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Extra Motor Stimulation and the Development of Optic Flow Perception in Infancy: A High-Density EEG Study

Master's thesis in Psychology

Supervisor: Audrey van der Meer

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Table of Contents

1. ACKNOWLEDGEMENTS	
2. ABSTRACT	
3. INTRODUCTION.....	1
4. METHODS.....	8
2.1 Participants	8
2.2 Optic Flow Stimuli	9
2.3 Data Acquisition.....	10
2.4 Procedure.....	10
2.5 Data Analysis	11
2.6 Artefact Removal	12
2.7 Peak Analysis at the Electrode Level.....	12
2.8 Time-frequency Analysis in Brain Space.....	12
3. RESULTS.....	15
3.1 VEP Responses	15
3.1.1 VEP Analysis	16
3.2 TSE Analysis.....	20
4. DISCUSSION	28
REFERENCES.....	37
APPENDICES.....	53
Appendix A	53

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Abstract

High-density electroencephalogram (EEG) was used for examining whether receiving extra motor stimulation during the first year of life facilitates the development of visual motion perception. Infants receiving extra motor stimulation (5 boys, 5 girls) and infants receiving a traditional Western upbringing (5 boys, 5 girls), were presented with an optic flow paradigm at 3–5 months of age, and then again at 8–12 months of age. The optic flow experiment comprised three different visual motion conditions simulating forwards optic flow, reversed optic flow, and random visual motion. EEG data was recorded using a 128-channel sensor array and subjected to analyses of visual evoked potentials (VEPs) and temporal spectral evolution (TSE – time dependent amplitude changes). For VEPs, traditionally-raised infants were not able to differentiate between motion conditions in the first session, but had significantly shorter latencies for structured optic flow (forwards optic flow and reversed optic flow) than for random visual motion in the second session. Extra-stimulated infants significantly differentiated between structured optic flow and random visual motion already in the first testing session, and processed structured optic flow significantly faster than they did random visual motion. In the second session, extra-stimulated infants significantly discriminated between each of the three motion conditions, with the shortest latencies observed for forwards optic flow, followed by reversed optic flow, and the longest for random visual motion. In addition, VEP results revealed overall latencies to be significantly shorter for extra-stimulated infants than for traditionally-raised infants across testing sessions. TSE results when comparing the three motion conditions with static non-flow revealed traditionally-raised infants' induced responses to be dominated by desynchronised activities in the theta frequency range in the first testing session, followed by an increase in desynchronised activities in the alpha frequency range in the second session. TSE maps of extra-stimulated infants revealed oscillatory activities in the theta frequency range in the first session, and oscillatory activities at higher frequencies in the alpha-beta frequency ranges in the second session. It was concluded that while the developmental progression observed in traditionally-raised infants could be attributed to neural maturation and onset of self-produced locomotion, extra motor stimulation was likely to have contributed to accelerated development of visual motion perception in extra-stimulated infants. Further research is warranted for examining the association between extra motor stimulation and development of visual motion perception in infancy.

Sammanfattning

Denna studie använde sig av elektroencefalogram (EEG) för att undersöka huruvida extra motorisk stimulering faciliterar utvecklingen av rörelseperception hos spädbarn. Spädbarn som mottagit extra motorisk stimulering (5 pojkar, 5 flickor) och spädbarn som mottagit en traditionell Västerländsk uppfostran (5 pojkar, 5 flickor), presenterades med ett optiskt flödeparadigm först vid 3–5 månaders ålder, och därefter vid 8–12 månaders ålder. Det optiska flödes-experimentet bestod av tre visuella rörelsebetingelser som simulerade framåt optiskt flöde, omvänd optiskt flöde och slumpmässig visuell rörelse. EEG-data registrerades med hjälp av 128 sammansydda elektroder jämnt fördelade på spädbarnets skalp, och utsattes för analyser av visuella framkallade potentialer (VEP) och tidsmässig spektral utveckling (TSE – amplitudförändringar över tid). VEP-resultat visade att traditionellt uppfostrade spädbarn var oförmögna att skilja mellan de tre rörelsebetingelserna vid den första test-sessionen, men skiljde signifikant mellan strukturerat optiskt flöde (framåt optiskt flöde och omvänd optiskt flöde) och slumpmässig rörelse vid den andra sessionen, med längst latenser för slumpmässig visuell rörelse. Extra-stimulerade spädbarn skiljde signifikant mellan strukturerat optiskt flöde och slumpmässig visuell rörelse redan vid den första test-sessionen, och bearbetade strukturerat optiskt flöde snabbare än slumpmässig visuell rörelse. Vid den andra test-sessionen skiljde extrastimulerade spädbarn signifikant mellan varje rörelsebetingelse och hade kortast latenser för framåt optiskt flöde, efterföljt av omvänd optiskt flöde, och längst latenser för slumpmässig rörelse. De totala latenserna visade sig vara signifikant kortare för extrastimulerade spädbarn än för traditionellt uppfostrade spädbarn vid båda test-sessionerna. TSE-resultat vid jämförelse av de tre rörelsebetingelserna med statisk icke-flöde visade att traditionellt uppfostrade spädbarns responser dominerades av desynkroniserade theta-oscillationer vid 3–5 månaders ålder, efterföljt av en ökning av desynkroniserade alpha-oscillationer vid den andra test-sessionen. TSE-kartor över extrastimulerade spädbarn avslöjade desynkroniserade theta-oscillationer vid 3–5 månaders ålder och en ökning av oscillerande aktiviteter i alpha-beta-frekvensintervaller vid den andra test-sessionen. Medan den observerade utvecklingsprogressionen hos traditionellt uppfostrade spädbarn tillskrevs neural mognad och erfarenhet av egenproducerad rörelse, bidrog extra motorisk stimulering sannolikt till en påskyndad utveckling av visuell rörelseuppfattning hos stimulerade spädbarn. Ytterligare forskning är motiverad för att undersöka sambandet mellan extra motorisk stimulering och utveckling av visuell rörelseuppfattning hos spädbarn.

1. Introduction

When navigating through the dynamic environment, the gathering of perceptual information allows for controlling and guiding forthcoming actions so that accidents might be avoided, and goals reached. According to Gibson (2014), locomoting observers accomplish this task by relying on patterns of visual flow (i.e., optic flow) arising from their movements through the ambient optical array. In view of this, Gibson argued that behaviour and perception are interdependent in that an organism's actions are continuously guided by what it perceives, and in turn, what is perceived is guided by its actions (Gibson, 2014). Thus, as observers locomote through three-dimensional space, they rely on visual information resulting from their movements for doing so safely and efficiently.

An extensive body of research has demonstrated optic flow to play a pivotal role in controlling posture (Bardy, Warren, & Kay, 1999; Jouen, Lepecq, Gapenne, & Bertenthal, 2000; Kang, Kim, Chung, & Hwang, 2012; Redfern & Furman, 1994), perceiving heading direction (Bruggeman, Zosh, & Warren, 2007; Crowell & Banks, 1993; Van den Berg, 1992; Van den Berg & Brenner, 1994), avoiding obstacles (Fajen & Warren, 2004; Menuchi & Gobbi, 2012), perceiving time-to-collision (Kayed & van der Meer, 2007; van der Weel, Agyei, & van der Meer, 2019), and in estimating distance travelled (Sun, Campos, & Chan, 2004; Sun, Campos, Young, Chan, & Ellard, 2004). The ability to perceive and use patterns of flow arising from our movements, may therefore be considered a critical aspect of the overall perceptual development and learning in infancy.

Attesting to the importance of visual motion perception for human function, newly born infants demonstrate rudimentary sensitivity to visual motion (Haith, 1966; Slater et al., 1990), and infants as young as 3 days of age respond with backward leaning of the head when presented with backward flow information (Jouen, 1990; Jouen et al., 2000). Although such findings have been argued to not solely arise from visual motion perception itself (Shirai & Yamaguchi, 2010), there is consensus among scholars that sensitivity to optic flow emerges early and undergoes prolonged postnatal development (Ball, Ballot, & Dibble, 1983; Bertenthal & Bai, 1989; Johnson et al., 2003; Nájuez Sr & Yonas, 1994; Sen, Yonas, & Knill, 2001). For instance, optic flow simulating an approaching object on a collision course has been found to elicit defensive motor responses in 3- to 6-week old infants (Nájuez Sr, 1988; Yonas, Pettersen, & Lockman, 1979). At approximately 8 weeks of age, infants show sensitivity to motion-carried information specifying object form (Arterberry & Yonas, 2000), and the use of smooth pursuit eye movements to track small moving objects undergoes rapid

improvement between 6 to 14 weeks of age (Rosander, 2007). Cortical responses to changes in heading direction have further been indicated to emerge at 5 weeks of age, and to increase in magnitude until 18 weeks of age (Braddick, Birtles, Wattam-Bell, & Atkinson, 2005). At around 6 months of age, infants have been demonstrated to successfully track and predict the reoccurrence of temporarily occluded objects on a horizontal path (Jonsson & von Hofsten, 2003). With age, this ability becomes more sophisticated, allowing for a more advanced coupling of visual information and subsequent adaptive actions such as catching a moving object (van der Meer, van der Weel, & Lee, 1994). Lastly, towards the end of the first year of life, infants show rapid improvements in their use of optic flow information for manoeuvring their surrounding environment (Higgins, Campos, & Kermoian, 1996; Ueno et al., 2018).

Considerable evidence from imaging and neurophysiological studies has pinpointed the medial superior temporal area (MST) and hMT+/V5 areas of the dorsal visual pathway to be implicated in the functional processing of visual motion, including optic flow (Duffy & Wurtz, 1997; Holliday & Meese, 2008; Morrone et al., 2000; Pitzalis et al., 2013; Ptito, Kupers, Faubert, & Gjedde, 2001; Smith, Wall, Williams, & Singh, 2006; Stevens, McGraw, Ledgeway, & Schluppeck, 2009; Tootell et al., 1995; Zeki, 2015). In macaque monkeys, neurons in the dorsomedial region of the MST (MSTd) show a preference for optic flow components (Duffy & Wurtz, 1991; Morrone et al., 2000), and a functionally homologous area to monkey MSTd has been identified in human hMT+/V5 (Culham, He, Dukelow, & Verstraten, 2001; Dukelow et al., 2001; Jong, Shipp, Skidmore, Frackowiak, & Zeki, 1994).

Motion-induced activation has further been reported in additional extrastriate areas including V6, V3/V3A, and areas in the intraparietal sulcus (Avila, Lakshminarasimhan, DeAngelis, & Angelaki, 2019; Fattori, Pitzalis, & Galletti, 2009; Jong et al., 1994; Merchant, Battaglia-Mayer, & Georgopoulos, 2004; Wattam-Bell et al., 2010). In neonates, evidence suggests visual motion processing in the occipitotemporal cortex to occur in the left hemisphere, with initial motion responses arising in the hMT+/V5 through a pathway involving the superior colliculus and pulvinar, after which a bilateral development and gradual involvement of visual areas takes place between 3 and 5 months of age (Rosander, Nyström, Gredebäck, & von Hofsten, 2007).

Complementary to physiological techniques such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), non-invasive electroencephalogram (EEG) has proven suitable for examining the functional cortical development and neural basis of motion perception in infancy 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 pyramidal 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). In adults, N2 latencies have been reported to occur at around 130–150 ms following stimulus onset (Probst, Plendl, Paulus, Wist, & Scherg, 1993), while N2 latencies in 11–12 month-old infants have been reported at around 180–270 ms (Agyei, Holth, van der Weel, & van der Meer, 2015; van der Meer et al., 2008).

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, infants show rapid improvements in their processing of optic flow stimuli between 3–4 and 11–12-months of age (Agyei et al., 2015). Moreover, and similar to adults (van der Meer et al., 2008), typically developing infants at 11–12-months of age are able to differentiate between different forms of visual motion, and process forwards visual motion faster than they do reversed and random visual motion (Agyei et al., 2015). The greater 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). However, contrary to findings in normally developing infants, preterm infants have been indicated to show abnormal development of visual motion perception across the first year of life, which has been attributed to a possible vulnerability of the dorsal visual processing stream (Agyei, van der Weel & van der Meer, 2016a; Braddick, Atkinson & Wattam-Bell, 2003).

As opposed to evoked activity, induced activity in the time-frequency domain pertains to frequency-specific modulations of the rhythmic activity of the brain in the ongoing EEG, also referred to as oscillations, which are time- but not phase-locked to an event (Pfurtscheller, Neuper, & Mohl, 1994; Pfurtscheller, Stancák, & Neuper, 1996). Several classes of oscillations have been distinguished – delta band (1–4 Hz), theta band (4–8 Hz), alpha band (8–13 Hz), beta band (13–30 Hz), and gamma band (30–150 Hz), each assumed to reflect specific cognitive processes (Buzsaki & Draguhn, 2004; Ganzetti & Mantini, 2013). Modulations in oscillatory activity may be observed as either an increase (i.e., event-related synchronisation, ERS) or a decrease (i.e., event-related desynchronisation, ERD), in the spectral amplitude of given frequency bands (Pfurtscheller, 1977, 1992), indicating more or

less synchrony in the rhythmic activity of underlying neuronal populations (Pfurtscheller, 2001).

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, Agyei, van der Weel, & van der Meer, 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). Contrary to adults, infants typically show low-frequency activation with higher amplitudes in response to visual motion stimuli. Such patterns of activity have been suggested to reflect immaturity of the functional circuits in the brain and the involvement of less specialised neuronal assemblies during visual motion processing (Pfurtscheller & Lopes Da Silva, 1999; Stroganova, Orekhova, & Posikera, 1999). For example, in a longitudinal study by Agyei and colleagues (2016a), full-term born infants at 4 months of age showed induced activities in the theta band range, and induced activities in the alpha-beta range at 12 months of age (Agyei et al., 2016a). Thus, in normally developing infants, the shift from lower to higher frequencies observed across the first year of life suggests a progression towards more adult-like responses to optic flow stimuli with age (Agyei et al., 2015).

Apart from the rapid maturation of the cortex, increased attention has been given to the role of experience in advancing psychological functions in infancy (Bertenthal & Campos, 1990; Gilmore, Baker, & Grobman, 2004; Higgins et al., 1996; James & Swain, 2011; Kermoian & Campos, 1988; Uchiyama et al., 2008; Ueno et al., 2018; Walle & Campos, 2014). Upon acquiring independent mobility, the possibilities for exploration drastically increase as infants transition from a state of being passively carried around to becoming active explorers of their surroundings (Gilmore, Baker & Grobman, 2004). This transition has been argued to herald an array of changes in psychological functions due to the many experiences it generates, and what these experiences demand of the infant in return (Campos et al., 2000).

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). For instance, the acquisition of independent mobility has been demonstrated to be associated with the emergence of adaptive behaviours in response to a visual cliff drop-off (Gibson, 1988). In these experiments, illuminating tiles or a patterned sheet are typically placed underneath a plexiglass surface to provide the illusion of either a solid surface or a drop-off on each end of the plexiglass-table (Anderson et al., 2013). When faced with the deep end of the visual cliff,

only infants who have acquired independent mobility tend to respond with avoidance or hesitance (Bertenthal & Campos, 1990; Campos, Bertenthal, & Kermoian, 1992; Ueno, Uchiyama, Campos, Dahl, & Anderson, 2012). Because of this, some scholars suggest self-produced locomotion to be the principal factor in the ontogeny of wariness of heights (Campos, Bertenthal, & Kermoian, 1992), while others argue that what is learnt is rather to perceive the possibilities for action that each new mode of locomotion (e.g., crawling or walking) affords (Adolph, Eppler, & Gibson, 1993; Adolph, Kretch, & LoBue, 2014). Similarly, the acquisition of independent mobility has been suggested to advance spatial cognitive development (Anderson et al., 2013; Bell & Fox, 1997; Campos, Anderson, & Telzrow, 2009; Clearfield, 2004; Horobin & Acredolo, 1986; Kermoian & Campos, 1988; Thelen, Schöner, Scheier, & Smith, 2001; Yan, Thomas, & Downing, 1998). In studies using a variety of search performance tasks, locomotor infants have been found to outperform their pre-locomotor peers in retrieving hidden objects, indicating that coding strategies of spatial information become increasingly sophisticated following the onset of self-produced locomotion (Bai & Bertenthal, 1992; Bell & Fox, 1997).

Taken together, the existing body of literature suggests that the many experiences acquired by exploring one's surroundings instigate advancements in psychological function including visual motion perception (Clearfield, 2011; Gibson, 1988; Herbert, Gross, & Hayne, 2007; Schwarzer, Freitag, Buckel, & Lofruchte, 2013; Vilhelmsen et al., 2019; Walle & Campos, 2014). However, and as argued by Campos et al. (2000), this does not negate the role of maturation in the emergence and subsequent development of such functions. Rather, the two are assumed to show varying degrees of interdependence, with maturation at times being of higher developmental importance, and vice versa (Campos et al., 2000). Considering the interplay between the two, the framework in which developmental changes take place needs also to be taken into account in order to understand developmental processes fully (Adolph & Hoch, 2019; Campos et al., 2000).

Cross-cultural studies have identified ways in which belief systems and caregiving practices might influence the developmental trajectories of infants living within a given culture (Bril, Zack, & Nkounkou-Hombessa, 1989; Keller et al., 2007; Keller, Kärtner, Borke, Yovsi, & Kleis, 2005; Keller & Lamm, 2005; Liu et al., 2019; Tamis-LeMonda, Song, Leavell, Kahana-Kalman, & Yoshikawa, 2012; Vierhaus et al., 2011). In the context of motor development, Western belief systems often proclaim infants to be fragile and in need of gentle handling, while some non-Western cultures consider age-appropriate, rough handling to be necessary for healthy motor development (Adolph & Hoch, 2019). For the latter, this might

involve practices such as stretching of the limbs, massage, stepping exercises, and postural manipulations from birth onwards (Carra, Lavelli, & Keller, 2014; Hopkins & Westra, 1990; Keller, 2003). 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). Intracultural differences in what is regarded as important skills to master, and more specifically, when and how such skills are to be acquired, may therefore affect infants' daily visuomotor experiences as it translates into caregiving practices (Adolph & Franchak, 2017; Karasik, Adolph, Tamis-LeMonda, & Bornstein, 2010). In view of previous studies demonstrating visuomotor experiences to bring about developmental change (Agyei et al., 2015; Anderson et al., 2013; Gilmore, Baker, & Grobman, 2004; Gilmore & Rettke, 2003), it is plausible that receiving enriched motor stimulation in the first postnatal year may also facilitate the development of visual motion perception.

The aim of the current study was to investigate whether receiving extra stimulation during the first year of life accelerates the development of visual motion perception. Western reared infants, of which one group had received extra motor stimulation and the other a traditional upbringing, were tested at two time points in a longitudinal design. High-density EEG was employed for recording cortical activity as a function of optic flow and random visual motion. Recorded EEG data were subjected to VEP and time-frequency analyses for investigating whether extra-stimulated infants displayed accelerated development of visual motion perception compared to their traditionally-raised peers. Previous optic flow studies have demonstrated N2 latencies to decrease with age and experience with self-produced locomotion, 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 world compared to traditionally-raised infants, and therefore to show an accelerated development of visual motion perception. It was hypothesised that extra-stimulated infants would display overall shorter latencies of VEPs in addition to induced activities at higher frequencies than infants receiving a traditional upbringing. Given the immediate and long-lasting developmental

effects of receiving extra stimulation in early infancy, extra-stimulated infants were expected to be developmentally advanced in their responses to the visual motion stimuli in both testing sessions.

2. Methods

2.1 Participants

A total of 20 infants, of which 10 had received extra stimulation, participated in the study. The extra-stimulated group (five boys, five girls) comprised infants that had participated in baby swimming classes for at least 10 weeks with one session per week, and one infant that had received baby massage on a daily basis from birth onwards. For extra-stimulated infants, recruitment entailed contacting parents directly at baby swimming classes held at Pirbadet in Trondheim, and the infant receiving baby massage was recruited by word of mouth. Out of 16 recruited infants who had received extra stimulation, six did not provide sufficient data in either the first or second testing session. These infants were therefore excluded from further analyses and were not matched up with traditionally-raised controls. Infants who had received a traditional upbringing (five boys, five girls) were recruited by contacting parents following birth announcements in the local newspaper or by word of mouth.

Infants were tested at two time points in a longitudinal design. Extra-stimulated infants were tested first at 3 to 5 months of age (M weeks = 21, SD = 1), and then again at 8 to 12 months of age (M weeks = 43, SD = 8). Experiences with self-produced locomotion were documented for both testing sessions, with self-produced locomotion being defined as crawling, walking, or in any other way achieving independent locomotion. At the first testing session, six of the infants had some experience with rolling over from back to stomach, but no experience with self-produced locomotion. At the second testing session, all of the infants were crawling and had been able to do so for a minimum of 4 weeks (M weeks of self-produced locomotion = 9.13). In addition, three of the infants were walking either independently or with help and had been able to do so for a minimum of 3 weeks.

Traditionally-raised infants who had not received extra stimulation were tested first at 3 to 5 months of age (M weeks = 19, SD = 2.12), followed by a second testing at 9 to 12 months of age (M = 49, SD = 1.29). For this group, four of the infants had experience with rolling over from back to stomach in the first testing session, but no experience with self-produced locomotion. At the time of the second testing, all infants except one were crawling and had been able to do so for at least 7 weeks. Additionally, six of the infants had mastered walking either independently or with help and had been walking for a minimum of 2 weeks (M weeks of self-produced locomotion = 10.43).

EEG recording is a non-invasive method that causes no known harm or physical pain to the participant. Parents were provided with sufficient information to give their informed consent, including their right to withdraw from the experiment at any time. The study gained approval by the Norwegian Regional Ethics Committee and the Norwegian Data Services for the Social Sciences.

2.2 Optic Flow Stimuli

E-Prime (Psychological Software Tools, Inc.) was used for generating the optic flow stimuli, which was presented to infants on an 84-inch display (Surface Hub, Microsoft Corporation). The display had a 16:9 ratio, a refresh rate of 120 Hz, and a resolution of 3840 x 2180 pixels. For the duration of the experiment, infants were seated at a distance of approximately 80 cm from the display with a visual angle of 68° horizontal and 46.7° vertical.

The optic flow experiment was presented to infants as the last of four visual motion paradigms. It comprised three visual motion conditions (i.e., forwards optic flow, reversed optic flow, and random visual motion), with each being presented to the infants in a randomised order and for a duration of 1500 ms. A frozen picture of the previous motion trial provided the baseline condition for TSE analyses and was shown for a duration of 1500 ms in-between each motion trial to prevent motion adaption. Visual motion was simulated using 100 black dot particles randomly occurring on a white background with a contrast of 99.5% and a mean luminance of 68 cd/m². A reference fixation point (1.69 mm in diameter) was positioned at the centre of the screen, subtending an angle of 0.16 degrees.

Dot particles appeared to either increase or decrease in size during the motion trials at a rate of 0.023 pixels, with the maximum and minimum dot size being 17 mm and 2 mm, respectively. In the forwards optic flow condition, dots moved in a coherent fashion parallel to the z-axis inwards and towards the eyes, simulating forward motion in three-dimensional space. To simulate backwards motion, dots coherently moved parallel to the z-axis in the reversed optic flow condition, but this time outwards and away from the eyes. For random visual motion, dots appeared to move in an incoherent fashion. Velocities in the x- and y-axes were kept at zero for each trial of each motion condition, and dot particles were repositioned automatically whenever moving out of the aperture. Lastly, for the non-flow condition made up of a frozen optic flow picture, the velocities in the z-, x-, and y-axes were kept at zero so that the dots remained at the same size and position at all times.

In the first testing session, extra-stimulated infants contributed on average 46 (SD = 14.2) motion trials and 48 (SD = 16.5) static non-flow trials, while traditionally-raised infants

contributed on average 57 (SD = 12.8) motion trials and 59 (SD = 14.2) static non-flow trials. In the second session, mean trial contributions for extra-stimulated infants were 58 (SD = 15) for motion, and 61 (SD = 13.7) for the static non-flow trials, while mean trial contributions for traditionally-raised infants were 49 (SD = 14.7) and 52 (SD = 18.7) for visual motion and static non-flow, respectively.

2.3 Data Acquisition

EEG recordings were carried out using a Geodesic Sensor Net (GSN; Tucker, 1993), consisting of an array of 128 electrodes evenly distributed across the infant's scalp. In line with recommendations for achieving optimal signal-to-noise ratio when using high input-impedance EGI amplifiers (Picton et al., 2000), impedances of the electrodes were kept below 50 k Ω . Cortical electrical activity was recorded at a sampling rate of 500 Hz on a Macintosh computer using Net station software and was subsequently stored on a hard disk for off-line analyses.

An infrared Tobii X50 camera was employed for monitoring the infant's gaze during the experiment. The visual feed was processed using ClearView software on an HP computer. In addition, two cameras positioned at different angles in front of the infant were used for monitoring their behaviour during the experimental session.

2.4 Procedure

On arrival at the laboratory, parents received sufficient information, verbally and in written form (see Appendix A), for providing their informed consent while their infant was given time to familiarise itself with the laboratory surroundings. After some time, an assistant measured the circumference of the infant's head for the appropriate selection of the net. Optimal conductivity was ensured by soaking the net in a saline solution, made with distilled water, and a small amount of baby shampoo for a duration of ten minutes. Once partially dried, the net was mounted on the infant's head. During the mounting of the net, the infant was placed on its parent's lap and distracted by colourful soap bubbles or small noise-emitting toys.

Upon successful mounting of the net, the infant was taken to the experimental room and seated in a baby car seat facing the rectangular display. The experimental room was dimly lit and separated by a glass partition from the adjacent control room, in which two or more assistants operated the computers necessary for data acquisition. At this time, and for the duration of the experiment, the parent, as well as an assistant, were present in the experimental room to minimise any possible distress of the infant, and to help the infant pay

attention to the screen. After connecting the net to the amplifier, the impedances of the electrodes were checked. If needed, more saline solution was added, or the position of the electrodes was adjusted. Upon successful calibration of the eye-movements using the infrared Tobii X50 camera, the testing session began.

Each infant typically performed the optic flow experiment as the last of 4 visual motion experiments. A typical testing session consisted of 90-120 trials per infant and lasted for 4-5 minutes on average. In the case of displays of disinterest or boredom on behalf of the infant, recording of data was temporarily stopped. To revive the infant's interest, the parent and the assistant played with the infant for a short period of time. Once sufficient data had been acquired, the experimental session came to an end.

2.5 Data Analyses

BESA (Brain Electrical Source Analysis) version 6.1 software was used for analysing the EEG raw data. Initial pre-processing entailed segmenting and exporting the EEG recordings as raw files using Net Station Software. Analysing procedures remained the same for both groups and both testing sessions. For the optic flow and visual motion responses, averaging epochs of interest were set from -200 to 800 ms, with a baseline definition of -200 to 0 ms. Low-cut and high cut-off filters were set at 1.6 Hz and 60 Hz, respectively, for removing slow drift in the data. Notch filter was set at 50 to avoid noise resulting from power line interference.

Two categories of oscillatory activity in the ongoing EEG were of interest in the present study; evoked and induced activity. Visual evoked potentials (VEPs) are proposed to represent the synchronous firing pattern of pyramidal post-synaptic neuronal populations during the processing of a visual stimulus (Pfurtscheller & Lopes Da Silva, 1999; Webb, Long, & Nelson, 2005). For detecting motion VEPs in EEG, averaging techniques are commonly applied as these brain responses are time- and phase-locked to the stimulus in question (Pfurtscheller, & Lopes Da Silva, 1999).

As opposed to evoked activity, induced activity is time-locked but not phase-locked to the stimulus, and is assumed to reflect specific event-related changes in the frequencies of brain oscillations (Pfurtscheller, & Lopes Da Silva, 1999). Due to being time-locked to the stimulus, time-frequency analysis makes for a more suitable method of extracting induced responses than averaging techniques.

2.6 Artefact Removal

Spherical spline interpolation was applied for removing or re-estimating artefact-contaminated channels and epochs resulting from ocular activity and bodily movements (i.e., head or arm movements) (Perrin, Pernier, Bertrand, & Echallier, 1989; Picton et al., 2000). Manual artefact correction designed to separate reoccurring ocular artefacts from activity in the brain regions of interest was carried out using spatial filters (Berg & Scherg, 1994). Threshold values were set at 0.1 μV for low signal, 75 μV for gradients, and 200 μV (220 μV for some participants) for maximum amplitude. Recorded data was excluded from further analyses if more than 10% of channels had been defined as bad, or if the gaze analysis revealed that the infant had not been paying attention during trials.

2.7 Peak Analysis at the Electrode Level

Evoked activity was examined by first re-referencing the EEG data to an artificial reference calculated from the average potentials across the scalp, and then exporting the data into the standard 81-electrode configuration of the 10-10 international system to obtain individual averages. Individual averages were combined yielding two grand averages per group and for each condition, and were used as a reference for identifying individual N2 components. For selecting the most dominant VEP waveforms of N2 activity in the occipito-parietal areas, 3D spherical spline whole-head voltage maps of scalp signal distribution were applied (Perrin et al., 1989). Each of the individual peak latency values was recorded and used for subsequent analyses.

2.8 Time-Frequency Analyses in Brain Space

For examining induced activity, TSE analyses using multiple source dipoles modelling the parietal and visual cortices were performed. As a consequence of the nature of dipole fields, and the smearing effect of the volume conduction in EEG, there is a wide distribution of focal brain activity at the scalp. Analyses were therefore carried out in brain source space rather than at the electrode level for separating brain activity from different underlying brain regions (Luck, 2005). Optimal separation was achieved by applying brain source montages derived from a multiple source model.

After appending the artefact-corrected files, a 4-shell ellipsoidal model (Berg & Scherg, 1994; Hoechstetter et al., 2004) was computed for each infant and then used for mapping and analysing the occipital and parietal regions associated with visual motion processing (Rosander et al., 2007). Selected regional sources are presented in Figure 1 and

were in line with Agyei et al. (2015). Per recommendations for infant data, a pre-defined template model for infants aged 0 – 18 months was applied for the analyses (BESA, GmbH information).

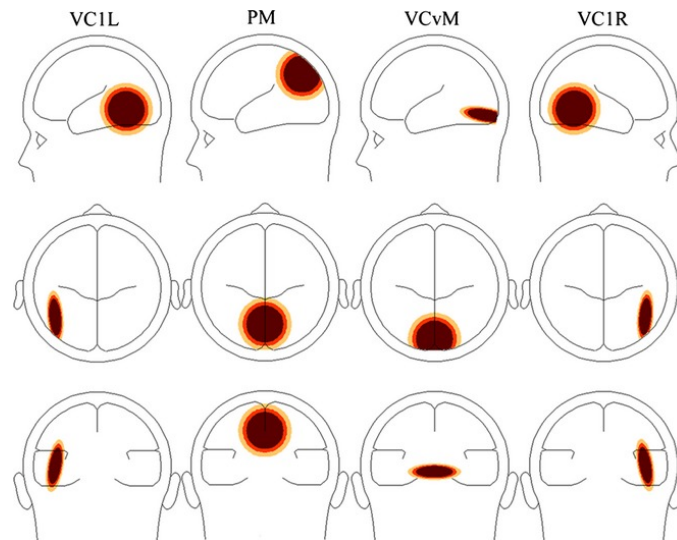


Figure 1. Head model of the regional areas of interest with approximate Talairach coordinates. From left to right: visual cortex lateral left (VCIL; $x = -45, y = -57, z = 6.5$), parietal midline (PM; $x = 0.0, y = -72, z = 37$), visual cortex ventral midline (VCvM; $x = 0.0, y = -85, z = -14.3$), and visual cortex lateral right (VCIR; $x = 45, y = -57, z = 6.5$). The signal magnitude reflects the estimated source activity if only one brain region were to be active.

Prior to computing the TSEs (change in amplitude over time in regional sources), averaged evoked activity was subtracted for focusing solely on induced oscillatory responses. Settings for epoch, filters and average parameters corresponded to those used for the VEP analyses. TSEs were computed separately for all infants for the three different motion conditions, the static non-flow condition, in addition to comparisons between each of the visual motion conditions and the static non-flow condition. Probability maps indicating significant differences in induced activity when comparing the three visual motion conditions with static non-flow were computed using Bootstrapping statistics. A Bonferroni correction procedure was used to address the multiple comparisons problem (Simes, 1986). Settings for frequency cut-off and time and frequency for the TSE displays and probability maps were 4–40 Hz, 1 Hz and 50 ms, respectively. Epoch length was -200 to 800 ms.

Paired sample t-tests were carried out using BESA Statistics 2.0 (BESA, GmbH) to test for significant differences between the three visual motion conditions and the static non-flow condition. Statistical comparisons were carried out for each group, and each testing

session, and a combination of permutation testing and data clustering was applied to correct for the multiple comparisons problem. As the results revealed no significant differences in amplitude values and frequency ranges in the TSE data, the visual motion conditions (forwards optic flow, reversed optic flow, random visual motion) were combined into one single motion condition (combined visual motion) and compared with the static non-flow condition. The results from the permutation test allowed for examining the individual TSEs according to the significant time-frequency ranges observed at the group level. The number of permutations was set at 512, and the cluster alpha level determining the significance level for building clusters in time and/or frequency was set at $\alpha = 0.005$. Settings for frequency cut-off, and time- and frequency sampling maintained the same as those stated above.

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 (see Figure 2). For infants receiving extra stimulation, the selected channels were POz, Pz, Oz, and O1 for the first testing session, while electrodes for control infants receiving a traditional upbringing were O2, PO4, POz, and Oz. Electrodes at the second session for extra-stimulated infants were O2, PO4, POz, Oz, and Pz, POz, Oz, and PO4 for control infants. Figure 3 displays the grand average VEPs for the three visual motion conditions for each group, and each testing session.

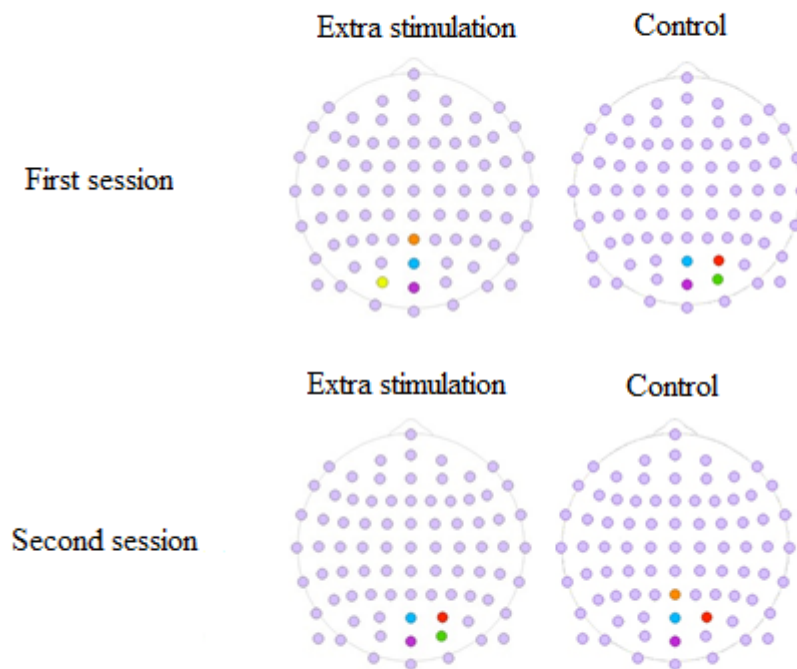


Figure 2. Head maps (nose up) illustrating the localisation of the 81 standard electrodes. From left to right and top to bottom: infants receiving extra stimulation and control infants in the first and second testing session. Selected electrodes are indicated as follows: Oz (purple), Pz (orange), O1 (yellow), POz (blue), O2 (green), PO4 (red).

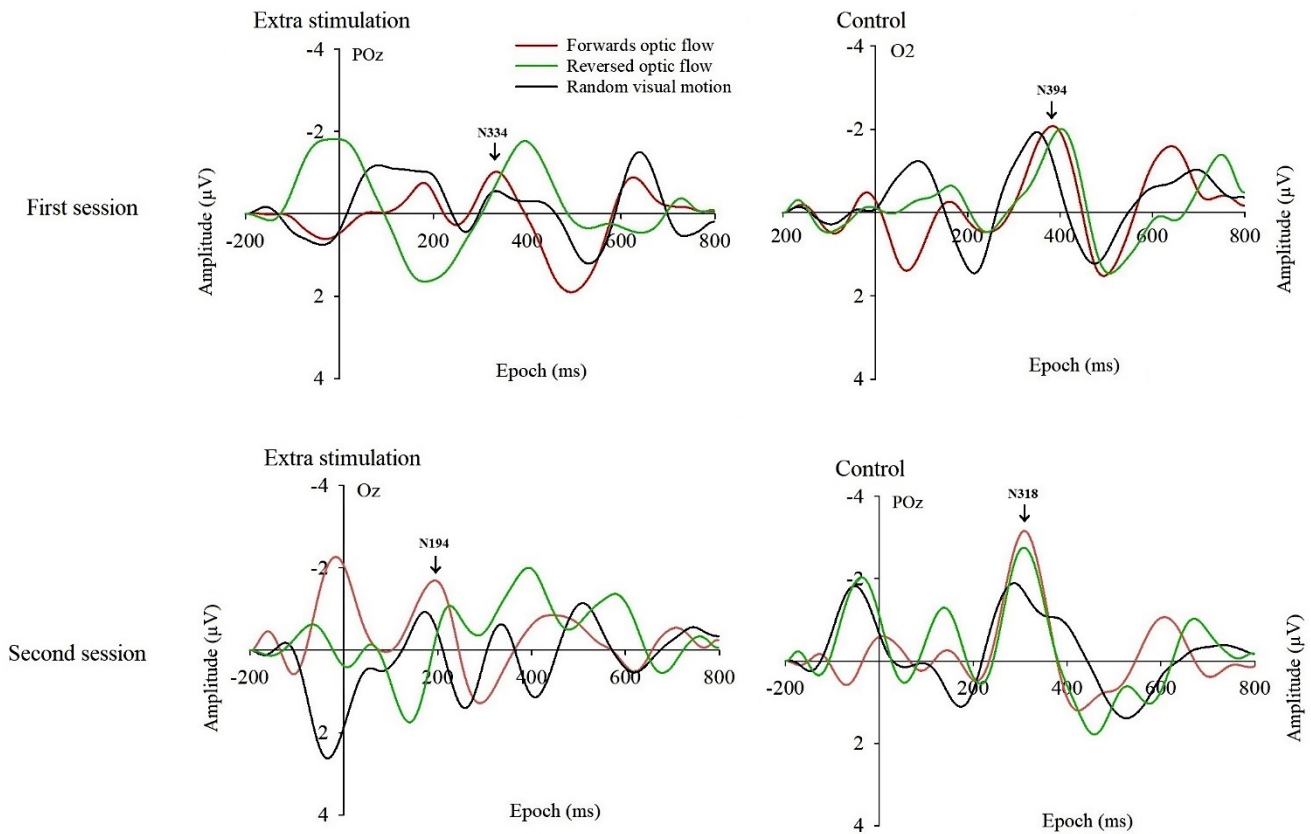


Figure 3. Grand average motion VEPs with epoch set at -200 and 800 ms. From left to right and top to bottom: infants receiving extra stimulation and control infants receiving a traditional upbringing in the first and second session. Motion conditions are illustrated with coloured waveforms and as follows: forwards optic flow (**red**), reversed optic flow (**green**), and random visual motion (**black**). Vertical arrows indicate actual N2 latencies for forwards optic flow.

3.1.1 VEP Analysis

Mean peak latencies were computed for the three visual motion conditions for each group and each testing session. For infants receiving extra stimulation in the first testing session (M weeks = 21, $SD = 1$), mean N2 latencies were 340 ms, 352 ms, and 399 ms for forwards optic flow, reversed optic flow, and random optic flow, respectively. For control infants receiving a traditional upbringing (M weeks = 19, $SD = 2.12$), mean N2 latencies were 394 ms for forwards optic flow, 391 ms for reversed optic flow, and 411 ms for random visual motion in the first session. In the second session for infants receiving extra stimulation (M weeks = 43, $SD = 8$), mean N2 latencies were 201 ms for forwards optic flow, 240 ms for reversed optic flow, and 298 ms for random visual motion, while mean peak latencies for traditionally-raised infants ($M = 49$, $SD = 1.29$) were 307 ms, 331 ms, and 382 ms,

respectively (see Figure 3). Mean weeks of experience with self-produced locomotion in the second testing session was 9.13 and 10.43 weeks for extra-stimulated and traditionally-raised infants, respectively.

A repeated measures ANOVA was performed on VEP latencies. Visual motion condition (forwards optic flow, reversed optic flow, random visual motion) and testing session (first or second) were within-subject factors, and groups (extra-stimulated infants, control infants) comprised the between-subjects factor. Out of the four chosen grand average electrodes, the electrode showing the highest N2 amplitude in the forward visual motion condition was selected and used in the analysis. Thus, selected electrodes varied across participants and sessions, but were limited to the four grand average electrodes at all times, and remained the same for each motion condition. Bonferroni correction was used to adjust for multiple comparisons.

The ANOVA revealed a significant three-way interaction effect of condition, testing session, and group, $F(2,36) = 8.51, p = 0.001$, suggesting that latencies were shorter for the structured optic flow conditions than for random visual motion in both groups, but only in the second session for control infants receiving a traditional upbringing. Additionally, latencies decreased significantly from random visual motion to reversed optic flow and to forwards optic flow for extra-stimulated infants in the second session. The results further revealed a main effect of group, $F(1, 18) = 37.34, p < 0.001$, suggesting that overall latencies were significantly shorter for extra-stimulated infants than for traditionally-raised infants across testing sessions.

As illustrated in Figure 4, the post-hoc analyses confirmed that only extra-stimulated infants were able to significantly differentiate between structured optic flow (forwards optic flow and reversed optic flow) and random visual motion in the first testing session, with the longest latencies for random visual motion and the shortest latencies at around 350 ms for structured optic flow. Traditionally-raised infants, on the other hand, were not able to differentiate between any of the different visual motion conditions in the first session, and had generally long latencies at around 400 ms. In the second session, only the extra-stimulated infants significantly differentiated between all three of the visual motion conditions, displaying the longest latencies for random visual motion followed by reversed optic flow and the shortest latencies at approximately 200 ms for forwards optic flow. Infants receiving a traditional upbringing significantly differentiated between structured optic flow and random visual motion, showing the longest latencies for random visual motion, and the shortest for structured optic flow with latencies at around 310-330 ms. Lastly, latencies for structured

optic flow were significantly shorter for extra-stimulated than for traditionally-raised infants in the first session ($p < 0.05$), with a difference of approximately 50 ms. In the second session, latencies for each of the three motion conditions were significantly shorter for extra-stimulated infants than for traditionally-raised infants ($p < 0.001$), and especially for forwards visual motion with a difference of around 100 ms.

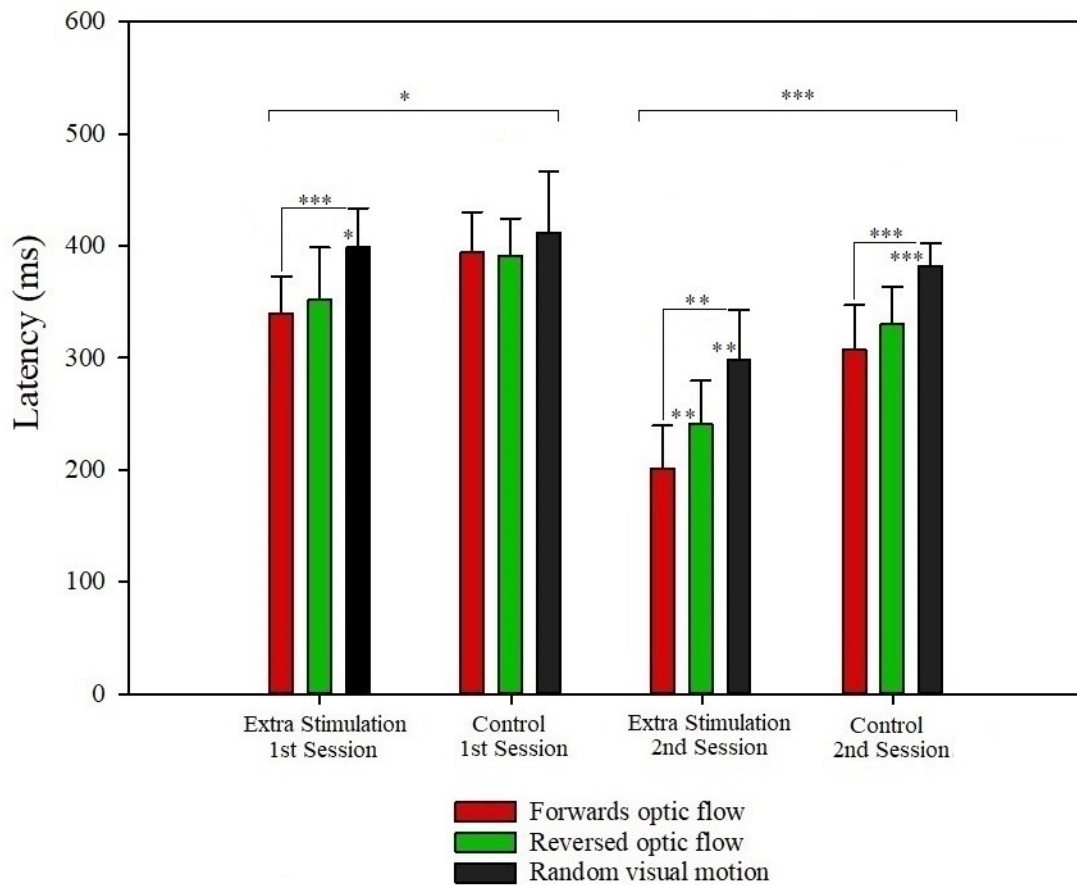


Figure 4. Illustration of mean group latencies (and SDs) for infants receiving extra stimulation and infants receiving a traditional upbringing (i.e., control). Overall mean latencies were significantly shorter for extra-stimulated infants across testing session, indicating faster processing of visual motion for extra-stimulated infants than for traditionally-raised control infants. In the first session, extra-stimulated infants significantly differentiated between structured optic flow (forwards and reversed optic flow) and random visual motion, with the shortest latencies observed for structured optic flow at around 350 ms, and the longest for random visual motion. Traditionally-raised infants showed no significant latency differentiations between the three visual motion conditions in the first session, and had generally long latencies at around 400 ms. In the second session, extra-stimulated infants had reduced their latencies considerably by 140 ms for forwards optic flow, and significantly discriminated between all three visual motion conditions, with the shortest latencies for forwards optic flow, followed by reversed optic flow, and the longest for random visual motion. Traditionally-raised infants, on the other hand, significantly differentiated between structured optic flow and random visual motion, with the shortest latencies at around 310–330 for structured optic flow, and the longest latencies for random visual motion.

*Significant at $p < 0.05$, **Significant at $p < 0.01$, ***Significant at $p < 0.001$

3.2 TSE Analysis

A time-frequency analysis was carried out for all infants separately for the three visual motion conditions and the static non-flow condition. Subsequent statistical comparisons between the visual motion conditions and the static condition yielded no significant differences in induced activity as a function of forwards optic flow, reversed optic flow, and random visual motion. The static non-flow condition was therefore compared with a single visual motion condition (combined visual motion) encompassing all three motion conditions.

Results from the permutation tests are displayed as follows: extra-stimulated and control infants in the first (Figure 5a, 5b) and second session (Figure 6a, 6b). Significant negative averaged clusters are illustrated with blue coloured areas and indicate significantly smaller t-values for the combined visual motion condition when compared with static non-flow. For each group and in each session, significant negative clusters were found in at least one of the four regional sources of interest.

The permutation test results for the first session suggested motion-induced responses for extra-stimulated infants to be dominated by desynchronised theta and alpha activity, and responses for control infants to be dominated by desynchronised activity in the theta, alpha, and beta bands. Theta activities in the first session appeared as less widespread for extra-stimulated infants compared to traditionally-raised infants. In the second session, frequencies of extra-stimulated infants had increased to include synchronised induced expressions of beta band frequencies, while control infants showed desynchronised oscillatory activities in the theta and alpha range.

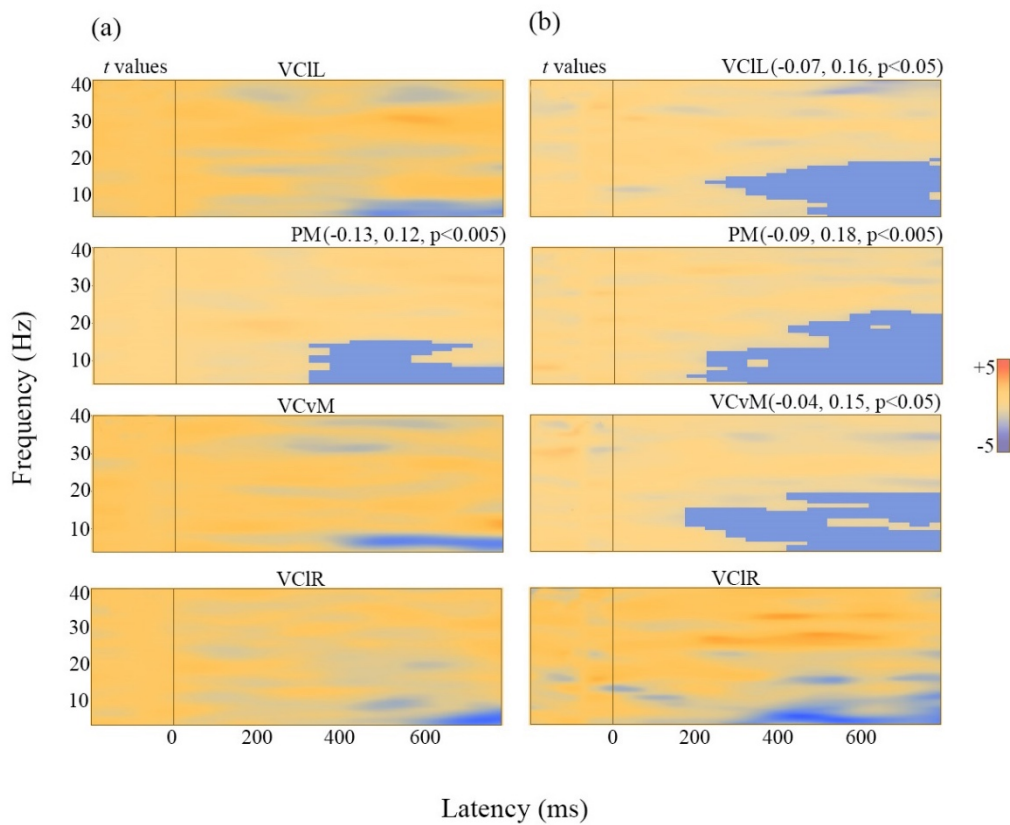


Figure 5. Illustrations of averaged clusters for **(a)** extra-stimulated infants, and **(b)** control infants at the first testing session when combined visual motion was compared with static non-flow. Negative clusters in the visual areas of interest (VCIL, PM, VCvM, VCIR) are represented with light blue areas and indicate significantly smaller t -values for combined motion than for static non-flow. Low-frequency desynchronised activity was observed in the first session for both groups in theta and alpha ranges, as well as in the beta range for traditionally-raised control infants. The theta desynchronisation appeared to be especially widespread for control infants. In parentheses, from left to right: cluster means for combined motion, cluster means for static-non flow, and the corresponding probability of significance value. A vertical line marks stimulus onset, and epoch is -200 to 800 ms.

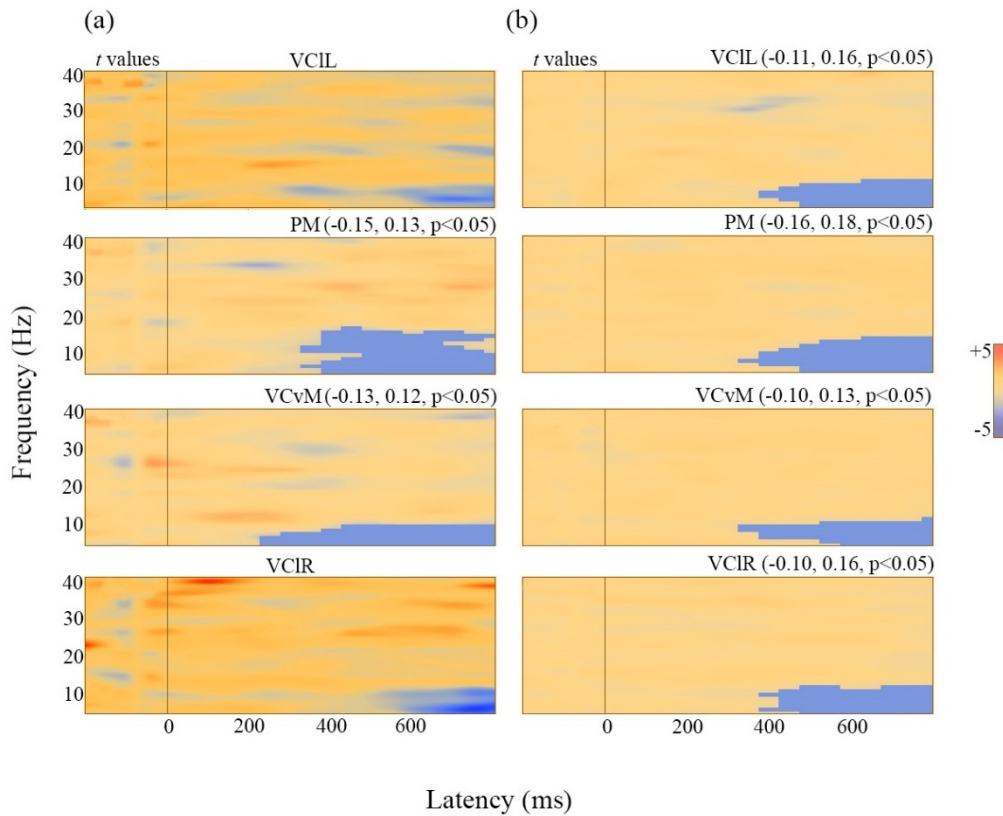


Figure 6. Visualisation of averaged significant clusters in the visual areas of interest for (a) extra-stimulated infants, and (b) control infants in the second session when comparing the combined visual motion condition with static non-flow. Blue coloured areas represent negative clusters indicating significantly smaller values for the combined motion condition than for static non-flow. Theta and alpha desynchronisations were observed in two or more of the visual areas of interest (VCIL, PM, VCvM, VCIR) for both groups, in addition to desynchronised beta band activity for extra-stimulated infants. Cluster means for combined motion, cluster means for static-non flow, and the corresponding probability of significance value are indicated within parentheses, in that order. Stimulus onset is indicated by a vertical line, and epoch length is -200 to 800 ms.

TSE (amplitude changes over time – temporal spectral evolution) maps and corresponding probability maps are displayed as follows: extra-stimulated infants and control infants in the first session (Figure 7a–d, Figure 8a–d), and the second session (Figure 9a–d, Figure 10a–d), in that respective order. When infants perceived the visual motion stimuli, a decrease in spectral amplitude (event-related desynchronisation) in the theta (4–7 Hz) band was seen for both groups of infants in the first session. Additionally, desynchronised oscillatory activities in the beta frequencies were observed for control infants. In the second session, a decrease in spectral amplitude in theta- and the alpha (7–13 Hz) range could be observed in both groups of infants. In addition, synchronised activities were observed in the

beta frequency band (13–30 Hz) for extra-stimulated infants.

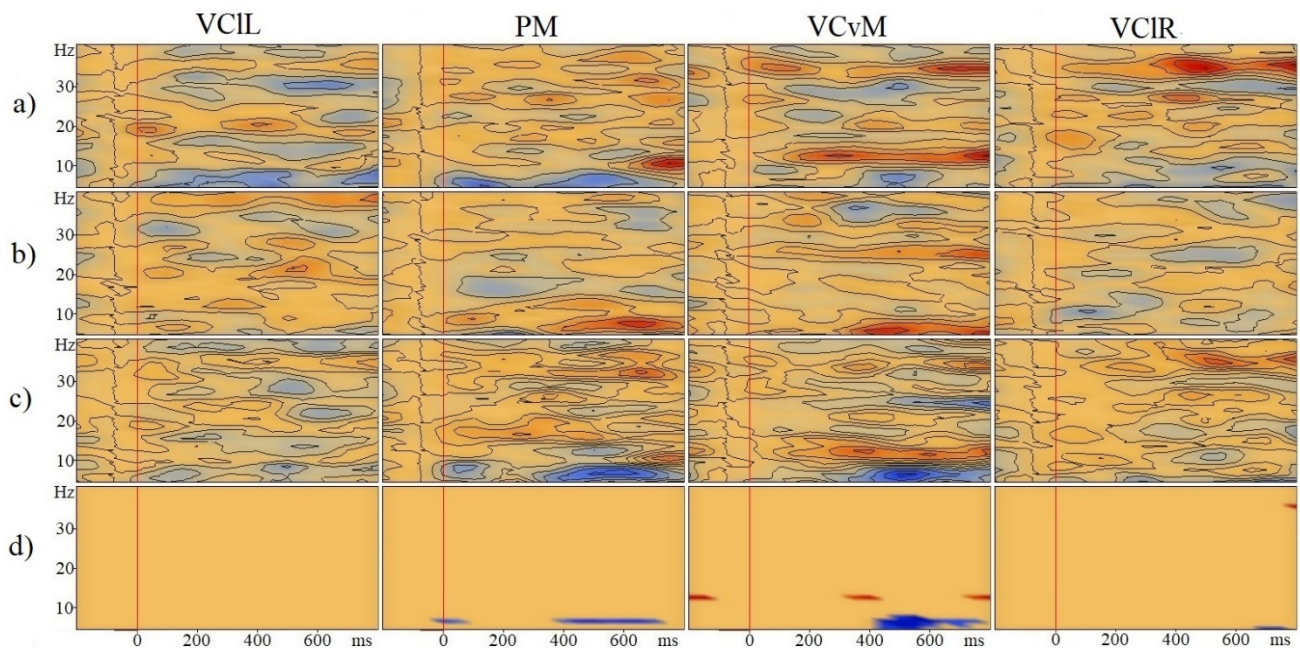


Figure 7. TSE maps of the visual areas of interest for a typical extra-stimulated infant (girl, 16 weeks of age) in the first testing session. The regional sources of interest comprised VCIL, PM, VCvM, and VCIR. Epoch length is -200 to 800 ms, with a baseline of -100 to 0 ms. A red line indicates stimulus onset at 0 ms. From **a-d**: combined visual motion (**a**), static non-flow (**b**), combined visual motion and static non-flow compared (**c**), and probability maps ($p < 0.05$) when the combined visual motion condition was compared with static non-flow (**d**). Desynchronised and synchronised activity is indicated by blue and red areas, respectively. Induced desynchronised activities in the theta band (4–7 Hz) were observed for the combined visual motion condition (**a**) in two or more of the visual areas of interest, while synchronised theta activities were observed for the static non-flow condition (**b**). When combined visual motion was compared with static non-flow (**c**), desynchronised activities appeared as induced theta oscillations in visual areas PM and VCvM in particular. The TSE probability maps display a significant increase (red areas) and decrease (blue areas) of TSEs ($p < 0.05$). Comparisons between combined visual motion and static non-flow showed significant decrease of TSE (desynchronisation) in the theta band in visual areas PM and VCvM (**d**).

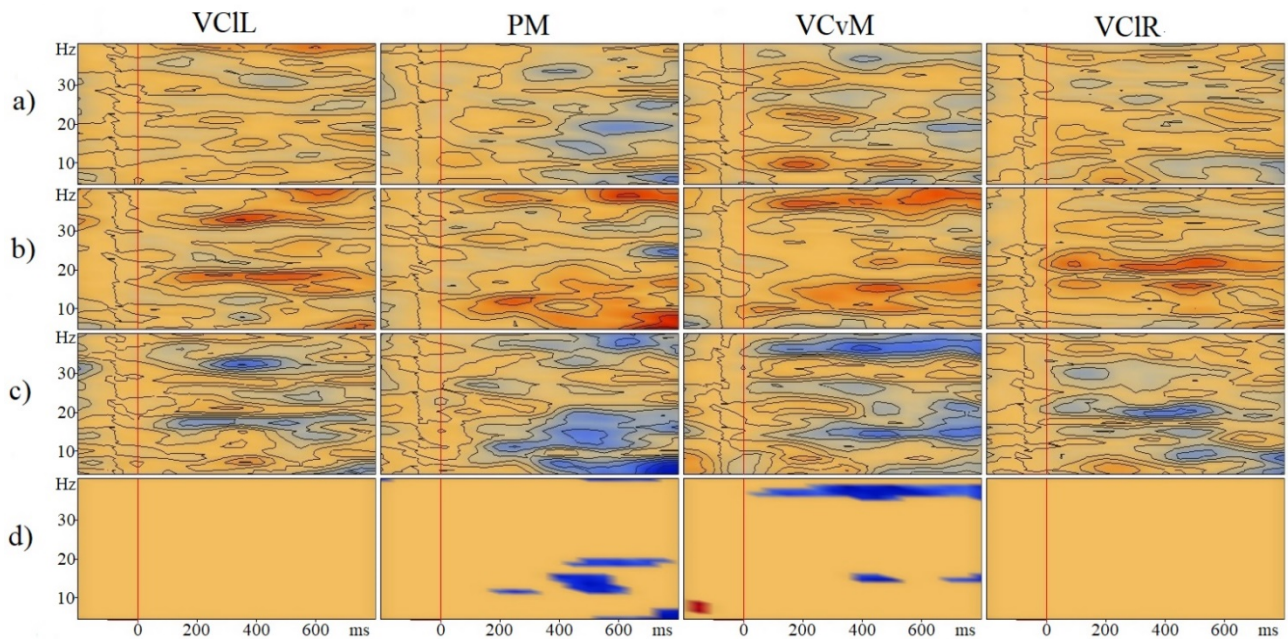


Figure 8. Visualisation of TSE maps in the visual areas of interest (VCIL, PM, VCvM, VCIR) for a typical control infant (girl, 20 weeks of age) receiving a traditional upbringing in the first session. Desynchronised and synchronised activity are indicated by blue and red areas, respectively. TSE maps are presented in the order of (a) combined visual motion, (b) static non-flow, (c) combined visual motion and static non-flow compared, and (d) corresponding probability maps ($p < 0.05$) for comparisons of combined visual motion and static non-flow. Baseline and epoch length is -100 to 0 and -200 to 800 ms, respectively. Desynchronised activities in the theta and beta frequency ranges were observed in visual regions PM and VCvM in particular (a), with synchronised activities showing up at the same frequencies for the static non-flow condition (b). Comparisons of combined visual motion and static non-flow (c) showed widespread theta desynchronisation, with the most prominent change in activity observed in visual area PM. In addition, desynchronised activities could be observed in the beta range (13–30 Hz). Probability maps of significance ($p < 0.05$) indicated significant decrease in TSE (desynchronisation) in the theta and beta range for visual area PM when comparing the combined motion condition with static non-flow (d).

In the first session, desynchronised theta activities were observed at around 300–800 ms post-stimulus in the TSEs of the combined visual motion condition in both groups of infants (see Figures 7a and 8a), while synchronised activities appeared at the corresponding frequency in response to the static non-flow condition (see Figures 7b and 8b). A decrease in spectral amplitude (desynchronised activity) could further be observed in the beta frequency band for control infants receiving a traditional upbringing. When comparing combined visual motion with static non-flow (see Figures 7c and 8c), theta band synchronisations showed up in the TSE maps of both groups and especially in regional sources PM and VCvM. Additionally, and as was observed for the combined visual motion condition, induced alpha

and beta band oscillatory activities appeared as desynchronisation for traditionally-raised control infants (see Figure 7c and 8c). Statistical testing of the comparisons between combined visual motion and static non-flow revealed that the desynchronised activities in the theta, in addition to activities in the beta frequency band for traditionally-raised infants, differed significantly ($p < 0.05$) from induced activities in response to static non-flow (see Figures 7d and 8d).

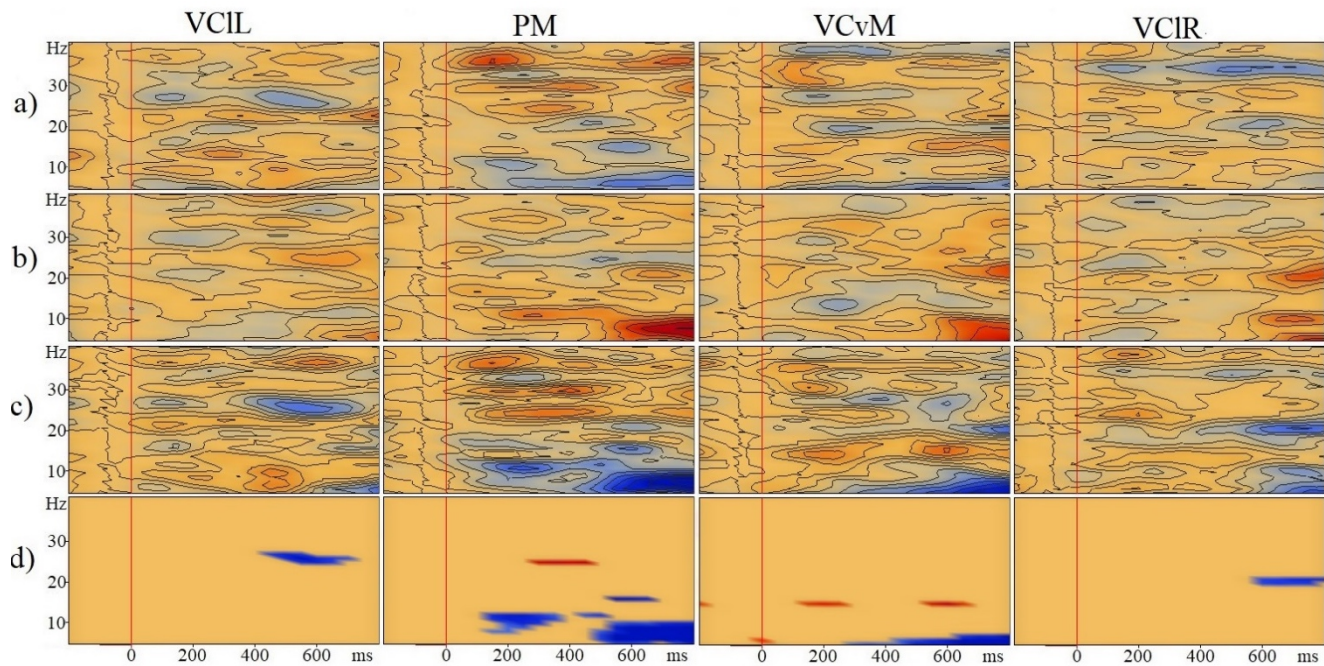


Figure 9. TSE maps for combined visual motion **(a)** static non-flow **(b)**, and the combined visual motion condition and static non-flow compared **(c,d)** for the same typical infant receiving extra stimulation in the second session at 32 weeks of age. Blue areas indicate desynchronised activity, whereas red areas indicate synchronised activity. Epoch length is -200 to 800 ms with baseline set at -100 to 0. Induced desynchronised activities in theta and alpha range, and synchronised activities in the beta band range, were observed in particularly visual areas PM and VCvM for the combined visual motion condition **(a)**. For static non-flow **(b)**, induced expressions of theta and alpha were seen as synchronisation, while induced expressions of beta appeared as desynchronisation. Prominent theta (4–7 Hz) and alpha (7–13) desynchronisations, as well as beta (13–30 Hz) synchronisations, were observed when comparing combined visual motion with static non-flow **(c)**, and particularly in visual areas PM VCvM starting at approximately 200 ms. The corresponding probability maps ($p < 0.05$) indicated that the induced desynchronised and synchronised activities in the theta, alpha, and beta ranges for the combined motion condition were significantly different from the static non-flow condition **(d)**.

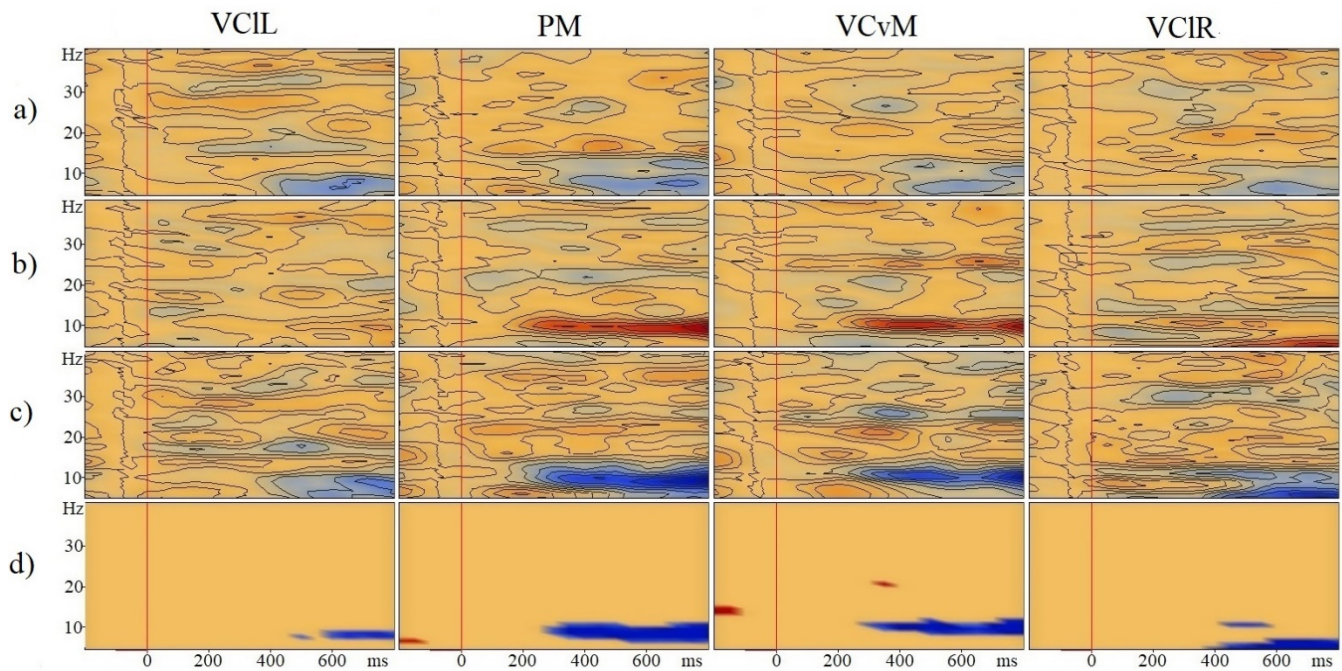


Figure 10. TSE maps illustrating desynchronised (blue areas) and synchronised (red areas) activities for combined visual motion (a) and static non-flow (b) across the visual areas of interest (VCIL, PM, VCvM, VCIR) for the same typical control infant receiving a traditional upbringing in the second session at 48 weeks of age. Settings for baseline and epoch length is -100 to 0 ms, and 800 ms, respectively. Desynchronised activities in the theta-alpha range were observed in the TSEs of the combined motion condition (a). Synchronised activities in alpha range were observed in TSE maps of the static non-flow condition (b).

(c) TSE maps for a typical control infant in the second session when comparing the combined visual motion condition with static non-flow. Induced ERD activities in theta and alpha band were observed in all visual areas of interest, and particularly in visual areas PM and VCvM peaking at around 200 ms.

(d) TSE probability maps from bootstrapping procedure for the same infant in the second session when combined visual motion was compared with static non-flow. Blue and red areas indicate a significant decrease and increase in TSE, respectively. A significant decrease of TSE (desynchronisation) was observed in all visual areas of interest in the theta-alpha band range.

In the second session, TSE maps of the combined visual motion condition revealed desynchronised induced activities in the theta-alpha range, and synchronised activities in the beta frequency range for extra-stimulated infants across all regional sources of interest (see Figure 9a). When extra-stimulated infants perceived the static control scene, the oscillatory activities in the theta-alpha range were rather observed as synchronisation, and the beta band activities as desynchronisation (see Figure 9b). TSE maps of the combined visual motion condition revealed prominent induced activities in the theta, alpha, and beta frequency bands

across all regional sources of interest (see Figure 9c). While induced expressions of theta and alpha oscillations were observed as desynchronisation, the induced beta oscillatory activities were seen as synchronisation (Figure 9c). The desynchronised and synchronised activities were especially prominent in visual areas PM and VCvM around 170–800 ms. The probability maps ($p < 0.05$) confirmed that oscillatory activities in response to visual motion in the theta, alpha and beta band across the regional areas of interest, and for PM and VCvM in particular, were significantly different from oscillatory activities in response to static non-flow (see Figure 9d).

For control infants receiving a traditional upbringing, oscillatory activities in the theta-alpha range appeared as desynchronisation in TSEs of the combined visual motion condition (see Figure 10a), with the same activities being observed as synchronisation in TSEs of the static non-flow condition (see Figure 10b). When comparing induced responses to combined visual motion and static non-flow (see Figure 10c), oscillatory activities could be observed as desynchronisation in the theta-alpha range. These activities were especially prominent around 250-800 ms in regional sources PM and VCvM. As illustrated in Figure 10d, the bootstrapping procedure revealed that amplitudes of the induced theta and alpha activities were significantly larger than oscillatory activities in response to static non-flow.

Taken together, the TSE findings suggest that during the course of the first year, induced responses to visual motion progressed from low frequency activity to oscillatory activity at increasing frequencies. However, as indicated by the synchronised activities in the beta frequency band, the progression appeared to be enhanced in infants that received extra stimulation.

4. Discussion

The present longitudinal study sought to examine the effects of receiving extra stimulation for the development of functional cortical responses to visual motion in the first year of life. Infants receiving extra stimulation and infants receiving a traditional Western upbringing were presented with a visual motion paradigm comprising of black dots simulating forwards optic flow, reversed optic flow, and random visual motion. VEP and TSE analyses were applied on infants' induced and evoked electrical brain responses, respectively, to ascertain whether extra stimulation was associated with enhanced development of visual motion perception.

The VEP analysis revealed that during the course of the first postnatal year, developmental improvements in visual motion perception appeared to be enhanced in extra-stimulated infants. In the first testing session at 3 to 5 months of age, extra-stimulated infants were able to discriminate between different forms of visual motion as they processed structured optic flow (i.e., forwards and reversed optic flow) significantly faster than they did random visual motion, with latencies for forwards- and reversed optic flow occurring at around 340 and 350 ms, respectively. When perceiving visual motion, extra-stimulated infants further processed structured optic flow significantly faster than traditionally-raised infants whose corresponding latencies occurred approximately 50 ms later. These results are contrary to previous findings in normally developing infants, showing visual motion processing in the first few months of life to be characterised by generally slow VEP responses at around 400–440 ms, and no evidence of young infants being able to differentiate between visual motion conditions (Agyei et al., 2015; Agyei, van der Weel & van der Meer, 2016b; Vilhelmsen, Agyei, van der Weel, & van der Meer, 2019). In line with such findings, however, traditionally-raised infants showed generally long latencies at around 400 ms, and showed no significant differentiation between any of the visual motion conditions.

Longer latencies of VEPs have been argued to indicate slower processing of moving visual stimuli (Langrová, Kuba, Kremláček, Kubová, & Vit, 2006), and are attributed in part to the ongoing maturation of neuroanatomical structures (Agyei et al., 2015). 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). In a series of experiments, an increase in cortical thickness has been observed in rat pups raised in stimulating environments (Bennett, Krech, & Rosenzweig, 1964; Forgays & Forgays, 1952; Sirevaag, Black, Shafron,

& Greenough, 1988). Among other things, this increase 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. Although literature on similar effects in humans remains relatively sparse (Jacobs, Schall, & Scheibel, 1993), enriched stimulation in early infancy has proven beneficial for facilitating visual development in preterm infants (Guzzetta et al., 2009), and to possibly enhance maturation of visual dorsal stream-related functions in primates (Kolb & Whishaw, 1998). Given 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, in water, or through baby massage during early infancy may increase processing speed by enhancing brain development of dorsal stream functions.

While traditionally-raised infants were not able to discriminate between motion conditions at 3–5 months of age, infants receiving extra stimulation displayed a greater sensitivity towards coherent visual motion. In explaining this finding, studies have indicated for infants receiving enhanced handling to have a richer perceptual-motor history compared to traditionally-raised infants (Lobo & Galloway, 2012). For example, 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 entail greater amounts of self-generated optic flow, which is argued by Gilmore and Rettke (2003) to provide the foundation from which perceptual information becomes functionalised. The current results may therefore suggest that by the time of the first testing session, 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.

In the second session, VEP results revealed further differences in the developmental trajectories of motion perception between extra-stimulated and traditionally-raised infants. Firstly, and akin to the first session, extra-stimulated infants showed significantly shorter N2 latencies than their traditionally-raised peers, but this time for all of the visual motion conditions and for forwards optic flow in particular, with latencies occurring approximately 100 ms earlier for extra-stimulated infants than for traditionally-raised infants. Secondly,

extra-stimulated infants differentiated between each of the visual motion conditions, showing the fastest processing of forwards optic flow, followed by reversed optic flow, and the slowest processing of unstructured random visual motion. Traditionally-raised infants, on the other hand, significantly decreased their latencies from random visual motion to structured optic flow, with latencies for structured optic flow occurring at around 310–330 ms. Thus, while developmental improvements could be observed for both groups, they appeared of greater magnitude for infants receiving extra stimulation. Interestingly, these results were found despite extra-stimulated infants being on average 6 weeks younger than their peers when tested for the second time, and despite that both groups had equivalent experiences with self-produced locomotion.

Previous longitudinal studies in normally developing infants have demonstrated faster responses to visual motion stimuli towards the end of the first postnatal year (Agyei et al., 2015; Vilhelmsen et al., 2019). In part, this has been attributed to neurobiological development allowing for a smoother flow of transmission with increasing age (Agyei et al., 2016b). Ongoing synaptogenesis, for instance, improves brain functioning by directing the formation of cortical pathways and the pruning of extraneous ones (Huttenlocher & Dabholkar, 1997; Huttenlocher, de Courten, Garey, & Van der Loos, 1982), while myelin formation of white matter fibres further improves conduction speed of nerve impulses (Bluml et al., 2013; Magoon & Robb, 1981). An increase in the rate of metabolic components has further been reported in occipital, parietal, and temporal lobe regions shortly after 3 months of age, followed by an increase in the frontal and association visual cortex at around 6-8 months of age (Gilmore et al., 2004; Klaver, Marcar, & Martin, 2011). As infants approach the end of the first year, ongoing structural and functional maturation of the brain thus facilitates their speed of processing. The significantly shorter latencies displayed by extra-stimulated infants compared to their traditionally-raised peers, despite their overall younger age, may therefore lend support to the notion of accelerated brain development of dorsal visual stream functions in infants receiving extra stimulation.

The ability to differentiate between different forms of visual motion has further been found to typically emerge towards the end of the first year in normally developing infants (Agyei et al., 2015). In addition to maturation, optic flow studies have demonstrated this emergence to be related to the onset of self-produced locomotion (Agyei et al., 2015; Vilhelmsen et al., 2019). Namely, achieving independent locomotion compels infants to pay attention to visual stimuli due to becoming increasingly reliant upon such information for being able to efficiently manoeuvre their surroundings. The improved abilities in

differentiating between different forms of visual motion are therefore likely to have been attributed to the fact that all but one out of the total sample of infants had acquired independent mobility by the time of the second session. However, although the onset of self-produced locomotion appeared to instigate greater sensitivities to optic flow in both groups, this effect was more prominent in extra-stimulated infants.

Scholars have demonstrated visuomotor experiences to play a vital role in the favouring of certain visual stimuli (Anderson et al., 2013; Bell & Fox, 1996; Gilmore, Hou, Pettet, & Norcia, 2007). For instance, an expansion bias during visual motion processing has been found in both adults and locomotor infants, likely due to ecological egomotion typically proceeding in a forwards manner (Agyei et al., 2015; Shirai et al., 2009; van der Meer et al., 2008). The presence of this bias in extra-stimulated infants therefore suggests that they had more experiences with self-generated optic flow than their peers, who were yet to differentiate between expanding and contracting patterns of flow. Considering the equivalent locomotion experience in the two groups, this furthers the proposition of enriched stimulation acting as a facilitating agent in advancing development through providing infants with active visuomotor experiences.

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 static non-flow, induced expressions of theta band (4–7 Hz) desynchronisation were seen in both groups. The finding corroborates earlier studies showing infant EEG to be dominated by low-frequency activity with larger amplitudes during processing of visual motion stimuli (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 view of this, Agyei et al. (2016a) propose 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. As such, the widespread theta activities observed in the present study may be interpreted as a general sign of immaturity. However, overall theta activities appeared as less widespread in extra-stimulated than in traditionally-raised infants. This could indicate that fewer yet more specialised neurons were employed during visual motion processing in extra-stimulated infants.

On the other hand, recent evidence suggests theta oscillations to be implicated in synaptic plasticity and the encoding of new information (Kahana, Seelig, & Madsen, 2001). Considering that optimal synaptic plasticity occurs in the first months of life (Huttenlocher et al., 1982), it is plausible that the increases in low-frequency power in part could have reflected the emergence of functional couplings between synapses employed in the processing of visual motion. Moreover, while induced changes in theta band frequency could be observed as desynchronisation in the TSE maps of visual motion, the same activities appeared as synchronisation in the TSE maps of static non-flow. Thus, whereas neurons were indicated to fire in synchrony when infants perceived a static scene, the same activity was instead suppressed when infants perceived visual motion. The present findings are comparable to previous observations indicating suppression of theta rhythms to be a general property of cortico-cortical communication during visual motion processing in infancy (Agyei et al., 2016b). Lastly, the prevalence of desynchronised theta band activities has further been proposed by Pfurtscheller and colleagues (1994) to reflect an increment in task complexity and mental effort. Differences in oscillatory activities can therefore be partially attributed to visual motion being perceived by infants as more complex than the relatively less complex static scene.

In conjunction with previous literature demonstrating an increase in higher frequency power with age (e.g., Vilhelmsen et al., 2019), the TSE results revealed induced changes in oscillatory activities in the alpha frequency band (7–13 Hz) for both groups of infants in the second session. These higher-frequency activities appeared as desynchronisation in the TSE maps when combined visual motion was compared with static non-flow, as was also found by Vilhelmsen et al. (2019). Several scholars propose enhancement of alpha suppression to reflect a preparatory state of neuronal networks (Lopes Da Silva, 1991; Pfurtscheller et al., 1994; Vilhelmsen, van der Weel, & van der Meer, 2015), and to be functionally linked to cognitive, visual, and attentional processes (Doppelmayr, Klimesch, Hodlmoser, Sauseng, & Gruber, 2005; Marrufo, Vaquero, Cardoso, & Gomez, 2001; Sauseng et al., 2005). As visual stimulation has been found to elicit induced alpha oscillations in adults, the present finding could be indicative of more adult-like responses coming online with age and experience towards the end of the first year of life.

In addition to induced alpha desynchronisation, synchronised activities in the beta band frequency (13–30 Hz) could be seen in the TSE maps for extra-stimulated infants when comparing the combined visual motion condition with static non-flow 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 oscillating neuronal networks responsible for rhythmic activity in the alpha frequency range, beta band rhythms are implied to involve fewer but more specialised neurons (Pfurtscheller, Stancak Jr, & Edlinger, 1997). As these rhythms have further been reported in response to optic flow stimuli in adults (van der Meer et al., 2008), expressions of beta oscillations in extra-stimulated infants, and the lack thereof in traditionally-raised infants, suggests that induced responses were developmentally advanced in the former. In support of this, extensive research has demonstrated gamma band activity in response to visual motion in adults (Hoogenboom, Schoffelen, Oostenveld, & Fries, 2010; Hoogenboom, Schoffelen, Oostenveld, Parkes, & Fries, 2006; Orekhova et al., 2015). As such, it is likely that the increase in frequency of oscillations with age is indicative of the emergence of more sophisticated brain operations affording more rapid couplings between smaller yet more specialised populations of neurons (Schmidt & Segalowitz, 2008).

Expressions of beta oscillations could further explain the significantly shorter latencies for VEPs displayed by extra-stimulated infants in the second session. Namely, 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). The simultaneous occurrence of desynchronised and synchronised responses within the alpha-beta band have therefore been implied to enhance functional connectivity, in turn allowing faster transmission and consolidation of sensory information (Ganzetti & Mantini, 2013). As cortical oscillations to a large degree depend on the constraints placed by the neocortical architecture of the brain, it is possible for a faster rate of brain development to have afforded an earlier increase in frequency of oscillations in extra-stimulated infants.

The results add 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). However, and perhaps most importantly, the interplay between the two was found to be affected by whether infants had received extra stimulation or not. Thus, while improvements in visual motion perception in traditionally-raised infants are likely to have been attributed to increased maturation and onset of self-produced locomotion, enriched stimulation constituted an important factor in facilitating visual motion perception in extra-stimulated infants. The present brain research therefore expands on previous findings demonstrating developmental behavioural advancements in infants receiving enriched

stimulation (Adolph & Hoch, 2019; Karasik et al., 2010) by examining this link from a neurodevelopmental perspective. Consequently, the results obtained may also prove beneficial for future attempts to minimise delays in infants at risk for abnormal visuomotor and neurological development.

Recent studies have implied EEG to be a suitable screening tool for uncovering atypical development of visual motion perception in preterm infants (Agyei et al., 2016b; Madan, Jan, & Good, 2005; Zotcheva & van der Meer, 2016). For instance, the development of visual motion perception in preterm infants born at gestational age of 33 weeks was found by Agyei and colleagues (2016a) to deviate from previously observed trajectories in which infants become increasingly skilled in detecting and processing visual motion across the first year of life (Agyei et al., 2016b; Agyei et al., 2015; Vilhelmsen et al., 2019). Similarly, Vilhelmsen, Stople, van der Weel, and van der Meer (2020) examined whether preterm birth was associated with long-term developmental delays in infants' cortical responses to visual motion. In line with earlier research showing preterm birth to be associated with long-term impairments (Braddick et al., 2003; Hammarrenger et al., 2007; Leung, Thompson, Black, Dai, & Alsweiler, 2018; Lindström, Winbladh, Haglund, & Hjern, 2007; Taylor, Jakobson, Maurer, & Lewis, 2009), children born preterm showed delays in their development at 6 years of age compared to children born full-term (Vilhelmsen et al., 2020). These findings have been proposed to be attributed to vulnerabilities of the visual dorsal stream (Braddick et al., 2003; Hammarrenger et al., 2007; Taylor et al., 2009). Early detection of possible anomalies could therefore be crucial for minimising future difficulties in abilities dependent upon this stream.

Existing interventions aimed at minimising delays in preterm infants have been suggested to be most beneficial 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 corroboration with such findings, cultural and theoretical studies have demonstrated daily handling and interaction patterns between caregivers and their infants to exert significant influence on developmental outcomes (Karasik et al., 2010; Karasik et al., 2015; Lobo & Galloway, 2012). Considering this, it is likely for the present results to have pertained not only to the specific enriched activities received by extra-stimulated infants, but also to the overall handling patterns of their caregivers. The current research therefore offers further testimony to the key role played by caregivers in the developmental trajectories of their infants.

Additional longitudinal investigations are warranted in order to fully understand the mechanisms by which enriched stimulation may facilitate the development of motion perception in normally developing infants, and to ascertain whether these effects are generalisable to preterm cohorts. Given the challenges associated with infant EEG data (Noreika, Georgieva, Wass, & Leong, 2020) and the relatively small sample used in the present study, future investigations should seek to address these issues and aim to include a larger sample for increasing statistical power for findings. Moreover, future studies may wish to more closely examine whether different amounts of extra-stimulation results in developmental differences, as this was not the focus of the current paper.

In conclusion, the present longitudinal study is among the first to demonstrate an association between receiving extra motor stimulation in infancy and accelerated development of visual motion perception. Results revealed that infants receiving a traditional upbringing follow 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 the course of the first year of life. When the TSEs of combined visual motion were compared to the TSEs of static non-flow, traditionally-raised infants displayed a progression from low-frequency desynchronisation in theta band frequencies to higher frequency desynchronisation in alpha band frequencies with age. These improvements have been attributed to neurobiological maturation and increased experience with self-produced locomotion.

Infants receiving extra stimulation, on the other hand, showed an overall greater sensitivity to visual motion than their traditionally-raised peers during the whole of the first year as reflected by their shorter latencies in response to visual motion. Further, extra-stimulated infants processed structured optic flow more efficiently than they did random visual motion in the first session, and forwards optic flow more efficiently than they did reversed optic flow and random visual motion in the second session. TSE maps showing extra-stimulated infants' induced responses when comparing combined visual motion with static non-flow, revealed desynchronisation in theta band frequencies in the first session, and induced oscillatory activities in alpha-beta band frequencies in the second session. Hence, an enhanced development of visual motion perception was demonstrated in extra-stimulated infants, likely due to having been provided with early enriched stimulation experiences by their caregivers. This finding does not only attest to the important role played by experience in advancing development, but challenges the often assumed universality of developmental trajectories of psychological functions in Western cultures as well (Adolph & Hoch, 2019). As the ways in which cultures view motor development are likely to affect the boundaries set

for the possibility to influence it, the current research may therefore prove beneficial for infants at risk for abnormal development of visual motion perception.

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APPENDICES

Appendix A - Information leaflet provided to parents prior to the start of the experiment.



Fakultet for samfunns- og utdanningsvitenskap
Institutt for psykologi
Nevrovitenskapelig utviklingslaboratorium (Nu-Lab)

Vår dato
07.07.2020

Vår referanse
Audrey van der Meer

FORESPØRSEL TIL FORESATTE OM FORSKNING PÅ BARN

EEG-STUDIE AV HJERNEUTVIKLING HOS SPEDBARN

Vi ønsker å finne ut hvordan spedbarn oppfatter omverdenen. Dere som får dette brevet har en baby under 12 måneder. Hensikten med prosjektet er å undersøke hjernens funksjon og dens utvikling ved å registrere elektrisk hjerneaktivitet, mens barnet holder på med enkle visuelle og auditive oppgaver på en skjerm. Vi ønsker å få kunnskap om hvordan en babyhjerne fungerer og hvordan den utvikler seg med alderen hos terminfødte og for tidlig fødte spedbarn. Det forventes at grunnleggende kognitive ferdigheter (sansemotoriske evner, hukommelse, oppmerksomhet) blir kartlagt. Dette kan lære oss å forstå de minste bedre, og på sikt hjelpe barn der hjernen ikke fungerer helt som den skal.

HVA INNEBÆRER PROSJEKTET?

Studien innebærer som regel to oppmøter i løpet av det første leveåret ved Nevrovitenskapelig utviklingslaboratorium (Nu-lab) på NTNU Dragvoll. Deltakelsen i prosjektet vil foregå under en times besøk. Barnet vil ha på seg en helt ufarlig hette med små sensorer og ledninger, og se på film mens det sitter på fanget til mor/far eller i en bilstol med en av foreldrene rett ved siden. Prosjektet vil pågå til slutten av 2030.



MULIGE FORDELER OG ULEMPER

Opgaven til babyen er å se på bevegelige ting på skjermen mens det har på seg sensorhetten. Undersøkelsen er ufarlig og vil ikke medføre ubehag. Hvis barnet ikke trives med situasjonen blir forsøket avsluttet med en gang. Dersom deltakelse i prosjektet skulle gi mistanke om sykdom eller skade hos barnet, kan dere få henvisning til riktig helsetjeneste. For oppmøte og testing ved Nu-lab på NTNU/Dragvoll dekkes bussbillett eller parkeringsavgift.

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7491 Trondheim
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Org.nr. 974 767 880
kontakt@ips.ntnu.no
<http://www.ntnu.no/psykologi>

Besøksadresse
Nu-lab
Bygg 12, nivå 2 (12-296)
NTNU Dragvoll

Telefon
+47 73 59 19 60

FRIVILLIG DELTAKELSE OG MULIGHET FOR Å TREKKE SITT SAMTYKKE

Det er frivillig å delta i prosjektet. Vi tar kontakt og dersom du ønsker at barnet ditt skal delta, undertegner du samtykkeerklæringen på siste side og leverer det ved oppmøte hos oss. Du kan når som helst og uten å oppgi noen grunn trekke ditt samtykke. Dersom dere trekker dere fra prosjektet, kan dere kreve å få slettet innsamlende prøver og opplysninger, med mindre opplysningene allerede er inngått i analyser eller brukt i vitenskapelige publikasjoner. Dersom du senere ønsker å trekke barnet ditt eller har spørsmål til prosjektet, kan du kontakte Audrey van der Meer, tlf. 918 97 522, audrey.meer@ntnu.no.

HVA SKJER MED OPPLYSNINGENE OM BARNET?

Opplysningene som registreres om barnet skal kun brukes slik som beskrevet i hensikten med prosjektet. Dere har rett til innsyn i hvilke opplysninger som er registrert om barnet og rett til å få korrigert eventuelle feil i de opplysningene som er registrert. Dere har også rett til å få innsyn i sikkerhetstiltakene ved behandling av opplysningene.

Alle opplysningene vil bli behandlet uten navn og fødselsnummer eller andre direkte gjenkjennende opplysninger. En kode knytter barnet til dets opplysninger gjennom en navneliste. Det er kun prosjektleder og prosjektkoordinator som har tilgang til denne listen. Det vil ikke være mulig å identifisere barnet når resultatene offentliggjøres. Hvis barnet har deltatt tidligere i denne studien, ønsker vi å sammenholde tidligere og nåværende opplysninger.

FORSIKRING

Pasientskadeloven gjelder for barnets undersøkelse ved NTNU Dragvoll.

OPPFØLGINGSPROSJEKT

Det kan bli aktuelt å invitere barnet til nye undersøkelser i denne langtidsstudien.

ØKONOMI

Prosjektet er delvis finansiert av NTNU og EU, og utstyret er finansiert av Norsk forskningsråd.

GODKJENNING

Regional komité for medisinsk og helsefaglig forskningsetikk har vurdert prosjektet, og har gitt forhåndsgodkjenning (Saksnummer [2010/1273](#)).

Etter ny personopplysningslov har dataansvarlig og prosjektleder Audrey van der Meer et selvstendig ansvar for å sikre at behandlingen av deres opplysninger har et lovlig grunnlag. Dette prosjektet har rettslig grunnlag i EUs personvernforordning artikkel 6a og artikkel 9 nr. 2 og ditt samtykke.

Du har rett til å klage på behandlingen av barnets opplysninger til Datatilsynet.

KONTAKTOPPLYSNINGER

Dersom du har spørsmål til prosjektet kan du ta kontakt med:

Prosjektleder: Audrey van der Meer e-post: audrey.meer@ntnu.no tlf: 918 97 522
Personvernombud ved institusjonen er Thomas Helgesen, thomas.helgesen@ntnu.no.

