidly processing information (Oldham & Fornito, 2019). Evidence suggests that perception, thoughts, emotions, and actions are more likely to emerge from interactions between neuronal assemblies that are distributed across the brain than from local computations in restricted brain areas (Bullmore & Sporns, 2012; Engel et al., 2001; Tononi, 2004). A plausible premise is therefore that the operation of every cognitive act requires the integration of distributed activity, as implemented through dynamic long-range neuronal communication within a network of structural connections (Ganzetti & Mantini, 2013). Functional brain connectivity reflects the brain's abilities to process and integrate information and can be investigated with EEG coherence connectivity analysis. In this analysis, the correlation between two scalp electrode sites is analysed, and oscillatory interactions reflect the degree of connectivity and synaptic elaboration between the two recording sites (Corbetta, 2012; Friston, 2002; Ganzetti & Mantini, 2013). Studies have found structural connectivity in

infants that overlap with adult networks, such as subcortical and visual regions, indicating that some structural connectivity is present in neonates (Oldham & Fornito, 2019). The localization of functional connectivity to primary sensory and motor areas of the prenatal/neonatal brain is thought to be linked to the initial development of cognitive, motor, and visual areas. Thus, early observed structural connectivity supposedly reflects immaturity and plays a limited role in integrative behaviour (Ganzetti & Mantini, 2013; Oldham & Fornito, 2019). However, functional connectivity networks appear to develop through childhood leading to more functional connectivity and complex processing of information (Ganzetti & Mantini, 2013). Given that optimal brain plasticity occurs in the first few months of life (Bonnier, 2008), it is possible that visual experience may accelerate the development of visual motion perception and the development of more functional connectivity in infants (Johansen-Berg & Rushworth, 2009; Kanwisher, 2010; Lamblin et al., 2017; Marek et al., 2015; Marrus et al., 2018; Varela et al., 2001).

1.4. Development of visual motion perception in normally developing infants

In response to visual motion processing, EEG studies using VEP and TSE analysis show a rapid improvement of optic flow perception during the first year of life in normally developing infants (Agyei et al., 2016b; van der Meer et al., 2008; Vilhelmsen et al., 2019). Vilhelmsen et al. (2019) found in an optic flow study on the visual discrimination between speeds and directions in infants and adults that the younger infants neither differentiated between visual motion speeds nor directions. Further, infants displayed the longest latencies in all visual motion conditions compared to adults, while the older infants displayed significantly shorter latencies for low speeds than for high speeds. The older infants also showed shorter latencies in response to forwards motion compared to reversed motion at low speed. Similar findings have been reported in other studies, where infants at 3-4 months could not differentiate between structured forwards and reversed optic flow, while 11- to 12-month-old infants could (Agyei et al., 2015; Agyei et al., 2016b). Studies investigating induced activity show that low-frequency theta-band activity is often found in younger infants at 4-5 months, while higher alpha-beta band activity is found in older infants at 8-12 months in response to visual motion stimuli (Agyei et al., 2016b; Borge Blystad & van der Meer, 2022; Rasulo et al., 2021; van der Meer et al., 2008; Vilhelmsen et al., 2019). The improvement in visual motion perception in the course of the first year of life has been attributed to the increasing maturity of visual pathways during the first year of life (Casey et al., 2000;

Chugani et al., 1996; Fields, 2008; Lebel et al., 2008) and experience with self-produced locomotion (Agyei et al., 2016b; van der Meer et al., 2008; Vilhelmsen et al., 2019).

1.5. Extra motor stimulation

Increased attention has been given to the link between locomotor experience and the development of advancing psychological functions in infancy (Anderson et al., 2013; Campos et al., 2000; Held & Hein, 1963; James & Swain, 2011; Keller et al., 2012). It has been suggested that the onset of locomotion can be accelerated with the appropriate stimulation (Zelazo et al., 1972). Extra motor stimulation is associated with less time spent in a stationary position and accelerated onset of motor behaviour such as crawling, standing, independent walking, and improved postural control (Adolph et al., 1993; Adolph & Hoch, 2019). Enriching the environment in the form of baby swimming, body massage, and other multisensory stimulation is suggested to have a positive influence on early brain development and, in particular, development of the visual system in infants (Bril & Sabatier, 1986; Guzzetta et al., 2009; Karasik et al., 2018; Lobo & Galloway, 2012; Sigmundsson & Hopkins, 2010; Super, 1976; van der Meer & van der Weel, 2020). For example, due to the anti-gravity property of water, young infants are able to experience self-produced and self-guided locomotion which is suggested to have a positive effect on the infant's cognitive and motor development (Sigmundsson & Hopkins, 2010). Considering previous research on the effect of visuomotor experience on developmental trajectories, it is plausible that extraordinary motor stimulation in forms of baby swimming and baby massage may facilitate the development of visual motion perception in infants during the first year of life.

1.6. The present study

The present study explored the effect of receiving extra motor stimulation in early infancy on the development of visual motion perception. Using longitudinal EEG data, infants receiving extra motor stimulation in the form of baby swimming and baby massage and control infants receiving a traditional Western upbringing were tested twice during the first postnatal year, before and after they had acquired self-produced locomotion. The first testing session was at 4-5 months, and the second session was at 8-12 months, after the infants had at least seven weeks of crawling experience. Analyses of VEP, time-frequency, and coherence connectivity were carried out to investigate differences in brain responses to visual motion stimuli between the two infant groups. VEPs were assumed to represent responses of cortical neurons to

changes in afferent activity (Brecelj, 2003; van der Meer et al., 2008), while event-related time-frequency responses were thought to represent interactions of local cortical neurons that control the frequency components of an ongoing EEG (Pfurtscheller & Lopes da Silva, 1999). EEG coherence connectivity was assumed to reflect structural and functional connectivity between neuronal assemblies (Bell & Fox, 1996). Based on previous EEG studies on optic flow, it was expected that perception of visual motion would rapidly improve with age and locomotor experience, observed as shorter N2 latencies for motion in the second session compared to the first session. A progression in induced activity from lower frequencies to higher frequencies was expected, in addition to an improvement in functional connectivity networks observed as more connectivity between relevant brain sources. Crucially, it was expected for infants receiving extra motor stimulation to show accelerated development of visual motion perception during the first year of life compared to traditionally-raised control infants.

2. Method

2.1. Participants

Thirty healthy, full-term infants were recruited for this longitudinal study. For recruitment of infants receiving extra motor stimulation (nine girls, six boys), parents were contacted directly at baby swimming classes at Pirbadet in Trondheim or by the snowball technique. For the control group (eight girls, seven boys), parents were contacted by following birth announcements in the newspaper or by word of mouth.

Fifteen infants were assigned to the extrastimulation group, and fifteen infants were assigned to the control group. The groups were matched according to gender, experience with self-produced locomotion, and age at the first testing session at 4 to 5 months. Experience with self-produced locomotion was defined as crawling, walking, or in any other way achieving independent locomotion, and was documented for both testing sessions. In this longitudinal design, infants were tested twice. In the first testing session, infants had no experience with self-produced locomotion, but some infants were rolling over from back to stomach. In the second session, infants had at least seven weeks of experience with self-produced locomotion.

Infants receiving extra motor stimulation were born between gestational weeks 37 and 41 and attended the first testing session at a mean age of 4 months and 25 days ($SD=35$ days). Twelve infants had already started baby swimming classes, with an average swimming experience of 2 months and 26 days ($SD=41$ days). Infants attended classes once a week, focusing on face-to-face communication in the warm water, while parents held their infant in an upright and prone position. There was also some optional diving and standing with straight legs in the instructor's hand. One infant had not attended swimming classes yet, and one infant received baby massage twice a day from birth. Finally, one infant was using "Little Climby" in addition to receiving adequate tummy-time from birth and starting baby swimming classes at 4 months. "Little Climby" is a new Norwegian brand under development that designs sustainable products for infants that stimulate the senses and early motor skills.

Eleven extrastimulated infants rolled over from back to stomach before the first testing session, while four infants had not been rolling over yet. In the second session, extrastimulated infants were on average 10 months and 6 days ($SD=51$ days) with an average of 3 months and 10 days ($SD=36$ days) of self-produced locomotor experience. Twelve infants were still attending baby swimming classes, two infants were taking up the classes

again soon, and one infant received daily baby massage twice a day until 8 months of age. The extrastimulated infants started crawling on average at 30 weeks ($SD=52$ days).

Infants in the control group who received a traditional Western upbringing spending a lot of their awake time in a supine position, were born between gestational weeks 39 and 41. They attended the first testing session on average at 4 months and 8 days ($SD=22.5$ days). Eleven infants in the control group rolled over from back to stomach before the first testing session, while four infants did not. At the second testing session, control infants were on average 11 months and 9 days ($SD=25$ days) and had on average 3 months and 23 days ($SD=39$ days) experience with self-produced locomotion. Infants in the control group started crawling at the mean age of 33 weeks ($SD=47$ days), which is on average 3 weeks later than infants receiving extra motor stimulation.

An information letter explaining the aim of the study and the possibility to withdraw from the study at any time was given to the parents to sign. EEG is a non-invasive procedure that has no harmful or painful consequences. The Norwegian Regional Ethics Committee and the Norwegian Centre for Research Data approved the study.

2.2. Experimental stimuli and design

E-prime software generated the optic flow pattern that was projected onto a large screen (108 cm wide, 70.5 cm high). Infants were seated approximately 70 cm away from the screen so that the screen subtended an angle of 71.5° by 50.4° . The optic flow experiment was presented as the last of four experiments on motion perception and occurred about fifteen minutes into the testing session. It lasted for about five minutes and comprised three visual motion conditions, i.e., forwards optic flow, reversed optic flow, and random visual motion, presented in randomized order. Each motion trial lasted for 1500 ms. The optic flow stimuli consisted of 100 black circles on a white background simulating movement in space. The dots were 5 mm in virtual radius and either increased or decreased in size at a rate of 0.025 pixels per pixel with reference to the position of the fixation point. In this way, particles appeared small when simulated far away from the eye in virtual space and big when simulated closer to the eye. When simulating forwards optic flow, the dots moved away from the centre of the screen, giving the impression of the infant moving forwards. For simulating reversed optic flow, the dots moved towards the centre of the screen, giving the impression of the infant moving backwards. When presenting random visual motion, the dots moved in random directions on the screen. A static non-flow trial lasting 1500 ms followed every motion

condition to reduce motion adaption. The static trials were also used as a control condition in the time-frequency analysis. The extrastimulated infants contributed, on average, 39 motion trials ($SD=12$) and 41 static trials ($SD=14$) in the first testing session, and 57 motion trials ($SD=16$) and 59 static trials ($SD=15$) in the second testing session. Control infants contributed, on average, 47 motion trials ($SD=10$) and 50 static trials ($SD=10$) in the first session, and 44 motion trials ($SD=13$) and 46 static trials ($SD=13$) in the second session.

2.3. Data acquisition

EEG activity was recorded using an Electrical Geodesic Inc. (EGI) sensor Net 200 (Tucker, 1993), consisting of 128 Ag/AgCl sponge sensors evenly distributed over the scalp. The net was connected to a high-input EGI amplifier set at a maximum impedance of 50 k Ω to ensure an optimal signal-to-noise ratio (Ferree et al., 2001; Picton et al., 2000). Amplified EEG signals were recorded with Net Station software on a Macintosh computer with a sampling rate of 500 Hz. To ensure that the infants were looking at the screen, an infrared Tobii X50 eye tracker monitored their gaze. Eye-tracking data were processed by Clear View software on an HP computer. Two additional digital cameras collected behavioural data during the experiment. Recorded data were further stored for offline analysis.

2.4. Procedure

The experiment was conducted at the Developmental Neuroscience Laboratory (Nu-Lab) at the Department of Psychology at the Norwegian University of Science and Technology (NTNU) in Trondheim, Norway. Parents arrived with their infant some time before the experiment so that the infant could get used to the laboratory environment. Meanwhile, parents were informed about procedures and provided information about their infant's locomotor experience. An assistant observed the infant's locomotor capabilities while the infant explored the playground and got acclimatized to the lab. The infant's head was measured to select the appropriate net which was then soaked in saline solution for a minimum of 10 minutes to ensure good impedance. The net was slightly towel-dried and gently placed on the infant's head while the infant sat on the parent's lap. Meanwhile, an assistant distracted the infant with soap bubbles and small noise-emitting toys. Parents received a digital photo of the infant wearing the net at the first testing session.

The parent carried the infant into the dimly lit experimental room, where the infant was placed in a baby car seat in front of the large screen (see Figure 1). The parent was

always seated next to the infant to ensure comfort and reduce stress. An assistant was present in the experimental room to monitor the experiment and help the infant focus on the screen. The net was connected to the amplifier, and impedance was checked. Two assistants controlled the computers with Net Station and the E-prime software in an adjoining room separated from the experimental room with a soundproof window. The infant's eye movements were calibrated to the eye tracker just before the experiment started.

The optic flow experiment was carried out in one block of approximately 3-4 minutes. In case of distress, boredom, or tiredness, the experiment was paused, and the assistant or parent would play with the infant to revive interest. The experiment ended if the infant no longer paid attention to the screen.

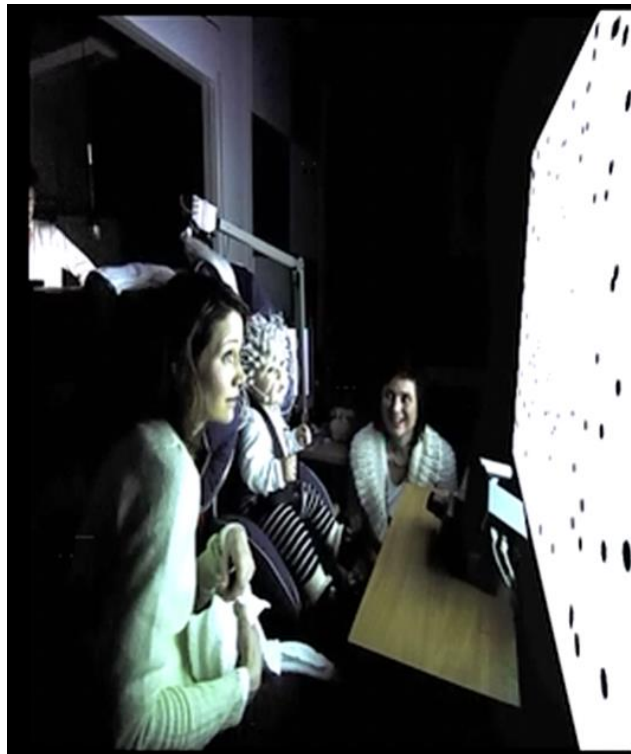


Figure 1. The experimental set-up with a 9-month-old infant secured in a baby car seat in an adjustable chair in front of a large screen. Forwards optic flow, reversed optic flow, and random visual motion is simulated by moving dots on the screen. The infant is wearing an electrode net consisting of 128 sensors. An eye tracker is placed on the desk in front of the infant to monitor gaze. An assistant from the lab is present to the infant's left to monitor the experiment and help the infant focus on the screen. The parent is always seated to the infant's right and is present during the entire session to ensure comfort and reduce stress.

2.5. Brain data analysis

EEG raw data were segmented using Net Station Tools software version 5.4.2.1 and analysed offline in Brain Electrical Source Analysis (BESA, GmbH) 6.0 research software. All data analysis was performed blind to avoid researcher bias. An assistant removed the participants' names from the segmented EEG raw data files and assigned the participant files numbers from 1 to 30. Thereafter, the files were placed in either "group 1" or "group 2", one group including extrastimulated infants and the other group including control infants. Analysis procedures remained the same for all participants and both testing sessions.

Averaging epochs were set from -200 to 800 ms, with a baseline definition set at -100 to 0 ms. A low cut-off filter was set at 1.6 Hz to remove slow drift from the data, and a high cut-off filter was set at 60 Hz to remove channels contaminated with high-frequency activities. The notch filter was set at 50 Hz to avoid line interference. Artefact-contaminated channels caused by eyeblinks or head- or body movements were visually inspected and either removed from further analysis or re-estimated using spherical spline interpolation (Perrin et al., 1989). A manual artefact correction was designed with spatial filters (Berg & Scherg, 1994) to separate brain activity from eye movement artefacts. Threshold values for gradient and low signal were set at 75 μV and 0.1 μV , respectively, and the maximum amplitude value was set at 200-300 μV .

Participants with more than 10% bad channels or less than 50% accepted trials were excluded from further analysis. Two participants, one extrastimulated infant and one control infant, did not meet these criteria and were therefore excluded from further analysis.

2.6. VEP peak analysis

VEP peak analysis at electrode level was carried out to investigate VEP responses. Individual EEG data were averaged and interpolated to a standard 81-electrode configuration of the 10-10 international standard system (Perrin et al., 1989; van der Meer et al., 2008). The individual averages were then combined into a grand average and used as a reference while selecting individual N2 components. 3D spline whole-head voltage maps were used to visually identify the N2 components of the individual averages over occipital areas. Values for peak latencies and peak amplitudes of the individual averages were recorded. Peak latencies were measured from stimulus onset to the peak of scalp N2 component, while peak amplitudes represented maximum amplitudes of the N2 components relative to the pre-stimulus baseline. Latencies were computed and subjected to further analysis.

2.7. Time-frequency analysis in brain space

In addition to VEP peak analysis, time-frequency analysis was carried out to investigate amplitude changes over time. Focal brain activity generates a widespread EEG voltage pattern, making it difficult to interpret findings of significant coherence between electrodes. To reduce this problem, source coherence was used by applying a filter based on a discrete multiple source model (Figure 2) as obtained by brain electrical source analysis (BESA) (Bornfleth et al., 2020). In the first step of source coherence analysis, a distinct multiple source model was made by transforming recorded surface EEG activity into brain space. As a result, single-trial data were converted from channel space into brain source space and further transformed into time-frequency space to calculate the amplitude and phase of each brain activity as a function of frequency and latency (Bornfleth et al., 2020). The change of power (=squared envelope amplitude) of each source with reference to the baseline was averaged over trials and displayed as a function of frequency and latency in event-related (de)synchronisation plots (ERD/ERS) (Pfurtscheller & Lopes da Silva, 1999). ERD/ERS illustrates the increase or decrease of activity in the time-frequency domain for each modelled brain region separately (Bornfleth et al., 2020). In the last step, TSE plots with desynchronisations/synchronisations were computed from the obtained source waveforms to determine the strength of coupling between the modelled brain regions (Hoechstetter et al., 2004).

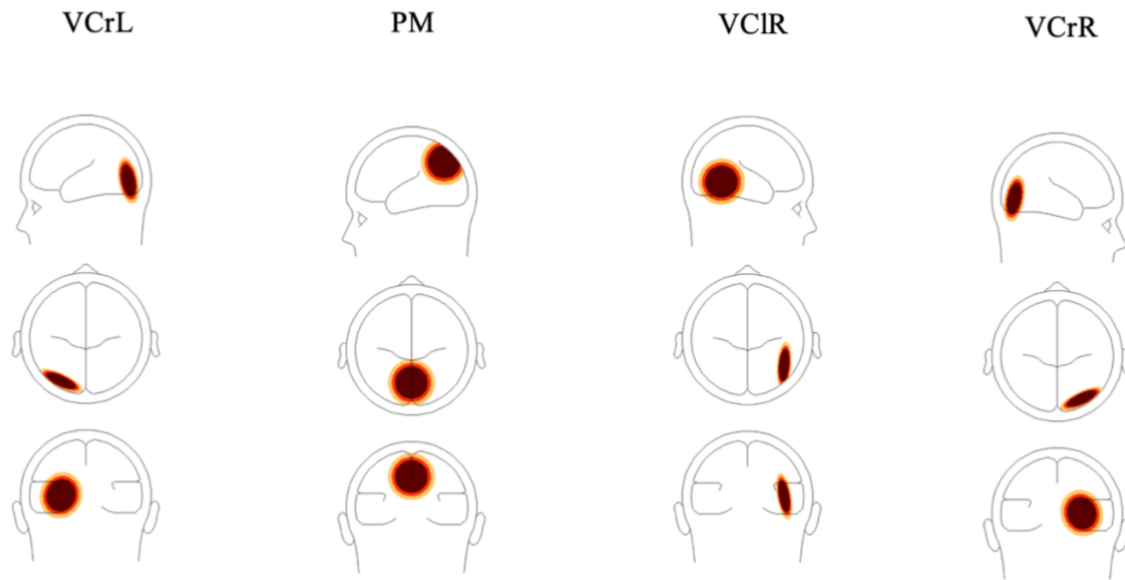


Figure 2. Head model of associated brain sources in the visual cortical areas of interest. From left to right: visual cortex radial left (VCrL), parietal midline (PM), visual cortex lateral right (VCIR), and visual cortex radial right (VCrR).

As recommended for infants, bone thickness was adjusted to 3 mm and conductivity to 0.02σ (Grieve et al., 2003). Epoch settings remained the same as VEP peak analysis, set at -200 ms to 800 ms. A low cut-off filter at 1.6 Hz, a high cut-off filter at 60 Hz, and a notch filter were set at 50 Hz. TSE displays were set from 2-40 Hz, and time samples were set at 1-50 ms. All thresholds and filters were the same for all participants in both groups, and the individual artefact corrected coordinate files were added for each participant.

BESA Statistics 2.0 was used for statistical comparisons of TSE source data. Because the evoked activity had already been analysed in the VEP analysis, regression analysis was carried out to remove the evoked activity from the data. Then, only induced activity remained and was used for further analysis. In the first step, a preliminary parametric statistics test was run to retrieve a preliminary statistical comparison between groups or conditions for cluster building (Bornfleth et al., 2020). Because of the multiple comparison error, a permutation test was followed to test for significant differences between the mean of two groups/conditions (Bornfleth et al., 2020). Cluster alpha, which determines the significance level for building clusters in time and frequency, was set to 0.05, and the number of permutations was set at maximum possibilities. In this way, all possible permutations were automatically computed.

Paired sample t-tests were carried out to compare the three motion conditions to static non-flow for both infant groups in each testing session. Unpaired sample t-tests were conducted to test for differences between motion condition and static non-flow between groups.

2.8. Coherence connectivity analysis

The computed time-frequency data were further used to investigate the functional connectivity between the visual areas of interest in extrastimulated infants and control infants. Using coherence connectivity analysis, we can identify the activity of neuronal networks and the connectivity between them during visual motion and static non-flow. TSE displays remained the same as in TSE-analysis, with the display set at 2-40 Hz, and time samples were set at 1-50 ms. EEG coherence analysis was performed in BESA Connectivity 1.0 using the coherence method separately for all participants in both groups. Coherence is a measure of linear covariance between two signals in a particular time-frequency bin. Hence, the coherence analysis describes the number of in-phase components of two brain source signals at a specific frequency (Bell & Fox, 1996).

T-tests were carried out in BESA Statistics 2.1 to test for the probability of significant coherence clusters between motion and the static control condition, followed by permutation tests. Paired sample t-tests were conducted to compare motion to static in each group and session. Unpaired sample t-tests were carried out to test for the probability of significant connectivity between the extrastimulated infants and the control infants in each session separately.

3. Results

3.1. VEP-analysis

Four channels from the VEPs grand average were selected based on the highest grand-averaged N2 peak amplitude in forwards optic flow. POz, PO4, Oz, and O2 were selected for both groups and sessions. Grand averaged latencies were identified and used as a guide to identify the individual N2 component for each participant in each session. As displayed in Figure 3, mean latencies for extrastimulated infants in the first session at 4-5 months for forwards optic flow were 369 ms ($SD=60$), for reversed optic flow 393 ms ($SD=69$), and for random visual motion 386 ms ($SD=76$). For control infants, mean latencies in the first session were for forwards optic flow 411 ms ($SD=47$), for reversed optic flow 424 ms ($SD=55$), and for random visual motion 424 ms ($SD=98$). In the second session, mean latencies reduced for the extrastimulated infants to 213 ms ($SD=63$) for forwards optic flow, to 285 ms ($SD=57$) for reversed optic flow, and to 274 ms ($SD=70$) for random visual motion. Mean latencies reduced for control infants to 325 ms ($SD=94$) for forwards optic flow, to 344 ms ($SD=68$) for reversed optic flow, and to 343 ms ($SD=77$) for random visual motion.

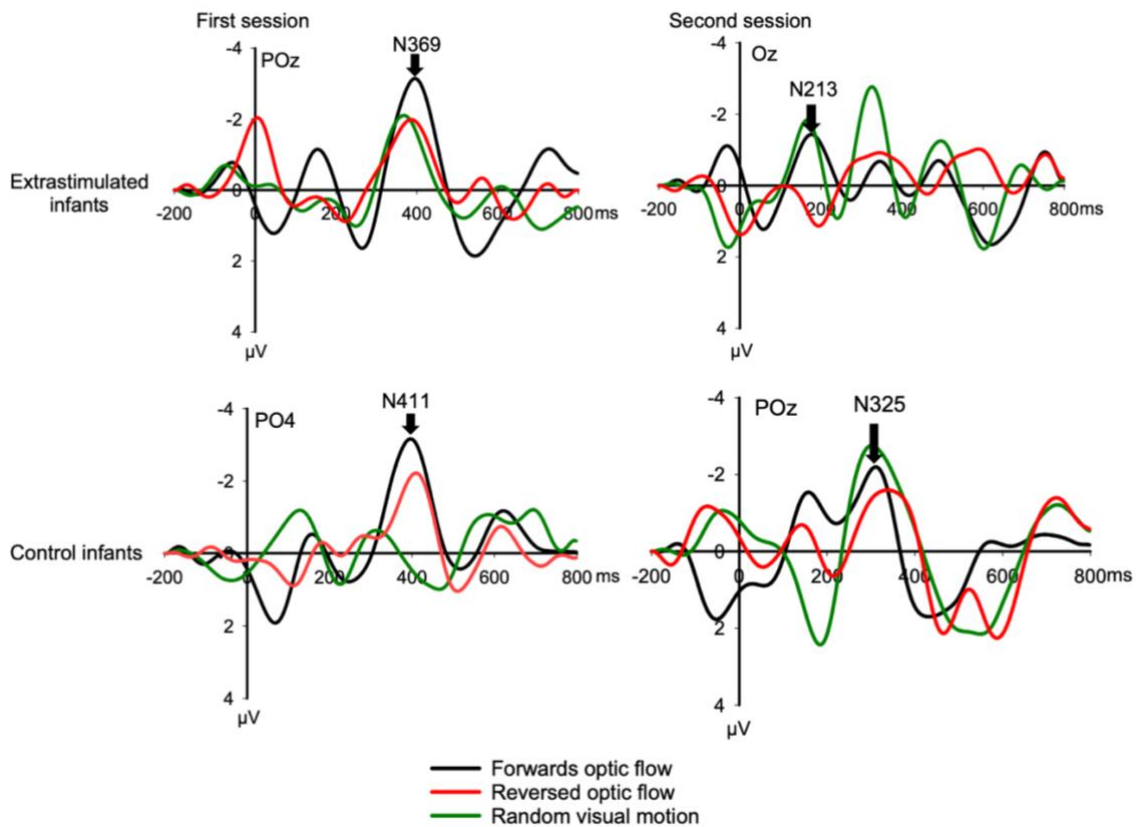


Figure 3. Grand averaged motion VEPs with epoch set from -200 to 800 ms. Amplitudes (μV) on the y-axis and latencies (ms) on the x-axis. From left to right and top to bottom: grand averaged VEPs in extrastimulated infants in the first (POz) and second (Oz) session, and control infants in the first (PO4) and second (POz) session. Vertical arrows indicate actual grand averaged peak N2 latencies for forwards optic flow. For extrastimulated infants, peak latency was reduced by 156 ms from 369 ms in the first session to 213 ms in the second session. Peak latency for control infants was reduced by 86 ms from 411 ms in the first session to 325 ms in the second session.

Latency values from the electrode with the highest N2 amplitude for forwards optic flow were selected and used in a subsequent ANOVA with Bonferroni correction to adjust for multiple comparisons. Latency values were selected from one of the four grand averaged channels (POz, PO4, Oz, and O2). The selected electrode varied between infants and sessions but remained the same for all three motion conditions in each participant. Repeated measures analysis of variance (ANOVA) tested for differences in N2 peak latency (Figure 4). Motion condition (forwards optic flow, reversed optic flow, and random visual motion) and testing session (session 1 and 2) were within-group factors, and group (extrastimulated infants and control infants) was the between-group factor.

A main effect for testing session was found, $F(2,26)=57.19$, $p<0.001$, indicating that latency decreased significantly with age from session 1 to session 2. Corresponding post hoc analysis confirmed a significant reduction in latency from session 1 to session 2 by, on average, 104 ms ($SD= 13.7$), $p<0.001$.

Furthermore, a significant main effect was found for motion condition, $F(2,25)=4.5$, $p<0.05$, indicating an overall significant increase in latencies from forwards optic flow, to reversed optic flow, and to random visual motion. Corresponding post hoc analysis confirmed a significantly shorter latency for forwards optic flow than reversed optic flow of, on average, 32 ms ($SD=11$), $p<0.05$.

Last but not least, a significant difference in latencies was found between extrastimulated infants and control infants, $F(1,26)=18.48$, $p<0.001$, showing significantly shorter overall latencies in response to visual motion for the extrastimulated infants than control infants by 58 ms ($SD=12.6$), $p<0.001$ in response to visual motion in both sessions combined.

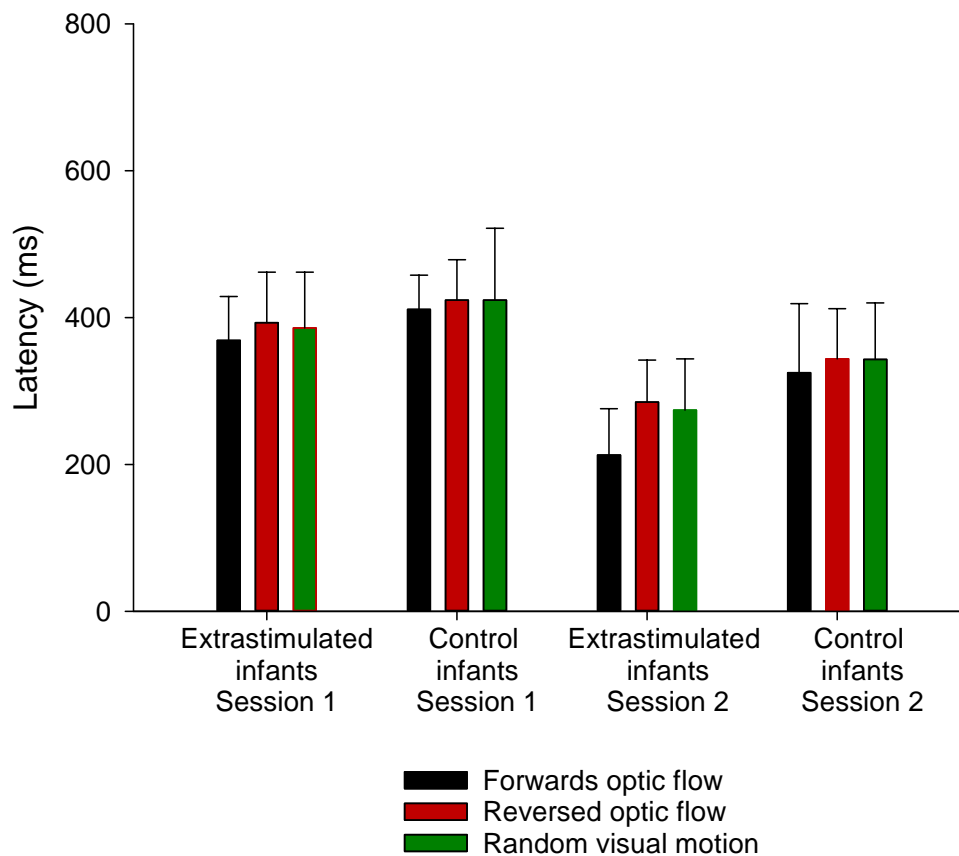


Figure 4. Illustration of group means with standard deviations of N2 peak latencies for extrastimulated infants and control infants in session 1 and 2. Motion conditions are visualised in colours, with forwards optic flow (**black**), reversed optic flow (**red**), and random visual motion (**green**). A significant main effect for session was found, $F(2,26)=57.19$, $p<0.001$, indicating that latency decreased from session 1 to session 2 for both extrastimulated and control infants. Corresponding post hoc analysis confirmed a significant reduction in N2 latencies for motion with age of just over 100 ms, $p<0.001$. A significant main effect was also found for visual motion condition, $F(2,25)=4.5$, $p<0.05$, indicating a significant increase in latencies from forwards optic flow, to reversed optic flow, and to random visual motion. Finally, extrastimulated infants showed significantly shorter latencies in response to visual motion than control infants, $F(1,26)=18.48$, $p<0.001$, by 58 ms on average.

3.2. Time-frequency analysis

Time-frequency analysis was carried out for the three visual motion conditions, with static non-flow serving as control condition. The permutation test showed no significant differences in data clusters between the three motion conditions when comparing forwards optic flow, reversed optic flow, and random visual motion. Thus, the three motion conditions were combined into one “motion” condition and compared to static non-flow. Figure 5 shows the permutation test results when combined motion was compared to static non-flow. Significant negative clusters ($p<0.05$) were found between motion and static non-flow in at least one of four visual areas of interest in both groups and sessions, indicating significantly lower amplitudes for combined motion than for static non-flow. In the first session, significant negative clusters ($p<0.05$) were observed in the theta-band in both extrastimulated infants and control infants (Fig. 5A and B). In the second session, significant negative clusters ($p<0.05$) was observed in the theta- and alpha-band in the extrastimulated infants (Fig. 5C). Theta-band activity was observed in the control infants (5D), whereas the activity appeared over a shorter period of time compared to the first session.

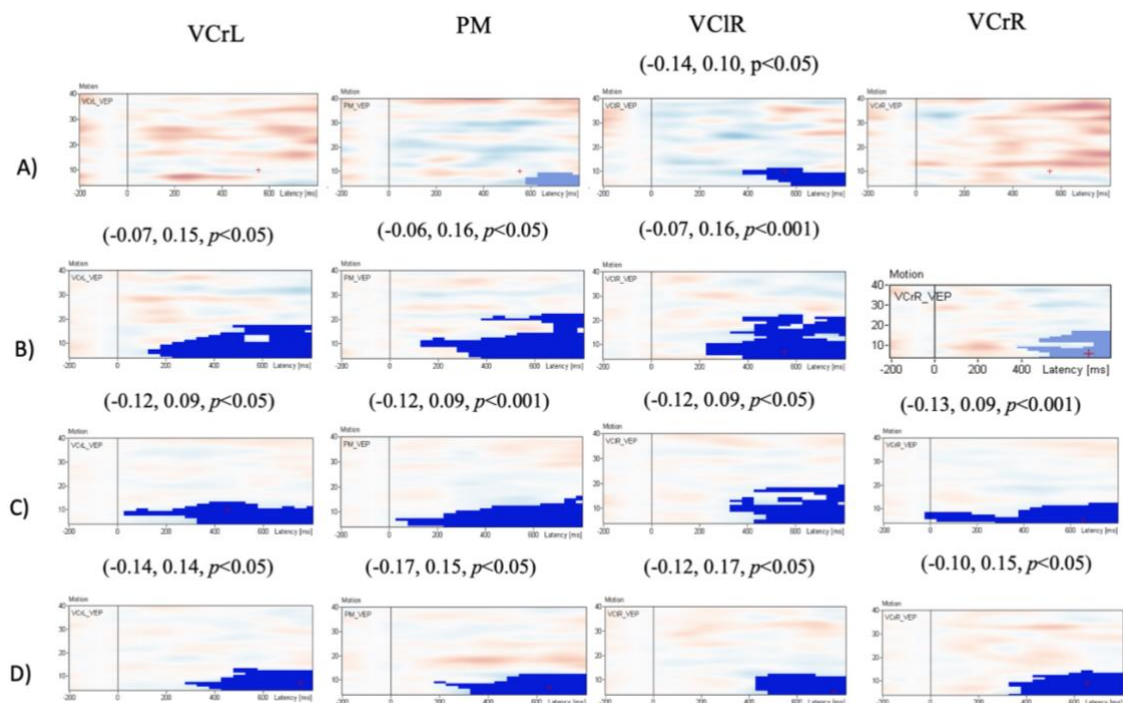


Figure 5. TSE probability maps ($p<0.05$) in sources VCrL, PM, VCIR, and VCrR represent averaged visualization of significant data clusters when visual motion was compared to static non-flow for extrastimulated infants in first (A) and second (C) session and for control infants in first (B) and

second (D) session. The vertical line marks stimulus onset at 0 ms. Epoch is set from -200 to 800 ms, with a baseline from -100 to 0 ms. Blue areas indicate significant negative clusters (i.e., combined motion has significantly smaller t -values than the static control condition), and red areas indicate significant positive clusters (i.e., combined motion has significantly higher t -values than the static control condition). Significant t -values are presented in parentheses. Significant negative clusters ($p < 0.05$) in the theta-band were found in each group and session (A to D) in at least one of four visual areas of interest. Extrastimulated infants also displayed alpha-band activity in the second session (C). Control infants displayed more widespread activity in the first session (B) compared to the second session (D).

Desynchronised oscillatory activity appears in TSE plots for both groups in both sessions (Figures 6A to D) in response to motion stimuli. In the first session, desynchronised theta-band activity appears for both extrastimulated and control infants (Fig. 6A and B). The activity is more widespread in control infants (Fig. 6B) than in extrastimulated infants (Fig. 6A). In the second session, desynchronised activity in the alpha-band range appears for both groups (Fig. 6C and D), although, extrastimulated infants also show expressions of beta-band activity (Fig. 6C). The activity occurs in relatively shorter periods in the second session (Fig. 6C and D) compared to the first session (Fig. 6A and B).

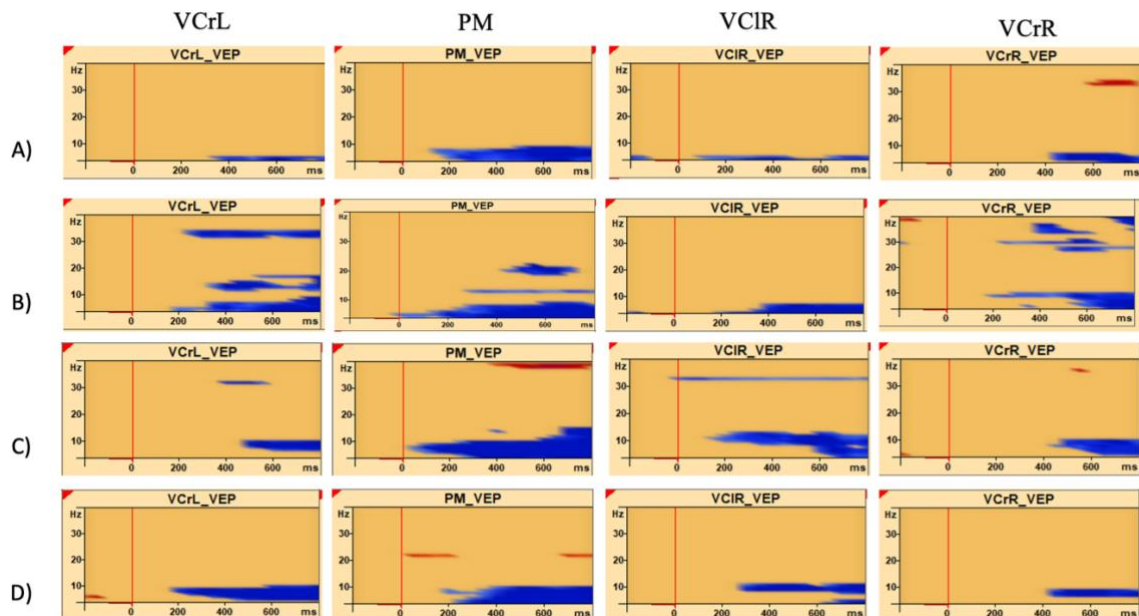


Figure 6. TSE plots of the visual areas of interest VCrL, PM, VCIR, and VCrR when combined motion was compared to static non-flow. TSE plots shows extrastimulated infants in the first (A) and second (C) session and control infants in the first (B) and second (D) session. The vertical red line

marks stimulus onset at 0 ms. The settings remained the same as in the TSE probability maps, with the epoch set from from -200 to 800 ms and the baseline from -100 to 0 ms. Induced synchronised activity is shown in red and desynchronised activity is shown in blue. Induced theta-band desynchronisation is prominent in both groups in the first session (A and B). However, control infants (B) exhibits more widespread activity than extrastimulated infants. In the second session, desynchronised alpha-band activity is prominent in both infant groups (C and D). Extrastimulated infants also showed expressions of beta-band activity in the second session (C). For both infant groups, oscillatory activity appears in relatively shorter periods in the second session (C and D) compared to the first session (A and B).

3.3. Coherence connectivity analysis

An EEG coherence connectivity analysis was carried out to identify the connectivity between neural networks during visual motion perception compared to static non-flow (Figure 7). For extrastimulated infants in the first session, significant coherence clusters was found between brain sources VCrL and VCIL ($p < 0.001$), VCrL and PM ($p < 0.05$), and VCIL and VCIR ($p < 0.05$), indicating greater coherence during visual motion perception compared to static non-flow. In the second session, significant coherence clusters was observed between brain sources VCIL and VCIR ($p < 0.001$), VCrR and VCbL ($p < 0.01$), VCrL and VCrR ($p < 0.01$), VCbL and VCIR ($p < 0.05$), and VCrL and VCIL ($p < 0.05$). Significant coherence clusters in the control infants in the first session was found between VCrL and PM ($p < 0.05$) and VCbR and VCIR ($p < 0.05$). In the second session, one significant coherence cluster was found between brain sources VCIL and CM ($p < 0.001$). Extrastimulated infants indicate greater coherence connectivity compared to control infants at 8-12 months.

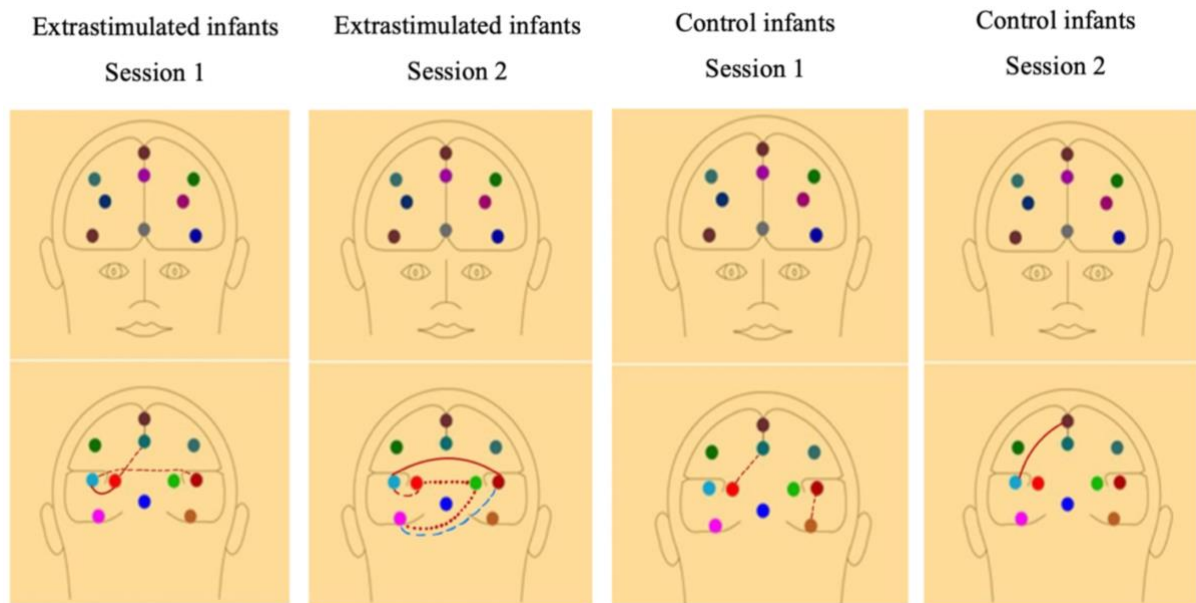


Figure 7. Head model with virtual brain sources **PM**, **VCIL**, **VCIR**, **VCrL**, **VCrR**, **VCbL**, **VCbR**, and **CM**, showing significant coherence clusters when combined motion was compared to static non-flow. Significant coherence at $p < 0.001$ marked with a solid line, $p < 0.01$ marked with dots, and $p < 0.05$ marked with straight dashes. Red lines indicate significantly higher t -values for motion than static, while blue lines indicate significantly lower t -values for motion than static. From left to right: significant coherence clusters was found in the extrastimulated infants in the first session between brain sources **VCrL** and **VCIL** (0.46, 0.36, $p < 0.001$), **VCrL** and **PM** (0.32, 0.19, $p < 0.05$), and **VCIL** and **VCIR** (0.50, 0.42, $p < 0.05$), indicating greater coherence during visual motion perception compared to static non-flow. Extrastimulated infants in the second session showed significant coherence clusters between brain sources **VCIL** and **VCIR** (0.48, 0.39, $p < 0.001$), **VCrR** and **VCbL** (0.36, 0.28, $p < 0.01$), **VCrL** and **VCrR** (0.33, 0.26, $p < 0.01$), **VCbL** and **VCIR** (0.34, 0.43, $p < 0.05$), and **VCrL** and **VCIL** (0.17, 0.27, $p < 0.05$). Control infants in the first session showed significant coherence clusters between sources **VCrL** and **PM** (0.31, 0.22, $p < 0.05$) and **VCbR** and **VCIR** (0.41, 0.33, $p < 0.05$). In the second session, only one connection was found between **VCIL** and **CM** (0.37, 0.26, $p < 0.001$). t -values are represented in parenthesis. These results indicate greater coherence in extrastimulated infants compared to control infants at 8-12 months.

4. Discussion

The present longitudinal study investigated the effects of receiving extra motor stimulation on the development of visual motion perception during the first year of life. Infants receiving extra motor stimulation in the form of baby swimming or baby massage and infants receiving a traditional Western upbringing were tested twice during the course of the first year of life. The first testing session was at 4-5 months with no experience with self-produced locomotion and the second testing session at 8-12 months with acquired self-produced locomotion. High-density EEG was used to observe cortical electrical activity as a perceptual response to structured optic flow (forwards and reversed) and random visual motion. Motion-specific N2 components of VEP waveforms were compared, with induced activity and coherence connectivity further analysed to investigate differences in cortical responses to visual motion stimuli.

4.1. Evoked responses to visual motion

The results of the VEP analysis showed an overall enhancement in latencies in extrastimulated infants compared to control infants in the course of the first year of life. In the first testing session at 4-5 months of age, extrastimulated infants showed slightly faster N2 latencies by, on average, 42 ms than control infants. In the second session at 8-12 months, extrastimulated infants showed overall shorter latencies by, on average, 112 ms than control infants. Both extrastimulated and control infants showed significantly shorter latencies in the second session than the first session, with the shortest latencies for forwards optic flow.

The observed improvement in overall N2 latency from 4-5 to 8-12 months corroborates previous longitudinal studies demonstrating that normally developing infants show faster responses to visual motion towards the end of the first postnatal year (Agyei et al., 2015; Rasulo et al., 2021; Vilhelmsen et al., 2019). These improvements are likely related to maturation of visual pathways causing more efficient processing of visual information. During the first year of life, an increase in glucose metabolic rate occurs in the posterior and temporal areas (Chugani et al., 1996), causing more efficient visual information processing (Vilhelmsen et al., 2019). At 4-6 months, infants show a peak of synaptogenesis, especially in the primary visual cortex, with a rapid formation and overproduction of cortical synapses during the first two years of life (Casey et al., 2000). Also, axonal pruning and white matter myelination during early development leads to more efficient network connections (Fields, 2008; Lebel et al., 2008). Thus, the rapid ongoing development in functional networks in

infancy could explain the faster processing of visual information in infants at 8-12 months in the present study.

Evidence suggests that functional detection of optic flow develops hand-in-hand with self-produced locomotion (Agyei et al., 2015; Anderson et al., 2013; Campos et al., 2000; Vilhelmsen et al., 2019). Held and Hein (1963) demonstrated in an experiment on visually-guided behaviour in kittens the importance of self-produced locomotion, where kittens who did not have the opportunity for active locomotion showed an abnormal development. Soon after birth, infants start to passively explore the environment either in a stroller or being carried by their caregivers until they can crawl or walk independently (Agyei et al., 2015). Considering passive exploration of the environment, a minimum level of improvement of sensitivity to optic flow has been observed between 3 to 6 months of age (Gilmore et al., 2004; Gilmore et al., 2007), as infants are experiencing directions chosen by their caregivers (Anderson et al., 2013). In contrast, with self-produced locomotion, infants voluntarily move the head and eyes to consistently point straight ahead, which allows them to make better use of optic flow information for navigating in the environment (Agyei et al., 2015; Anderson et al., 2013; Gibson, 1979/2015; Vilhelmsen et al., 2019).

Based on a series of classical animal studies, there is knowledge that cortical representations are dynamic and continuously modified by experience, which studies in humans support and complement. Previous findings suggest that infants show a preferential sensitivity to expanding stimuli compared to contracting stimuli (Giaschi et al., 2007; Gilmore et al., 2007; Shirai et al., 2009). In fact, infants in the present study appeared to show faster responses when perceiving forwards optic flow than reversed optic flow and random visual motion. Because humans typically move in forward direction, the acquired experience may develop accordingly, with a preference for expanding stimuli (Agyei et al., 2015; Shirai et al., 2009; van der Meer et al., 2008). Thus, experience from self-produced locomotion affords infants the ability to make better use of the information embedded in optic flow. Functional perception of structured radial flow have been found to develop with independent locomotion (van der Meer et al., 2008), with self-generated actions leading to a strong link between perception and action in the developing brain (James & Swain, 2011). Evidence is clear that experience produces multiple, dissociable changes in the brain, including dendritic length, increase in spine density, synapse formation, increased glial activity, and altered metabolic activity (Kolb & Whishaw, 1998). Considering the fact that brain plasticity has a foundational effect on the development of skills (Fox & Rutter, 2010; Kolb & Whishaw, 1998), it is plausible that, in addition to maturation, the active self-locomotion acquired by the older

infants may have led to faster recruitment and activation of neural networks responsible for motion recognition compared to the younger infants who passively experience the environment.

Nonetheless, in the present study, the extrastimulated infants showed significantly shorter latencies in response to visual motion compared to control infants by, on average, 58 ms shorter latencies in both sessions combined. Further, extrastimulated infants showed, on average, 42 ms shorter latencies than control infants in the first session and, on average, 112 ms shorter latencies than control infants in the second session. Hence, other external factors may influence the development of visual motion perception. In the context of motor development, Western cultures often proclaim infants to be fragile and in need of gentle handling, while some non-Western cultures believe that rough handling is necessary for healthy motor development (Adolph et al., 1993). For instance, Kenyan mothers believe they have to teach their children the most crucial motor milestones such as sitting, standing, and walking from birth (Super, 1976). Likewise, in Mali in West Africa, parents manipulate infants' arms and legs, use massage techniques, and both arms and legs are being stretched from an early age (Bril & Sabatier, 1986). In contrast, in Tajikistan and other parts of central Asia, infants are given minimal possibilities for movement, with a traditional child-rearing practice called gahvora cradling (Karasik et al., 2018). A traditional view in Europe is that infants are born with an underdeveloped brain and that early stimulation can be dangerous for the infant's physical development (van der Meer & van der Weel, 2020). Therefore, European caregivers are careful not to overstimulate their infants.

Enriched stimulation in early infancy has proven beneficial for facilitating brain development and, in particular, visual development (Guzzetta et al., 2009). Likewise, Lobo and Galloway (2012) found that infants receiving extra motor handling and positioning had richer perceptual-motor history than traditionally raised infants. This is in line with results in the present study where, interestingly, the extrastimulated infants were, on average, four weeks younger than control infants at the second testing session (8-12 months). Extra motor stimulation is associated with less time spent in a stationary position and accelerated onset of motor behaviour such as crawling, standing, independent walking, and improved postural control (Adolph et al., 1993; Adolph & Hoch, 2019). Baby swimming and baby massage include activities that are not typical for traditional Western upbringing, where infants spend considerable time placed in a supine position. With extra motor stimulation, infants are likely more experienced in processing different visual motion patterns than their peers because of more opportunities to interact with their surroundings (Guzzetta et al., 2009). Also, parents

who take their newborns to baby swimming classes or baby massage may, in general, provide a more stimulating motor environment. Extra motor stimulation may generate more opportunities for self-motion and accelerated brain development leading to faster responses to motion stimuli. Thus, extra motor stimulation may indirectly affect the development of visual motion perception observed in the improved brain responses to motion stimuli in the extrastimulated infants compared to the control infants.

4.2. Induced responses to visual motion

Investigating induced activity in the time-frequency domain, desynchronised oscillatory activity was found in motion processing compared to synchronised oscillatory activity observed in static non-flow. This finding is consistent with previous studies suggesting that desynchronised activity reflects aspects of visual motion processing (van der Meer et al., 2008). Furthermore, Pfurtscheller and Lopes da Silva (1999) proposed that task complexity contributes to enhancing theta desynchronisations. It is possible that during perception of the static dot pattern, neuronal assemblies may have fired in synchrony and that this synchronised activity was suppressed when motion stimuli were presented, resulting in the observed desynchronisation.

Infants in the present study showed desynchronised theta-band activity in the first session, while desynchronised alpha-band activity in the second session. Also, the extrastimulated infants showed expression of beta-band activity at 8-12 months. This finding corroborates previous studies that have found infant EEG to be dominated by low-frequency activity with larger amplitudes during the processing of visual motion (Agyei et al., 2015; Agyei et al., 2016b; van der Meer et al., 2008; Vilhelmsen et al., 2019). Amplitudes reflect the number of neurons firing in synchrony, and slowly oscillating cell assemblies are usually composed of more neurons than faster oscillating assemblies (Elul, 1972; Pfurtscheller & Lopes da Silva, 1999). The low-frequency theta-band activity in the younger infants could suggest the recruitment of more extensive neuronal networks during the processing of visual motion, which is a general indication of the involvement of less specialized cortical networks in motion information processing in infancy, that have been interpreted as signs of immaturity.

Evidence from EEG studies shows that infant oscillatory activities in response to visual motion progress from lower to higher frequencies in the first postnatal year (Agyei et al., 2015; Agyei et al., 2016b; van der Meer et al., 2008; Vilhelmsen et al., 2019). Vilhelmsen

et al. (2019) found in an EEG study on optic flow perception that adults displayed beta-band activity in response to visual motion, which have been attributed to a fully developed visual perceptual system. Furthermore, faster oscillating alpha-band activities in older infants give credence to the emergence of more specialized functional neuronal networks within the visual areas when processing motion information (Agyei et al., 2015). Given the acquired experience with self-produced locomotion in the second session, the progression from low-frequency theta-band activity to higher-frequency alpha-band activity may be apparent as infants develop more specialised visual perceptual systems. Moreover, expressions of beta-band activity observed in the extrastimulated infants at 8-12 months may indicate a more developed visual perceptual system compared to control infants resulting from the early motor stimulation. This finding could further explain the significantly shorter latencies in the extrastimulated infants for VEPs in the older infants.

4.3. Coherence connectivity in brain sources

Physiological, neuropsychological, and neuroimaging studies have revealed that functional specialization and integration are two distinct yet coexisting principles of human brain organization (Corbetta, 2012; Friston, 2002; Ganzetti & Mantini, 2013). Perception, thoughts, emotions, and actions are more likely to emerge from interactions between neuronal assemblies distributed across the brain than from local computations in restricted brain areas (Bullmore & Sporns, 2012; Engel et al., 2001; Tononi, 2004). Results from the present coherence connectivity analysis revealed that although some significant coherence was observed in both groups and sessions, extrastimulated infants showed a greater amount of significant coherence between the different brain sources in the visual areas of interest compared to control infants. This finding was especially prominent in the second session at 8-12 months. The human brain undergoes profound neuronal changes during the first two decades of life (Oldham & Fornito, 2019), and neuronal connectivity parallels the maturation of social, cognitive, and motor skills from birth to younger adulthood (Lamblin et al., 2017; Marek et al., 2015; Marrus et al., 2018). Previous findings suggest that structural connectivity is present from a very early age and that the location is consistent throughout development (Oldham & Fornito, 2019). The observed connectivity in the first session at 4-5 months in the present study may reflect the early structural connectivity that is found to be established before birth.

Functional connectivity is constrained but not completely determined by structural connectivity (Oldham & Fornito, 2019). Given that structural connectivity is present from birth, it seems plausible that control infants have not yet developed the functional connectivity necessary for effective visual motion processing, as observed in relatively few significant connections. Moreover, extrastimulated infants showed increased functional connectivity in the second session at 8-12 months. Previous studies suggest that beta-band activity may be important for cross-network functional connectivity and may consolidate and link actions across wide areas of the brain. Although the function of an area is highly specialized (Ganzetti & Mantini, 2013; Kanwisher, 2010), the information it processes is dependent on its precise connections with other parts of the brain (Johansen-Berg & Rushworth, 2009; Varela et al., 2001). For successful navigation in the environment, we need to process visual information in relation to the self, which requires efficient systems for integrating visual information with information from our joints, muscles, and the vestibular system to give the appropriate motor output (van der Meer et al., 2008). Since functional connectivity is thought to develop with experience, active exploration of the environment may accelerate the development of functional connectivity networks involved in visual motion processing. Considering the greater connectivity observed in the extrastimulated infants at 8-12 months, early motor stimulation may account for accelerated functional connectivity.

5. Conclusion

In conclusion, the present longitudinal study demonstrated a strong link between receiving extra motor stimulation in early infancy and accelerated development of visual motion perception observed in VEPs, TSEs, and coherence connectivity. During the first year of life, extrastimulated infants showed greater sensitivity to visual motion compared to traditionally-raised control infants, as reflected by shorter latencies in response to motion stimuli and oscillatory activity at higher frequencies. In addition, increased connectivity was observed in extrastimulated infants at 8-12 months, indicating more developed functional networks involved in visual motion processing. The greater improvement observed in extrastimulated infants was attributed to their caregivers' overall handling patterns, including enriched motor activities such as baby swimming and body massage, resulting in accelerated brain development for visual motion perception compared to control infants.

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