Longitudinal study of infants' and children's perception of optic flow and random visual motion using high-density EEG

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Abstract

A longitudinal electroencephalogram (EEG) study was performed with 5 participants tested for 3 sessions at age 4 and 12 months and 6 years to study brain electrical activity responses to perception of structured forwards optic flow, structured reversed optic flow, and non-structured random visual motion. Analyses of visual evoked potentials (VEP) and time-spectral evolution (TSE) were conducted on EEG data recorded with 128- and 256-channel Geodesic Sensor Net 200 (GSN). Children's motor skills were also tested with Movement ABC battery. A significant decrease in latency was found with increasing age. No significant effect of visual motion condition or interaction effect was found. Individual TSE analyses revealed that infants at 4 months primarily displayed desynchronized theta-band activity for motion stimuli, and synchronized theta-band activity for static non-flow stimuli. The 12-month-old infants showed much of the pattern of the children, however with more activity in alpha- and beta-band range. Children had a further increase in alpha- and beta-band activity, as well as increased synchronized activity to motion stimuli that is more in accordance to the previous findings in adults. The development of visual perception of optic flow is believed to be an interacting process between neurobiological development and increased self-produced locomotor experience. A larger number of participants is necessary to further investigate the development of visual motion perception from infancy to childhood.

1. Introduction

Visual motion perception is crucial for navigating in the environment and provides important information for prospective control, the ability to guide and control movements in an appropriate way in relation to the world around us (Lappe, Bremmer, & Van den Berg, 1999). Prospective control plays a role in every activity we perform, including movements, cognitive skills, and even social interactions (Bruce, Green, & Georgeson, 2003). How we move around other people or objects in the environment is largely a result of visual motion perception, including the perception of optic flow (Turano, Yu, Hao, & Hicks, 2005). The information from optic flow is an essential source to prospective control. Optic flow is the pattern of visual motion of the eye when we are moving relative to our environment (Gibson, 1950). If we travel in a straight line, the point that is straight ahead in the direction we are traveling will expand. A flow will radiate from the center of expansion, the point we are heading. Whenever we move backwards, the point we are moving away from will shrink and the flow will seemingly radiate towards the point (Bruce, et al., 2003). This means that people rely on optic flow when walking towards a goal (Warren, Kay, Zosh, Duchon, & Sahuc, 2001), and the information in the optic flow helps in the control of the force of each step, length of each stride, as well as walking direction and walking speed (Bruce et al., 2003).

Visual information leaving the retina through lateral geniculate nucleus (LGN) reaching higher cortical areas in visual cortex is divided into two main pathways after V2, the ventral and dorsal pathway. These two pathways work separately, but with some interaction. The ventral pathway is associated with object recognition, while the dorsal pathway is associated with visual motion perception. The dorsal stream runs through V3 and V3A before reaching V5/Medial Temporal (MT) and Medial Superior Temporal (MST) (Callaway, 2005). The neurons in V5/MT and MST are specialized in processing information of radial motion (Layton, & Fajen, 2016). This is supported by several physiological studies who have attempted to map the cortical areas associated with perception of motion, like functional magnetic resonance imaging (fMRI) (Duffy, & Wurtz, 1991; Smith, Wall, Williams, & Singh, 2006; Wall, & Smith, 2008) and positron emission tomography (PET) scan (Ptito, Kupers, Faubert, & Gjedde, 2001). Studies of transcranial magnetic stimulation (TMS) have also found that when magnetic stimulation was applied over the MT/V5 area the participants showed an impairment in motion perception (Stevens, McGraw, Ledgeway, & Schluppek, 2009).

The ability to perceive motion seems to develop within the first three months of human infancy (Gilmore, Baker, & Grobman, 2004), and becomes increasingly important as the infant grows older and movements are becoming increasingly independent and complex. Because motor abilities and movements in relation to the environment are linked intimately to visual motion perception, it is reasonable to think that children's visual and motor development are not two separate processes but rather one interactive process. Children with developmental coordination disorder have shown to score worse in visual perception skills, than children without the disorder (Prunty, Barnett, Wilmut, & Plumb, 2016). Premature children, who have been linked to clumsiness, have shown in electroencephalography (EEG) studies to develop later than their full-term peers in the ability to distinguish direction of optic flow and random motion (Agyei, Van der Weel, & Van der Meer, 2016).

Optic flow has been used studying infants and adults with eye-tracking tools. Infants younger than 12 months showed an advantage in detecting reversed optic flow, while adults showed an advantage in detecting forwards optic flow (Shirai & Imura, 2016). This may be attributed to young infants' avoidance response to approaching objects. Infants' neurological development and increasing ability to move themselves is what is believed to be the reason for improvement in distinguishing and processing optic flow patterns (Gilmore et al., 2004).

In EEG studies, one has investigated the visual evoked potentials (VEPs) of the electrodes in the brain areas associated with visual perception. Motion VEPs are characterized by a negative N2 peak. The N2 peak usually appears at 130-200 milliseconds (ms) in adults, 270-290 ms in 12-month-old infants and 400-430 ms in 4-month-old infants (Van der Meer, Fallet, & Van der Weel, 2008; Agyei, et al., 2015). Sensitivity of radial optic flow seems to improve with age, however it is still not fully developed at the age of 16. This may be attributed to involvement of higher cortical areas, like MST, and that this areas has yet to mature (Joshi, & Falkenberg, 2015). Infants tested at 4 months and 12 months show a significant decrease in latency of the N2 component, which is associated with visual perception (Agyei, et al., 2015). Infants as young as 3 months are able to discriminate between various directions of optic flow (Gilmore, et al., 2004). However, it seems that if infants have had a normal neurological development and locomotor experience, they will rely more on information from structured optic flow at the age of 12 months. At this age, the latencies are shorter for both forwards and reversed optic flow as well as for random motion. The 12-month-old infants are also better at discriminating between forwards optic flow, reversed optic flow and random motion, showing the shortest latency for forwards optic flow and the longest latency for random motion (Agyei, et al., 2015). There has been little research on visual evoked potentials in elementary school children looking at the N2 component. However, adults show shorter latencies overall than infants and are also better at discriminating forwards and reversed optic flow and random motion (Van der Meer, et al. 2008). In investigating adults' perception of structured forwards optic flow in different speeds, the findings were that the high speed resulted in shorter latencies than those of low and medium speed. Indicating that faster speed is more demanding to process (Vilhelmsen, Van der Weel, & Van der Meer, 2015). A non-EEG study found that from the age of 6 to 17 years of age, children seem to gradually improve at discriminating direction of motion and reaching mature level of visual motion perception at 14 years. (Bogjellmo, Bex, & Falkenberg, 2014). This may implicate that 6-year-old children will be better at discriminating direction of optic flow than when they were infants, but as they are not fully matured they will not show the same results as adults.

EEG-studies investigating the development of visual motion perception during human infancy have investigated induced time-spectral evolution (TSE). Eight-month-old infants showed theta-band event-related desynchronization (ERD) when watching optic flow whereas they showed theta-band event-related synchronization (ERS) when watching a static dot pattern. The adults in the study showed beta-band ERS for motion stimuli and beta-band ERD for static stimuli (Van der Meer, et al. 2008). Both 4- and 12-month-old infants have shown theta-band desynchronized activity. However, the 12-month-old infants in addition showed alpha-band synchronized activity, implicating that they are maturing towards a more sophisticated way of processing visual motion in the brain (Agyei, et al., 2015).

The aim of this current study is to investigate perception of optic flow and random motion 4- and 12-month-infants and 6-year-old-children using high-density EEG. In light of previous research it is believed that there will be an improvement in perception of optic flow with increasing age. However, 6-year-old children are likely not to have reached the same level of development that has been found in adults. The latency in general of the N2 component was expected to decrease with age. Compared to the 4-month-olds, the 12-month-olds and 6-year-olds are believed to be better at discriminating forwards optic flow, reversed optic flow and random motion, with the shortest latency of forwards optic flow and the longest for random motion. There is also an expectation that 6-year-olds will show increased beta-band activity.

2. Method

2.1 Participants

Five healthy, full-term Norwegian children were participating in this longitudinal study, three boys and two girls. As infants the subjects were recruited through birth announcements and by contacting parents. Participants were born 2009-2010. First and second sessions took place in 2010-2011, while third sessions took place in 2016-2017.

At the first session, infants had the mean age of 17 weeks (SD=2.4), ranging from 16 weeks to 22 weeks. The infants did not have any crawling experience at this age

The same subjects came back for a second testing session, when they had reached the mean age of 50 weeks (SD=1.6). The youngest was 49 weeks and the oldest was 52 weeks old. At this age the infants had crawling experience, but had not started to walk independently yet.

For the third testing session, the children had reached a mean age of 6.4 years (SD=0.6), the youngest being a few days away from turning 6 and the oldest being 7 years and 2 months. All children were right-handed.

EEG recording is completely safe and causes no physical harm or pain to the participant. Prior to the experiment, the parents were informed about the experiment and they gave their written consent. They were made aware that they at any time could withdraw from the experiment, either before, during or after. A parent would always be seated next to the infant or child during the experimental testing. The exception was for the Movement ABC, where the parent would be in an adjoined room with the door open so the child at any moment could make contact with the parent. The study has been approved by Norwegian Regional Ethics Committee and the Norwegian Data Services for the Social Sciences.

2.2 Experimental stimuli and paradigm

The stimuli of optic flow were programmed in E-Prime 3.0 and mirror-reversed projected onto a wide white screen (1.1 m x 0.8 m) with a visual angle of 68° horizontal and 47° vertical. Resolution of the images was 593 pixels per metre at a refresh rate of 60 Hz. In order to distinguish structured and non-structured radial motion, stimuli were shown in three conditions. These three conditions were forwards optic flow, reversed optic flow and random visual motion. In addition, there was a static non-flow condition. In all conditions, 100 black dots with a virtual radius of 5 mm were randomly positioned on the screen. All conditions were presented for a duration of 1.5 s, while the stimulus contrast was 99.5 % and mean luminance was 68 cd/m^2. The dots moved at a constant rate of 30 mm per frame at 6 fps in a manner of moving inwards and towards, or outwards and away, from a fixation point at the centre of the screen. The fixation point had a diameter of 1.69 mm and an angle of 0.16 degrees. When the dots appeared at the centre they were virtually far away and thus smaller and would grow larger as they came closer, or vice versa. The size of the dots could range from 2 mm to 17 mm in radius and the change in size happened at a rate of 0.025 pixel per pixel in reference to the fixation point.

In the forwards optic flow condition, the dots would move towards the child in a coherent manner, the movement was parallel to the z-axis towards the eye with zero velocity in the x- and y-axes. Reversed optic flow was very similar to the forwards optic flow with the exception that the dots moved in the opposite direction and away from the child. In the random motion condition, the dots moved incoherently in random directions. In the static condition the dots did not have any velocity and remained in the same position on the screen for the entire trial. The order the conditions were presented in was random, but the static condition was always appearing in between the motion conditions in order to avoid motion adaptation.

2.3. Data Acquisition/Materials.

Recording of the EEG activity was performed by a Geodesic Sensor Net (GSN) 200. A net consisting of 128 Ag/AgC1 sensors was evenly distributed across the infants' scalp. The 6-year old children used a net consisting of 256 Ag/AgC1 sensors. The sensors were evenly distributed across the infants' and children's scalp. A high-input EGI amplifier was connected to the GSN 200 so the signals would be amplified with maximum impedance set to the value of 50 KΩ for optimal signal-to-noise ratio. Net Station software on a Macintosh computer recorded and sampled amplified signals at 500 Hz. Eye movements and gaze of infants and children were tracked by using Tobii X50, with visual feed processed by ClearView software on a HP computer. Two additional cameras recorded digital videos to track the behaviour of participants during the experiment. Recorded data were stored for offline analyses.

Movement Assessment Battery for children was used to test the children when they came back for their third session. Movement ABC is an assessment battery for identifying motor function impairment in children, but can also be used in experimental studies. There is both quantitative and qualitative scoring. If the total score of the child is above 10.0 it can suggest motor impairment (Henderson & Sugden, 1992). A camera was also used to film this session, to later be able to monitor any deviating behaviour during the test.

Figure 1. *4-months-old infant with EEG-net with 128 electrodes placed on his scalp. The infant was seated on his mother's lap while the net was placed unto his head.*

2.4. Procedure

At their arrival for the first testing session, the parents of the infants signed the consent form before the onset of the experiment. The infants were given time to get used to and comfortable with the surroundings of the laboratory by playing with toys and exploring the environment. The 6-year-olds were shown a photo of them participating as infants to make it less intimidating to wear the electrode net. During this time an assistant measured the circumference of the participant's head to select the correct size of the GSN 200. The net was then immersed in a saline electrolyte solution to ensure the best possible electrical conductivity. The net was partially dried before it was placed on the participant's head, during which infants would be seated on their parent's lap and were distracted by soap bubbles and toys.

After the net was placed on the participant's head, they were moved into a dimly lit experimental room. Figure 1 displays infant with EEG-net on. Experimental assistants moved to the control room, where they managed the computers used for data acquisition. The experimental room and control room were separated by a transparent glass window. The infants were seated on their parent's lap or in a baby car seat during the first testing session, in a baby car seat during the second testing session, while the children were seated in a chair with a pillow in their backs during the third session. In all three sessions the parent sat close by in the experimental room. The net was connected to the amplifier and the impedance of the electrodes was controlled and improved if necessary. An assistant was present in the experimental room to monitor the experiment and help the infant or child to focus on the screen. The parent was present for the entire duration of the experiment to avoid any stress effect the absence of a parent may have on an infant or child.

The experimental session started immediately after calibrating the infants' and children's eye movement in virtual space to the Tobii X50 camera. The session began with the optic flow experiment followed by two other visual motion experiments. The optic flow experiments lasted for 5 to 7 minutes. Approximately half of the 80 to 120 trials presented per infant were static non-flow trials. Data acquisition was carried out in one block, however, when the infant showed sign of boredom or had lost interest, the session was paused so the assistant and/or parent could revive the level of interest by playing with the infant for a short time before resuming the experiment. An experimental session was ended when the participant showed considerable level of disinterest, fussiness or tiredness.

In the third testing session, the children would in addition be tested on the Movement ABC. After removal of the electrode net, the children would have a 15-minute break with some snacks and juice before they started the tasks of the Movement ABC. One assistant would explain and show the various tasks, and help the child to focus. Another assistant noted the scores and managed the video camera. The videos would later help to control the scoring results and the qualitative assessment. Qualitative assessment would be any observed emotional, motor or behavioural deviations. The Movement ABC tested the children's manual dexterity, ball skills and static and dynamic balance. The tasks for manual dexterity were posting coins, threading beans, and bicycle trail. The tasks for ball skills were catching bean bag and rolling ball into goal. The static and dynamic balance tasks were one-leg balance, jumping over cord and walking heels raised. In all the Movement ABC tasks the child would be shown by the experimental assistant and would then have a practice trial before the actual test. While the children performed the Movement ABC tasks, a parent would fill out a checklist to assess their views on their child's movements in everyday situations. The checklist consisted of specific situations, where the parent would give a score from 1-5.

2.5. Data analysis.

Analysis of EEG data was performed with Brain Electrical Source Analysis (BESA) research software version 6.1 and BESA statistics 2.0 (BESA GmbH). The EEG recordings were segmented with the Net Station software and exported as raw files for further analysis. Files consisting of the appropriate trigger and sensor information were imported and attached. Averaging epoch was set at -200 to 800 ms at baseline definition of -100 to 0 ms. For the data from the first two sessions, high-pass filter was set at 1.5. Hz to remove slow-drift, while low-pass filter was set at 60 Hz. For removal of line interference from recorded data, notch filter was set at 50. Channels and epochs that were artefact-contaminated caused by head or body movements or participant not looking at screen were interpolated or excluded from analysis when required. During the artefact scan the threshold values for gradient and low signal were set at 75 μV and 0.1 μV, with maximum amplitude set at 200-230 μV. Artefacts, e.g. blinking and eye movements, were corrected by using manual and semi-automatic artefact correction that was designed to separate brain activities from artefacts using the fitting spatial filters. All threshold values and filters were set to the same values for all participants

Individual EEG data from each infant and child were averaged and interpolated into standard 81-electrode configuration of 10-10 international system and re-referenced to an artificial reference calculated from average potentials over the scalp. VEP peak analysis was performed by using these individual averages and combining them into grand averages for each of the three sessions. Individual N2 component at different electrode sites were chosen by the approximate time intervals given by grand average VEPs. 3D spherical spline whole-head voltage maps of EEG scalp signals aided in visualizing N2 activity in occipito-parietal areas for the most dominant VEP waveforms. The values for peak latencies and peak amplitudes of individual averages were recorded for further VEP analysis. Peak latencies were measured as time of stimulus onset to peak of each scalp N2 component. Peak amplitudes were measured as maximum amplitudes of N2 component in relation to the pre-stimulus baseline.

Time-frequency analysis was carried out in brain space using pre-defined multiple source dipoles that modeled activities in the visual areas of the parietal and visual cortical regions. In order to obtain optimal separation of focal activities, a source montage was used. The source montage was a multiple source model where source waveforms separated activities and the various brain regions, and had 17 sources modelling activities in the visual pathway and residual activities in other areas of the brain. The sources were relevant brain areas, which were the visual cortex bilateral left (VCbL), visual cortex lateral left (VClL), visual cortex radial left (VCrL), parietal midline (PM), visual cortex radial right (VCrR) and visual cortex lateral right (VClR). For the analysis of the brain activities, a head model for the appropriate age groups with source dipoles (Figure 1) inserted was created and the artefact-corrected coordinate files were added.

The same settings for epoch, filters and averages parameters as in the VEP analysis were used. Time-frequency displays represent changes in amplitude over time and frequency normalized to baseline of each frequency. The displayed graphs were a plot of spectral amplitude density of one montage channel over time and frequency normalized to the baseline for each frequency. Because only TSE displays of induced brain activities were investigated, the signals from average evoked responses were subtracted from single trial time series before calculation of TSE. Computation of comparisons between motion conditions and static non-flow condition were performed. Frequency cut-offs of TSE-displays were set to 4-40 Hz and frequency and time sampling set at 1 HZ and 50 ms.

3 paired t-tests were conducted in BESA statistics 2.0 (BESA, GmbH) to calculate for significant differences in amplitude and frequency values in all visual motion conditions and static non-flow in the TSEs for all three sessions. There were separate t-tests for each sessions, where TSE data from all participants were averaged and analyzed together. BESA statistics uses a combination of permutation testing and data cluster (Maris, & Oostenveld, 2007) in order to avoid multiple comparison problem. There were 32 permutations for each t-test. Epochs and frequency ranges were the same as in time-frequency analysis.

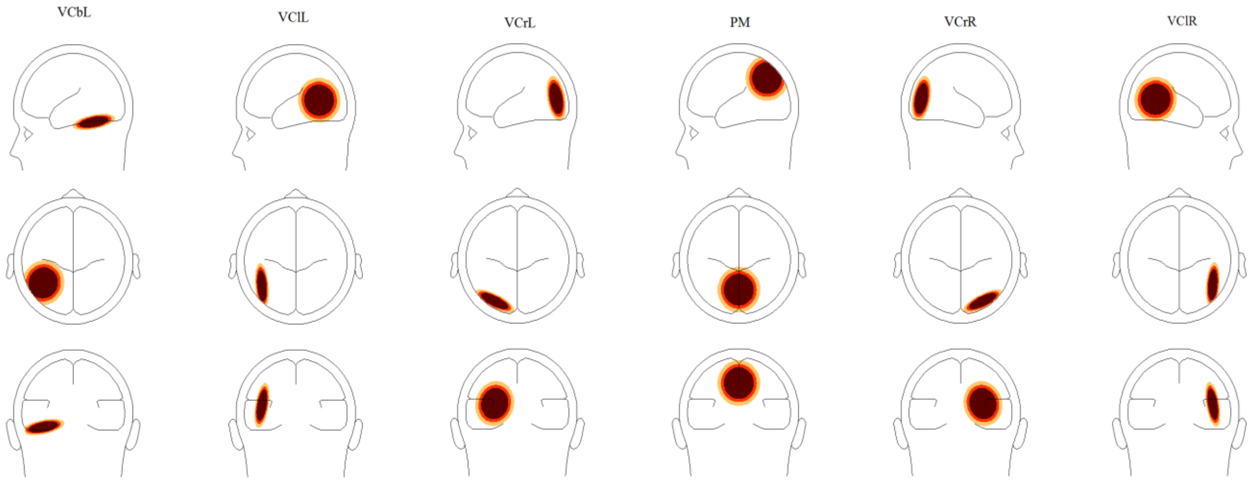

Figure 1. *Head model showing visual cortical areas of interest. From left to right VCbL, VClL, VCrL, PM, VCrR. and VCrL.*

3. Results

3.1. VEP responses.

For the infants at both 4 months and 12 months, 4 posterior electrodes were chosen for further analysis. These electrodes had the highest N2 amplitude values in the forwards optic flow condition of the grand average VEPs. For the 4-month-old infants, electrodes POz, PO3, Oz and O2 were chosen. The electrodes chosen for the 12-month-old infants were POz, PO8, Oz and O2, while the electrodes for the 6-year-olds were POz, PO4, Oz and O2 (Figure 2).

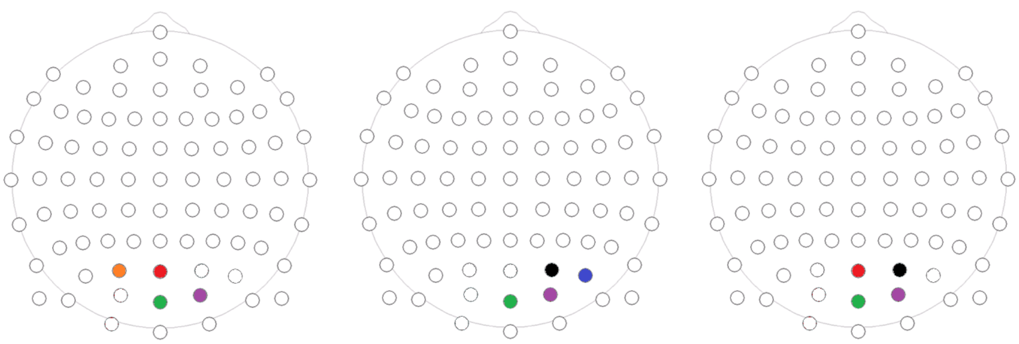

Figure 2. *Head map (nose up) showing scalp localization of the 81 standard electrodes. From left to right: infants at 4 months, infants at 12 months and children at 6 years. The four electrodes of interest are marked with the colours: POz (red), PO3 (orange), PO4 (black), PO8 (blue), Oz (green) and O2 (purple).*

VEP latencies and amplitudes were separately analyzed with repeated-measures ANOVA. The within-group factor was motion condition (forwards optic flow, reversed optic flow, random motion) and age (4 months, 12 months, 6 years). Adjustment for multiple comparisons was made by a Bonferroni correction. VEP latencies and amplitudes are displayed in Figure 3.

The mean N2 peak latency (Figure 4a) for the 4-month-old infants in forwards optic flow condition was 358 ms (SD=38). The values for reversed optic flow and random motion were 348 ms (SD=55) and 414 ms (SD=52), respectively. For the 12-month-old infants in the forwards optic flow condition the mean N2 peak latency had declined to 267 ms (SD=36). The latencies for reversed optic flow and random motion were 305 ms (SD=70) and 324 ms (SD=77), respectively. Latencies for forwards and reversed optic flow for the 6-year-olds were 260 ms (SD=56) and 266 ms (SD=41). For random motion the latency was 298 ms (SD=72).

There was a significant main effect of age, $F(2,8) = 8.71$, $p < 0.01$, indicating that latency decreased with age. There was also a nearly significant main effect of visual motion condition, $F(2,8) = 3.44$, $p = 0.08$, suggesting increasing latencies from forwards optic flow to reversed optic flow to random visual motion, but only for the infants at 12 months and the 6-year-olds. No significant interaction effect between condition and age was found.

The mean N2 peak amplitudes (Figure 4b) for 4-month-old infants were for forwards optic flow 6.06 μV (SD=4.3), reversed optic flow 3.8 μV (SD=2.1), and random motion 5.64 μV (SD=3.8). For the 12-month-old infants the mean N2 peak amplitudes for forwards optic flow were 5.77 μV (SD=1.95), while the N2 amplitude for reversed optic flow and random motion were 4.95 μV (SD=3.1) and 5.72 μV (SD=4.3),respectively. For the 6-year-olds the amplitudes for forwards and reversed optic flow were 2.14 μV (SD=1.8) and 1.73 μV (SD=1.9). The amplitude for random motion was 2.32 μV (SD=1.8).

For amplitude, there was a significant main effect of age, $F(2,8) = 4.65$ $p < 0.05$), indicating that amplitude decreases with age. There was no significant main effect for motion condition, nor a significant interaction effect.

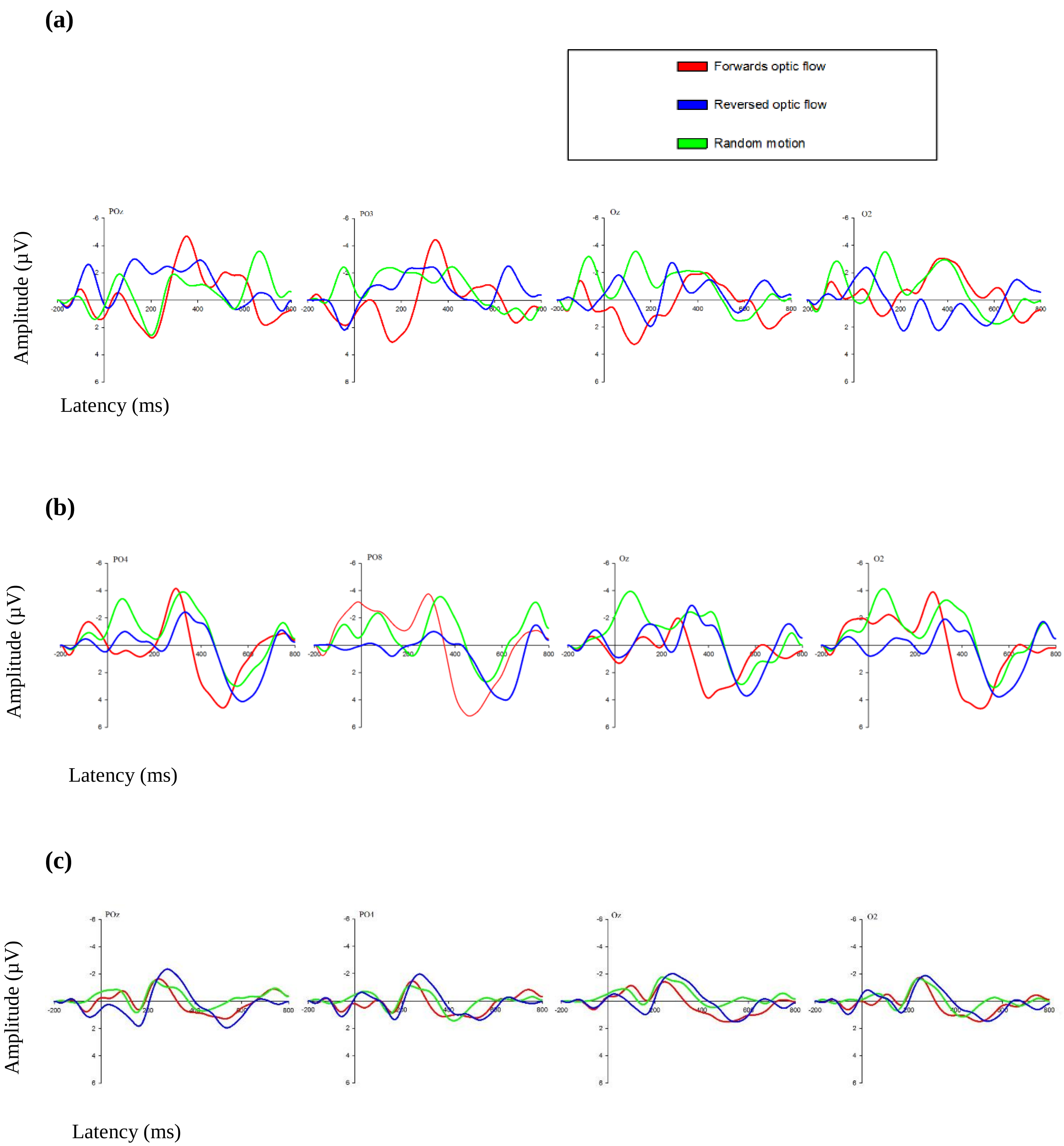

Figure 3. *Grand average motion VEPs of infants at 4 months (a), infants at 12 months (b) and 6-year old children (c) for forwards optic flow, reversed optic flow and random motion.. Peak latencies significantly decreasing in optic flow and random motion as the age of the participants is increasing*

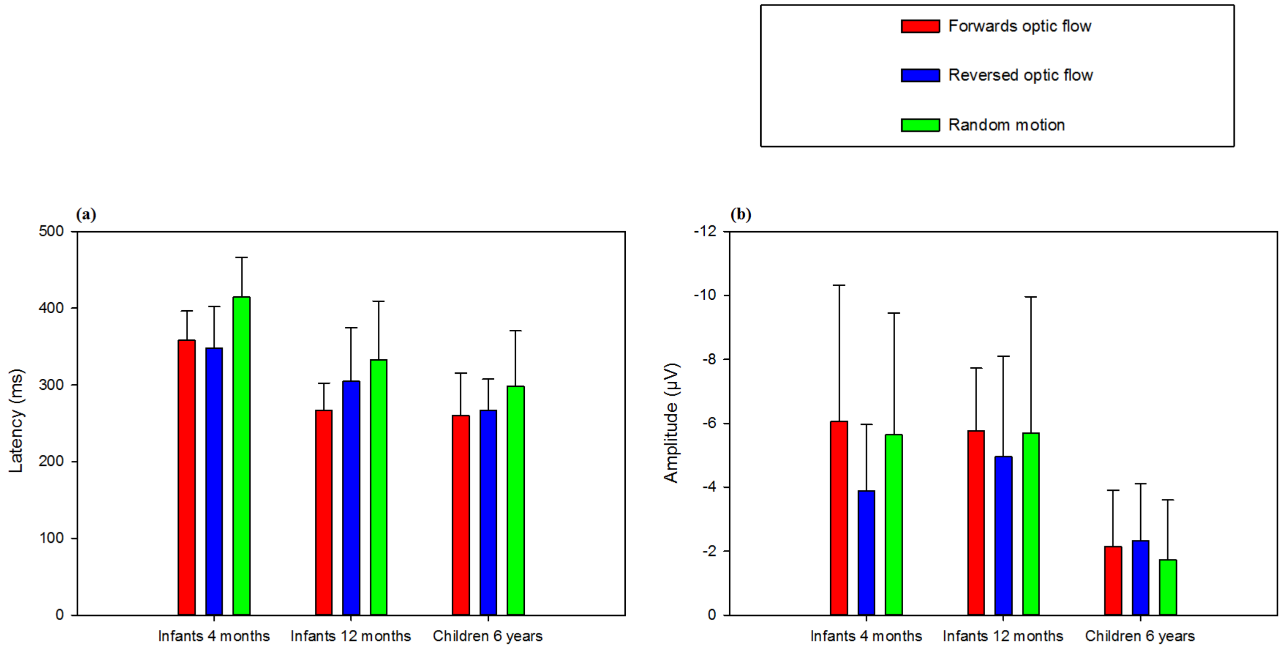

Figure 4: *Group means (and SDs) of N2 peak latencies (a) and amplitudes (b) for forwards optic flow, reversed optic flow and random motion. There is a significant decrease in both latency and amplitude, as participants grow older.*

3.2. Time-frequency analysis

The permutation tests of the average of all participants in all 3 sessions in motion conditions and static non-flow are displayed in Figure 5. The permutation tests revealed significant negative clusters in infants at 4 months and children at 6 years. The significant clusters for 4-months-old infants were found in visual areas VClR, VCrL and VCbL (figure 5a), while significant clusters in the 6-years-old infants were VCrR, PM and VClL (figure 5c). The 12-months-old infants did not display any significant clusters (figure 5b). The significant negative clusters found when motion was compared to static non-flow in the visual area of interest indicates that motion conditions had significantly lower amplitude values than in the static condition.

Theta-band range activity was present both in 4-months-old infants and 6-year-old children, but over a shorter period of time at 6 years.

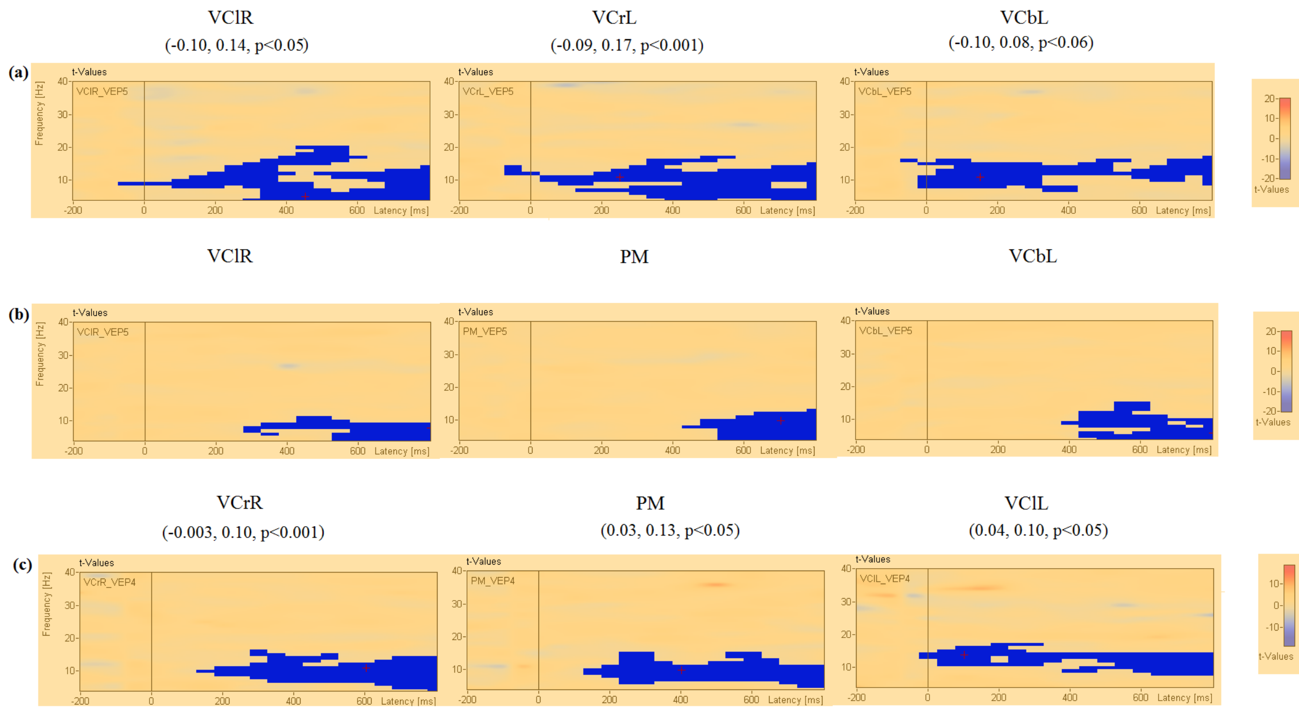

Figure 5. *Average visualization of significant clusters of visual areas of interest when motion conditions was compared with static non-flow in infants at 4 months (a), infants at 12 months (b) and children at 6 years (c). Negative clusters are indicated with light blue (t-values were smaller in motion conditions than static non-flow), while positive clusters are indicated with light red (t-values were greater in static non-flow than motion conditions). Blue voxel marks in each visual area indicates significant negative clusters. Both 4-month-old infants and 6-year-old children display theta-band activity, but over a shorter time period in children (c) than the 4-month-old infants (a). 12-month-old infants had no significant clusters, the figures displays visual areas closest to a significant value (b). The values in the parantheses are presented in the following order for each visual source: respective cluster means for motion, static non-flow, and the probability level. Stimulus onset is indicated at 0 ms with a black vertical line with epoch set from -200 to 800 ms.*

3.2.1. Individual analysis.

Analysis of TSE maps across the visual areas of interest when motion conditions were compared with static non-flow were conducted for each participant. Participants showed some individual variations in their responses to motion and static non-flow and which visual areas of interest that displayed the most activity. However an overall pattern of development was found at 4-months (Figure 6), 12 months (Figure 7) and 6 years (Figure 8).

Activity observed in 4-month-old infants was of desynchronized oscillatory activity in motion conditions (Figure 6a, 6c) and synchronized activity in static non-flow (Figure 6b, 6d) and . The band range was somewhat widespread, although 4-month-old infants primarily showed activity in theta-band range, with some alpha-band activity. Activity was usually observed around 200-800 ms.

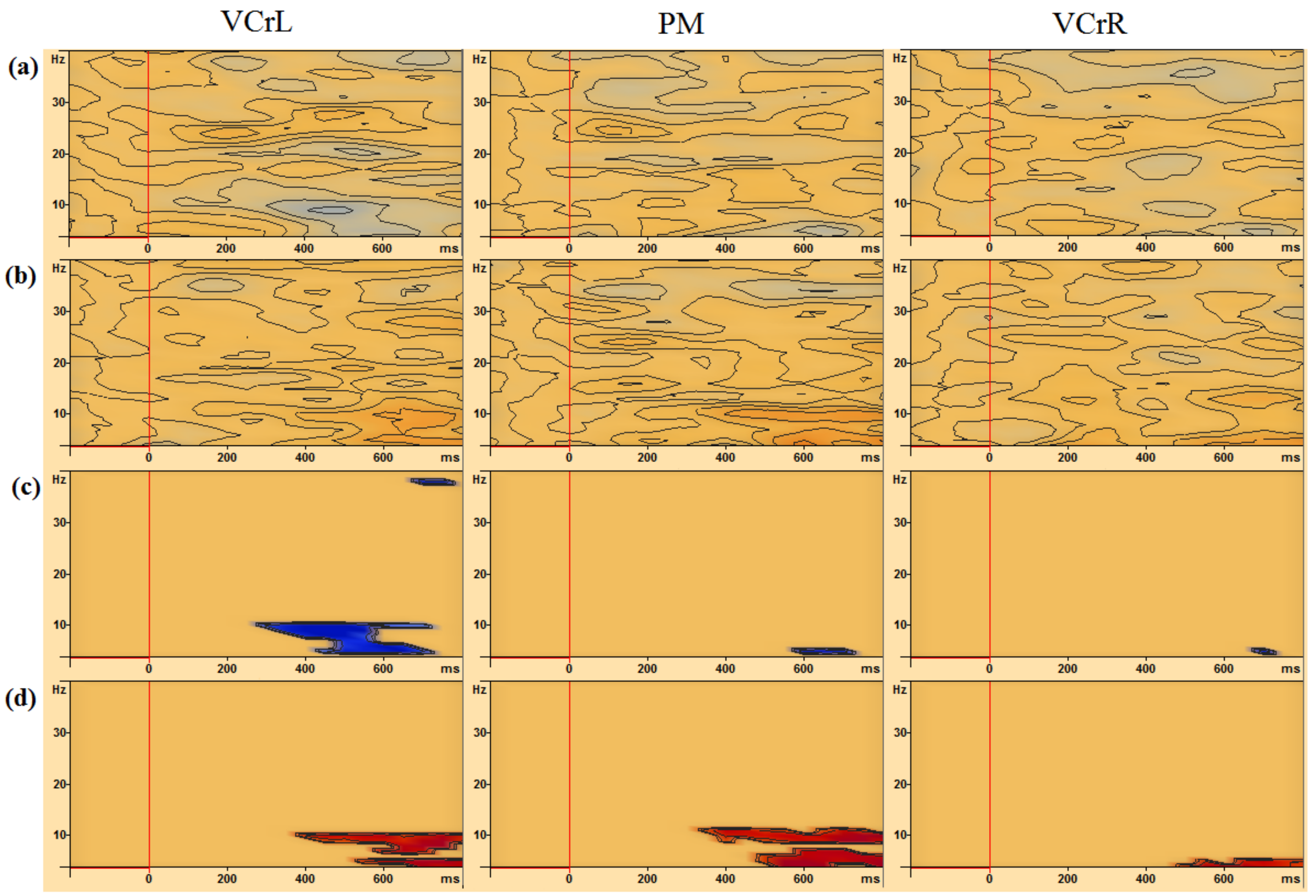

Figure 6. *TSE maps across visual areas of interest of motion a) and static b) in a typical infant at 4 months with epoch length is from -200-800 ms. Blue areas represent desynchronized activity and red areas represent synchronized activity. Desynchronization in theta- and alpha-band range can be observed in the TSE of motion a), synchronization in theta-band range can be observed in static non-flow b). Results of bootstrapping procedure showing TSE probability maps for motion c) and static non-flow d). TSE probability maps of motion show desynchronization in theta- and alpha-band range, at 200-700 ms c). Synchronized theta-band range is observed in the static non-flow at 200-800 ms d).*

12-month-old infants showed both desynchronized and synchronized activity in motion, but primarily synchronized (Figure 7a, 7c). There was less significant activity in static non-flow; however, it was always synchronized activity (Figure 7b, 7d). Theta-band activity was observed in the 12-month-old infants but there was increased activity in the alpha- and beta-band as well. Activity was usually observed around 200-800 ms..

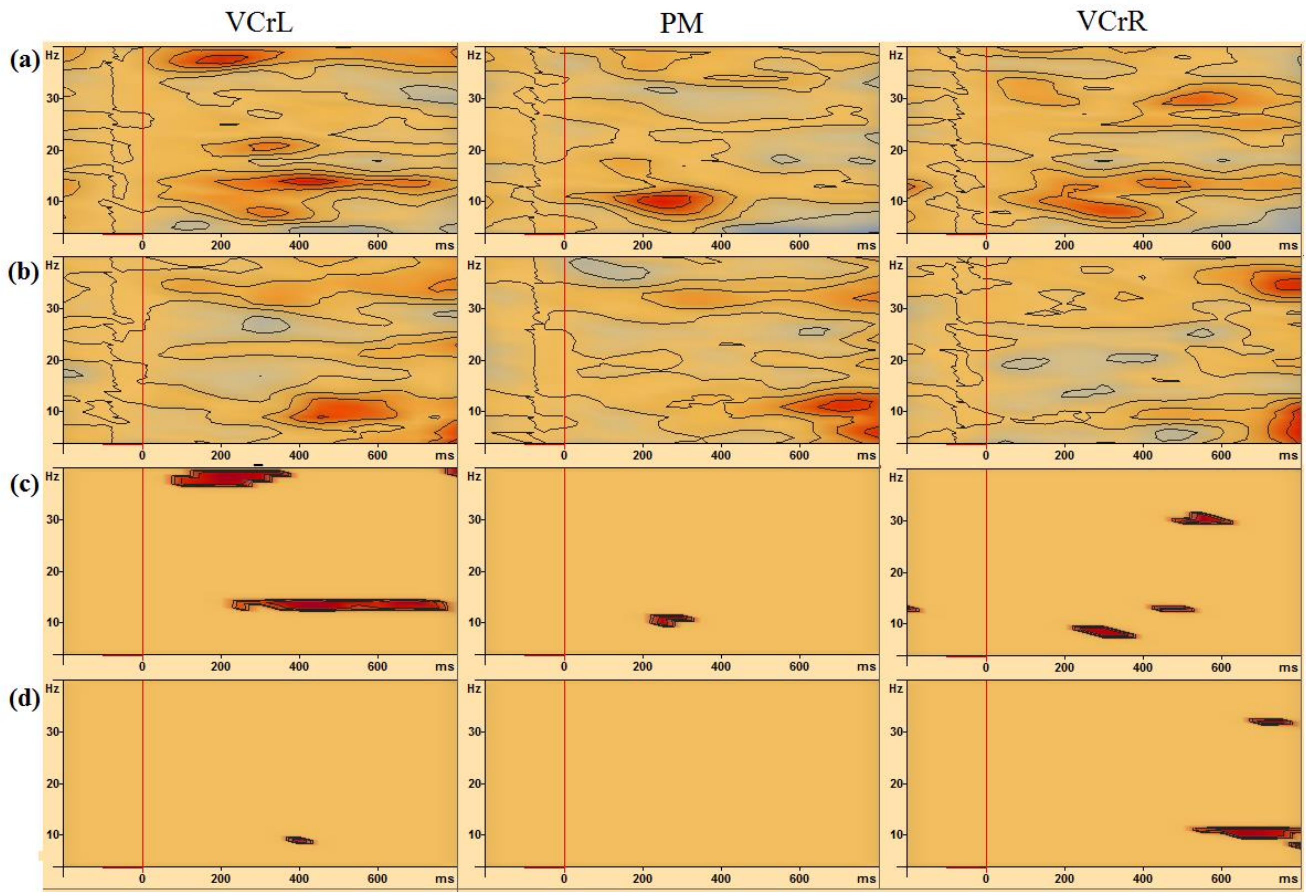

Figure 7. *TSE maps across visual areas of interest of motion a) and static b) in a typical infant at 12 months with epoch length from -200-800 ms. Blue areas represent desynchronized activity and red areas represent synchronized activity. Desynchronization and synchronization are observed in theta-, alpha- and beta-band range in motion a) while synchronization is observed mainly in theta-band range in static non-flow. Results of bootstrapping procedure showing TSE probability maps for motion c) and static non-flow d). TSE probability maps of motion show synchronization in alpha- and beta-band range, at 200-800 ms c). Synchronized theta-band range is observed in the static non-flow condition at 400-800 ms d).*

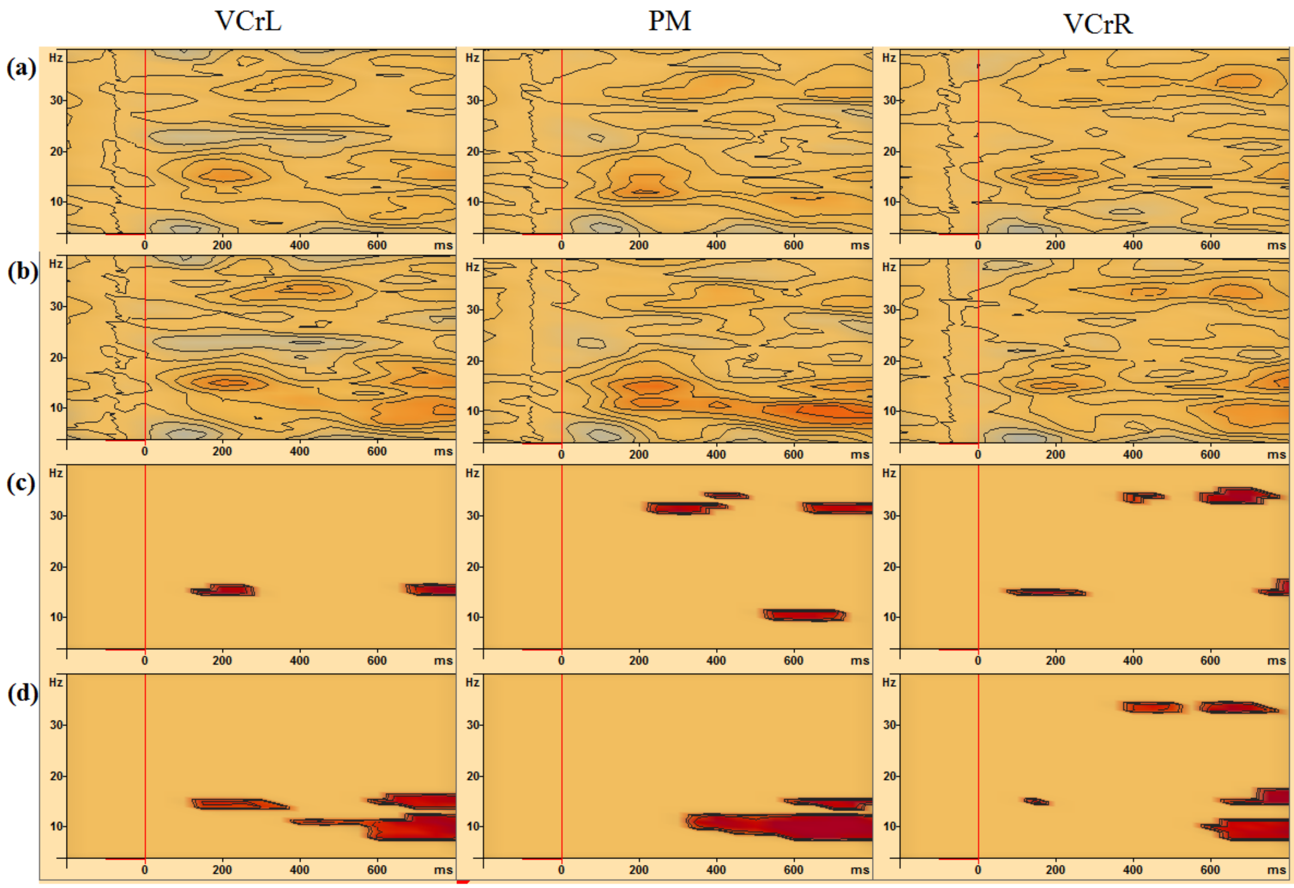

Figure 8. *TSE maps across visual areas of interest of motion a) and static b) in a typical child at 6 years with epoch length from -200-800 ms. Blue areas represent desynchronized activity and red areas represent synchronized activity. Desynchronization and synchronization is observed in alpha- and beta-band range in motion a). Synchronization is observed alpha- and beta-band range in static non-flow. Results of bootstrapping procedure showing TSE probability maps for motion c) and static non-flow d). TSE probability maps of motion show synchronization in alpha- and beta-band range, at 150-800 ms c). Synchronized alpha- and beta-band range is observed in the static non-flow condition at 150-800 ms d).*

Activity observed in 6-year-old children was primarily synchronized in both motion (Figure 8a, 8c) and static non-flow (Figure 8b, 8d). Activity in alpha- and beta-range was observed, while no theta-range activity was seen in the children. The activity usually appeared around 150-800 ms.

3.4. Movement ABC.

The mean scoring of manual dexterity in Movement ABC was 5.4 (SD=2.5). The scoring results for ball skills were 3 (SD=2.9) and balance 0.8 (SD=0.8). The total scoring results were 9.2 (SD=3.8). A total score in the motor task above 10.0 may indicate a motor impairment. Total score was 21.2 (SD=7.4) when the score of the checklist the parent filled was included. No child had any qualitative marks, which means they did not show any behavioural or motor deviations while performing the tasks.

4. Discussion

The present longitudinal study investigated the development of perception of optic flow and random motion in infants at 4 and 12 months, and again when they had turned 6 years old and had started school. High-density EEG was used to study brain electrical activity in response to visual motion. VEP and TSE analyses were conducted to investigate differences in brain activity when participants were presented with structured radial motion and non-structured random motion. Movement ABC battery was also used to test the motor skills of the children. There were only five participants in this study. One of the challenges that arose during this study was the lack of significant data, a consequence of the low number of participants. As it is a longitudinal study, only the data of the participants that came back for a third session could be included.

Despite the low number of participants, we found that there was a significant decrease in overall latency of the N2 component with age. This is in accordance to previous research, when 12-month-old infants displayed significantly shorter latencies than 4-month-old infants (Agyei, et al., 2015). The 6-year-old children had shorter latencies than the infants, but as expected, the latencies were not as short as 130-200 ms found in adults (Van der Meer et al., 2008). This decline in latency with age, may be attributed to the increasing reliance on optic flow as a source of information for moving effectively around in the surroundings. The 12-month-old infants have more crawling experience and are moving increasingly independently. An attributed reason for the decline in latency in the infants is the neurobiological development, as it would contribute to more effective perception of visual motion. During the first two years of life an overproduction of synapses takes place, reaching a peak around the age of 4-6 months in primary visual cortex (Huttenlocher, 1990). Increased local glucose metabolic rates have been observed in occipital, parietal and temporal lobes (Chugani, Muller, & Chugani, 1996; Gilmore et al., 2004). The increased rate of metabolism would allow for increased neuronal energy and more efficient information processing. The development of functional networks in infancy and, in addition, neuronal myelination of white matter tracts allows for faster processing of visual information with age (Grieve, Emerson, Fifer, Isler, & Stark, 2003). The ongoing neural development and increased locomotor experience may be an explanation of the decrease in latency with age.

The latency of the N2 component was found to decrease with age in forwards and reversed optic flow and random motion, however there was no significant effect of condition or interaction effect between condition and age. Agyei et al., (2015) found that only 12-month-old infants differentiated between the motion conditions, whereas they displayed the shortest latency for forwards optic flow and the longest for random. The same trend is also observable in this present study, observable in the latency means of the 12-month-old infants and the 6-year-old children. At these ages, the participants showed shortest latency for forwards optic flow and the longest for random motion. This trend may suggest that the 12-month-old infants and 6-year-old children have better ability to differentiate between the three motion conditions. A significant interaction effect was most likely not found because of a lack of statistical power caused by a low number of participants.

Reliance on optic flow becomes greater in order to move more efficiently around the environment (Bruggeman & Warren, 2007). Increased locomotor experience and sensitivity to optic flow develops interactively (Anderson, et al., 2001). 4-month-old infants have little to no experience with self-produced locomotion such as crawling. While they do have experience in passive locomotion as they are carried by parents or in a stroller, it is believed that it is self-locomotion that is a vital factor to develop visual motion perception (Hein & Held, 1963). The 12-month-old infants have had crawling experience, and may have started to take their first steps, while the 6-year-old children have even more locomotion experience in walking and running. The experience of structured optic flow from real-life would make the participants become more reliant on this information. The lack of structure in random motion was negatively affecting all the participants at all ages, as there was no structure to help them.

Amplitudes did decrease as the ages of the participants increased, the greatest decrease occurred from the infants at 12 months old to children at 6 years old. This is most likely due to a thinner skull in infants than in children (Grieve, et al., 2003). However, differences in skull-thickness are corrected for in TSE analysis.

The individual TSE analysis revealed increasing activity in alpha- and beta-range and decreasing theta-band activity with increasing age. The 4-month-old infants displayed primarily desynchronized activity in the motion conditions, while 6-year-old children displayed primarily synchronized activity. The theta-band activity in 4-month-old infants and increased alpha-band activity in the 12-month-old infants, has also been found in previous studies (Agyei, et al., 2015).

Low-frequency activity has been attributed to immaturity (Pfurtscheller, & Lopes da Silva, 1994), which may be a reason for the primarily theta-band activity among the 4-month-old infants, which is also somewhat prevalent in the 12-month-old infants. The reason that infants mainly display desynchronized activity for motion stimuli and synchronized activity for static non-flow pattern may be explained by motion stimuli being more complex than static pattern. Alpha/theta desynchronization is associated with increased task complexity, more efficient task performance and more attention required (Pfurtscheller, & Lopes da Silva, 1999). The increasing activity in the alpha- and beta-band range and shift to more synchronized activity can be explained by a gradually maturing brain. Synchronized beta-band activity has been found in studies of adults processing motion stimuli, indicating that this activity is a sign of more mature and sophisticated activity (Van der Meer, et al., 2008).

Amplitude of oscillation is proportional with number of neurons firing in synchrony, slower oscillating cell assemblies as in theta-band activity would involve more neurons than the faster oscillating cell assemblies in beta-band activity (Pfurtscheller, & Lopes da Silva, 1999). The development from the slower oscillating theta-band frequency to the faster alpha-band frequency, could imply a progression from larger and less specialized oscillatory cell assemblies towards fewer and more specialized neurons as the participants grew older. This is in accordance with adult studies, where participants displayed beta-band activity (Van der Meer, et al., 2008; Vilhelmsen et al., 2015).

For the third session in the present study, participants were also tested in movement ABC, as development of motor skills and visual motion perception are closely connected. Although not reaching the threshold that can be worrisome, the movement ABC total score was somewhat high. A likely reason for this may be that one of the participants had higher scores than the others, and may have distorted the means as the number of participants are low.

In conclusion, there was a development in the processing of visual motion information as latency decreased with increased age and proportional to more locomotor experience. In addition, both the VEP and TSE results showed a trend in development of motion sensitivity. Infants at 12 months and children at 6 years may be better at differentiating forwards and reversed optic flow and random motion. Increasing alpha- and beta-band activity with increasing age do indicate a maturing brain. These findings is positive for further research on the topic. Additional children who was tested as infants will be called back for testing when they reach the appropriate age, and it is likely that with the greater number of participants significant findings in effect of condition and interaction effect of condition and age will appear. Investigating the development of perception of visual motion and Movement ABC will be interesting with a greater number of participants, when comparing with prematurely born children to investigate if they inhabit some deviations in visual motion perception and motor skills in comparison to the full-term children.

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