

A high-density EEG study of differentiation between two speeds and directions of simulated optic flow in adults and infants

Kenneth Vilhelmsen, Seth B. Agyei, F. R. (Ruud) Van der Weel, Audrey L. H. Van der Meer

Developmental Neuroscience Laboratory, Department of Psychology, Norwegian University of Science and Technology (NTNU), Trondheim, Norway

Correspondence

Kenneth Vilhelmsen, Developmental Neuroscience Laboratory, Department of Psychology, Norwegian University of Science and Technology (NTNU), NO-7491 Trondheim, Norway

Email: kenneth.vilhelmsen@ntnu.no

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Abstract

A high-density EEG study was carried out to investigate cortical activity in response to forward and backward visual motion at two different driving speeds, simulated through optic flow. Participants were prelocomotor infants at the age of 4–5 months and infants with at least 3 weeks of crawling experience at the age of 8–11 months, and adults. Adults displayed shorter N2 latencies in response to forward as opposed to backward visual motion and differentiated significantly between low and high speeds, with shorter latencies for low speeds. Only infants at 8–11 months displayed similar latency differences between motion directions, and exclusively in response to low speed. The developmental differences in latency between infant groups are interpreted in terms of a combination of increased experience with self-produced locomotion and neurobiological development. Analyses of temporal spectral evolution (TSE, time-dependent amplitude changes) were also performed to investigate nonphase-locked changes at lower frequencies in underlying neuronal networks. TSE showed event-related desynchronization activity in response to visual motion for infants compared to adults. The poorer responses in infants are probably related to immaturity of the dorsal visual stream specialized in the processing of visual motion and could explain the observed problems in infants with differentiating high speeds of up to 50 km/h.

KEYWORDS

development, EEG, ERPs, oscillation/time frequency analyses, visual processes

1 INTRODUCTION

Optic flow, the pattern of visual motion on the retina resulting from an observer's own motion, has been shown to guide locomotion and postural stability (Bruggeman, Zosh, & Warren, 2007). Optic flow provides information about an organism's speed (Cabrera & Theobald, 2013; Wei, Kang, & Zhou, 2013) and direction (Bruggeman & Warren, 2010; Warren, Kay, Zosh, Duchon, & Sahuc, 2001) and is therefore important for navigating in the real world. Physiological evidence shows that human medial temporal/visual area 5 (hMT/V5) is involved in processing radial motion (Dukelow et al., 2001; Morrone et al., 2000; Smith, Wall, Williams, & Singh, 2006), and the medial superior temporal (MST) area (Duffy, 1998; Holliday & Meese, 2008; Yu, Page, Gaborski, & Duffy, 2010) of the dorsal visual stream is implicated in the processing of optic flow. Global motion elicits activity in areas such as visual area 3a (V3a) and the parietal areas (Wattam-Bell et al., 2010). Adults show greater response to expanding radial motion as compared to contracting radial motion and translational motion (Holliday & Meese, 2005). In response to visual motion stimuli, infants show rapid perceptual development during the first year of life. Direction-specific neuronal pathways develop around 3 months of age, and infants are able to perceive contracting and expanding stimuli (Shirai & Imura, 2014; Van der Meer, Svantesson, & Van der Weel, 2012; Van der Weel & Van der Meer, 2009). At around 4–5 months, infants are able to detect large changes in heading (Gilmore, Baker, & Grobman, 2004), and directional selectivity starts at low speeds and increases to higher speeds as infants mature (Wattam-Bell, 1992, 1996). By 3 months of age, infants are able to respond to speeds of up to 20 degrees/second ($^{\circ}/s$; Wattam-Bell, 1991), and Shirai, Kanazawa, and Yamaguchi (2008) found that at this age infants are only able to perceive differences between fairly low speeds (2.66 and $5.5^{\circ}/s$). In preferential looking studies, infants prefer expansion to contraction in radial motion stimuli (Brosseau-Lachaine, Casanova, & Faubert, 2008; Shirai, Kanazawa, & Yamaguchi, 2006). Infants also rely on information from optic flow from an early age (Brosseau-Lachaine et al., 2008; Gilmore, Hou, Pettet, & Norcia, 2007; Vaina & Rushton, 2000). At 4–8 weeks, infants

respond to optic flow patterns (Arterberry & Yonas, 2000) and use optic flow fields to stabilize gaze and head movement at around 3 months (Von Hofsten & Rosander, 1996).

To investigate responses to visual motion and optic flow in very young infants, EEG is often used. EEG is a noninvasive technique that allows for high temporal accuracy and is complementary to other physiological methods. EEG waveform activity is dominated by a motion-sensitive N2 component found in occipital and parietal areas in response to visual motion (Pitzalis, Strappini, De Gasperis, Bultrini, & Di Russo, 2012; Probst, Plendl, Paulus, Wist, & Scherg, 1993). In adults, N2 is found at approximately 130–150 ms after stimulus onset (Kremláček, Kuba, Chlubnová, & Kubová, 2004; Probst et al., 1993), while infants have been shown to display latencies of 180–220 ms in visually evoked potential (VEP) studies using optic flow stimuli (Van der Meer, Fallet, & Van der Weel, 2008). Infants at 3–4 months were unable to distinguish between forward and backward radial motion, and random motion, while at 11–12 months the same infants were able to differentiate between the different forms of visual motion in a VEP study (Agyei, Holth, Van der Weel, & Van der Meer, 2015). A recent study showed longer N2 latencies and lower amplitudes in response to higher speeds compared to lower driving speeds in adult participants (Vilhelmsen, Van der Weel, & Van der Meer, 2015).

As opposed to evoked activity, induced activity is not phase-locked to the stimuli and cannot be extracted with linear techniques used in ERP research, since these event-related frequency changes are rather time-locked (Handy, 2005; Pfurtscheller & Lopes Da Silva, 1999). A time-frequency analysis investigates induced nonphase-locked activity, which allows for the detection of signals lost in averaging. These event-related (de)synchronizations (ERD/ERS) are modulations of ongoing natural frequencies in the underlying neuronal populations. Motion-induced power increases in the gamma band (Hoogenboom, Schoffelen, Oostenveld, Parkes, & Fries, 2006), beta band (Van der Meer et al., 2008), and alpha band (Pfurtscheller, Neuper, & Mohl, 1994; Vilhelmsen et al., 2015) in occipital and parietal areas in adults have been reported. Alpha oscillations are common findings in response to radial motion. Power decreases in the

alpha band in 5 posterior regions in adults reflect activation in response to visual motion. Synchronizations (increased amplitude) in occipital sites in the alpha band reflect a state of cortical idling in underlying neuronal populations (Pfurtscheller & Lopes Da Silva, 1999; Pfurtscheller, Stancák, & Neuper, 1996). Evidence has been emerging for how visual motion stimuli modulate natural frequencies in infants. Neuronal oscillations in posterior areas that are modulated by visual motion increase in frequency as infants get older. Amplitude in EEG rhythms reflects the number of neurons firing in synchrony, from larger and slower neuronal assemblies comprising more neurons to smaller and faster oscillating assemblies (Pfurtscheller & Lopes Da Silva, 1999). An increase in amplitude is thought to be the result of more efficient performance and higher task difficulty (Pfurtscheller & Lopes Da Silva, 1999). A longitudinal study (Marshall, Bar-Haim, & Fox, 2002) found a peak in 6–9 Hz oscillations that match alpha-range bands from the end of the first year of life to early childhood. Low-frequency activation in infants has been linked to signs of immaturity (Orekhova, Stroganova, Posikera, & Elam, 2006). Optic flow studies (Agyei et al., 2015; Agyei, Van der Weel, & Van der Meer, 2016b) found that during the first year of life infants show a decrease in amplitude in neuronal theta-band oscillations.

Investigating how infants and adults respond to ecologically relevant stimuli is important for understanding the perception of optic flow information. By using EEG, it is possible to investigate how early responses to speed and direction sensitivity develop in the brain. Previous findings have identified how infants respond to changes in direction of optic flow and how they perceive random motion (Agyei et al., 2015, 2016b; Van der Meer et al., 2008; Vilhelmsen et al., 2015). However, the development and perception of both speed and direction in infants and adults in response to ecological visual motion need further investigation. A previous study (Vilhelmsen et al., 2015) investigated adult responses to optic flow speed, but it did not account for changes in optic flow direction.

The present study investigated how adults and infants process different speeds and directions of visual motion simulated through optic flow, using analyses of VEPs and time-frequency oscillations. Latency differences between infants at 4–5 months, infants at 8–11 months, and adults were examined together with frequency changes in oscillations in the temporal and occipital areas. Previous studies have shown that infants around 3–4 months are unable to distinguish between forward and backward motion (Agyei et al., 2015), and that perception of speed differences in response to optic flow stimuli develops during the first year of life (Brosseau-Lachaine et al., 2008). It was therefore hypothesized that only the oldest infants and adults would be able to differentiate between speeds and directions. Furthermore, neuronal assemblies have been shown to oscillate at higher frequencies as infants mature (Agyei et al., 2015), with the fastest oscillations observed in adults (Van der Meer et al., 2008; Vilhelmsen et al., 2015). Frequencies in response to radial motion were expected to increase with age.

2 METHOD

2.1 Participants

Infants were recruited by contacting parents through birth announcements in the local paper. All babies were born full term (≥ 39 weeks of gestation) and healthy without birth complications or any neurological deficits as determined by parental report. The adults were recruited from the university campus, and all had normal or corrected-to-normal eyesight.

This study followed a cross-sectional design where three different age groups were tested. There were two infant groups and one adult control group. The three different groups (15 participants each) were infants at 4–5 months (7 female), infants at 8–11 months (4 female), and adults (8 female). Mean ages were 19 weeks ($SD = 1.9$) for the 4- to 5-month-old infants, 41 weeks ($SD = 3.6$) for the 8- to 11-month-old infants, and 24 years ($SD = 1.8$) for the adults. In total, 20 infants at 4–5 months and 26 infants at 8–11 months were tested, resulting in an attrition rate of 25% for the youngest infants and 42% for the oldest infants. The youngest infants had no experience with self-produced locomotion at the time of testing, but some had started rolling over. Infants had no self-produced locomotion if they were unable to crawl or achieve any form of forward motion. All infants at 8–11 months had at least 3 weeks of experience with self-produced locomotion: creeping, crawling on hands and knees, or walking with help. An assistant observed if infants were able to either walk assisted or crawl. EEG is noninvasive and has no known harmful consequences. All parents and adult participants gave their informed consent and were informed that they could withdraw at any point without adverse consequences. The Norwegian Regional Ethics Committee and the Norwegian Data Services for the Social Sciences approved this study.

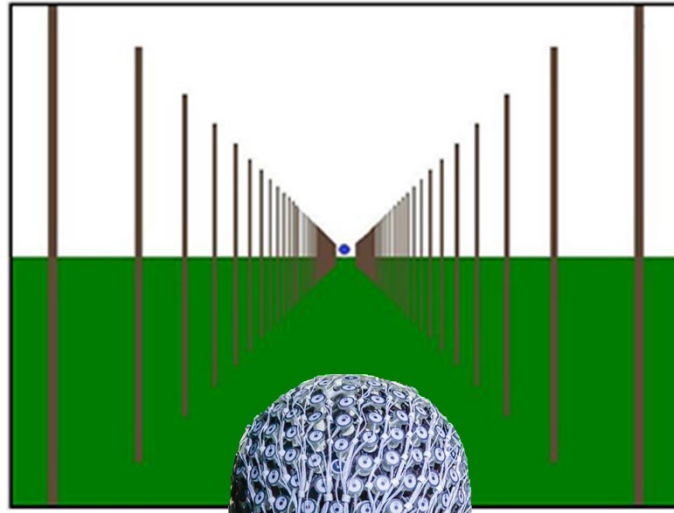


Figure 1. Optic flow pattern simulating forward motion at high speed (50 km/h) down a virtual road with an adult participant wearing the Geodesic Sensor Net consisting of 256 sensors. Blue dot indicates where adult participants were instructed to look but was not present during the experiment.

2.2 Experimental stimuli and paradigm

The optic flow pattern was generated by E-Prime software (Psychological Software Tools, Inc.) and mirror-projected onto a large screen (1.08 m × 0.705 m) by an ASK M2 projector with a refresh rate of 60 Hz. The screen had a resolution of 593 pixels per meter. The participants were seated approximately 75 cm from the screen so that the screen subtended an angle of 71.5° by 50.4°. This study simulated optic flow at two different speeds (low and high) and directions (forward and backward). When simulating forward motion, poles moved outward from the center of the screen at speeds of 17 km/hr and 50 km/hr, leaving the screen at each side. Poles that disappeared from the screen were immediately replaced at the center. This gave the impression of moving down a road (Figure 1). When simulating backward motion, poles moved in the opposite direction but with the same two speeds as in the forward condition. The visual angles, defined by the first pole position (road end) and last pole position (road start), resulted in a road length of 30

m to the horizon. Simulated pole height was 1.3 m, eye height from the ground was 0.65 m, and simulated distance between poles was 1.69 m. Each of the motion conditions was randomly presented for 1.5 s. A static condition was presented in between each motion condition to avoid motion adaptation, and this also lasted for 1.5 s. The static condition was a nonmoving scene of the preceding visual motion condition. To simulate higher speeds, the number of poles on each side of the screen was increased, which effectively decreased the distance between the poles.

2.3 Data acquisition

EEG activity was recorded using the Electrical Geodesics Inc. (EGI) Sensor Net 200 (Tucker, 1993) consisting of an array of 128 Ag/AgCl sponge sensors for infants and 256 Ag/AgCl sponge sensors for adults. The net was evenly distributed over the scalp. A high-input EGI amplifier connected to the net ensured amplification of signals at maximum impedance of 50 k Ω as recommended for an optimal signal-to-noise ratio (Ferree, Luu, Russell, & Tucker, 2001; Picton et al., 2000). NetStation software on a Macintosh computer recorded amplified EEG signals at a sampling rate of 500 Hz, with 200 Hz low-pass and 0.1 Hz high-pass online filters. Gaze was monitored with an infrared Tobii X50 camera to ensure that the participants were looking straight ahead at the screen. Two digital cameras monitored behavior during the experiment for all participants. Video files containing eye movement information were processed on an HP computer by Clear View software, and these files were stored and inspected offline. On average, 11 trials ($SD = 4.1$) were lost for the youngest infants, while for the older infants on average 16 trials ($SD = 5.2$) were lost because the infants looked away from the screen.

2.4 Procedure

Parents arrived with their infants some time before the experiment so that the infants could get used to the laboratory environment. Procedures were explained, and parents provided information about the infant's locomotor experience and signed the consent form. While the infants were

acclimatizing to the environment, an assistant observed the infants to confirm their locomotor capabilities. The infant's head was measured, and an appropriate net was selected. The net was soaked in a saline solution to ensure good impedance, slightly dried with a towel, and mounted on the head while the infant sat on the parent's lap. The infant was distracted with soap bubbles and small noise-emitting toys during the application of the net on the head. The parent carried the infant into a dimly lit experimental room where he/she was placed in a baby car seat, with the parent always at the side. The net was connected to the amplifier, and impedance was checked. If needed, extra saline solution was added. An assistant was present in the room at all times and helped with keeping the infant's attention on the screen and monitoring the experiment. Two assistants who controlled the computers for the experiment were in an adjoining room that was separated from the experimental room by a soundproof window. Immediately before the experiment started, infants' eye movements were calibrated in virtual space. The optic flow experiment was the first experiment carried out in a session consisting of three experiments in total. The current experiment was carried out in one block, but could be paused for a while if the infant became too fussy or bored, at which time the parent and the assistant would play with the infant to revive interest. The experiment was aborted if the infant refused to keep watching the screen or started fussing. Each testing took about 5 min. The stimuli were presented in a random sequential order for about 100–120 trials, where the static nonflow condition accounted for half of the trials.

When adult participants arrived at the laboratory, the experiment was explained to them and they signed the consent form. Adult participants were given instructions to focus on the middle of the screen and had no assistant present during the recordings. However, two assistants monitored the sessions from the adjoining room and could respond to any arising issues. Adults' sessions lasted for about 15 min, with 75 trials in each of the four motion conditions and 300 static trials. After the session, the adults were debriefed and asked how they experienced the experiment. All participants reported being able to differentiate between the visual motion conditions.

2.5 Analyses

2.5.1 Data analyses

Brain Electrical Source Analysis (BESA, GmbH) 6.0 research software was used to analyze EEG raw data. The raw data recordings were first segmented using NetStation software and exported to another server for analyses. Averaging epochs were from -200 ms to 800 ms with a baseline definition set at -100 to 0 ms. Notch filter was set at 50 Hz to avoid line interference, and low cutoff filter was set at 1.6 Hz to remove slow drift in the data. High cutoff filter was set at 60 Hz for infants and 80 Hz for adults to remove channels contaminated with high-frequency activities. Artifact-contaminated channels and epochs resulting from head and arm movements and eye activity were removed from further analysis or re-estimated using spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989; Picton et al., 2000). Manual artifact correction was carried out, with threshold values for low signals and gradients set at 0.1 μV and 75 μV , respectively, and maximum amplitude set at 200 μV (220 μV for some infants). The manual artifact correction was designed to separate brain activity from eye movement artifacts with spatial filters (Berg & Scherg, 1994; Ille, Berg, & Scherg, 2002). Participants with more than 10% of electrodes defined as bad were excluded from further analysis, while trials where participants were not looking at the screen were removed by visual inspection. If infants looked away from the screen for more than two trials, the experimenter would either attempt to get the infants to pay attention or the experiment would be paused. Mean trial contributions for the youngest infants were 11 for each of the four motion conditions and 48 ($SD = 4.9$) for the static condition. For the oldest infants, they were 13 for each of the motion conditions and 55 ($SD = 15.3$) for the static condition. Finally, adults' mean trial contributions were 73 (out of 75) for each of the motion conditions, and 297 (out of 300) for the static condition. Participants with eight or fewer trials accepted per condition were excluded from the data set.

2.5.2 Peak analyses at the electrode level

EEG data were exported into the standardized 81-electrode configuration of the 10–10 International system after rereferencing to an artificial reference calculated from the average potentials over the scalp such that individual averages were obtained. The signal for the reference-free (10-10) montage was estimated with spherical spline interpolation (American Electroencephalographic Society, 1991). Individual averages were computed and analyzed for each participant before the individual averages were combined into a grand average and used as a reference for selecting the individual N2 components. The N2 components of the individual averages were then identified using 3D spherical spline whole-head voltage maps identifying maximum N2 activity over posterior areas for the most dominant waveform (Perrin et al., 1989). Latencies were recorded and subjected to further analysis. Peak latency was measured from stimulus onset to the peak of each N2 component.

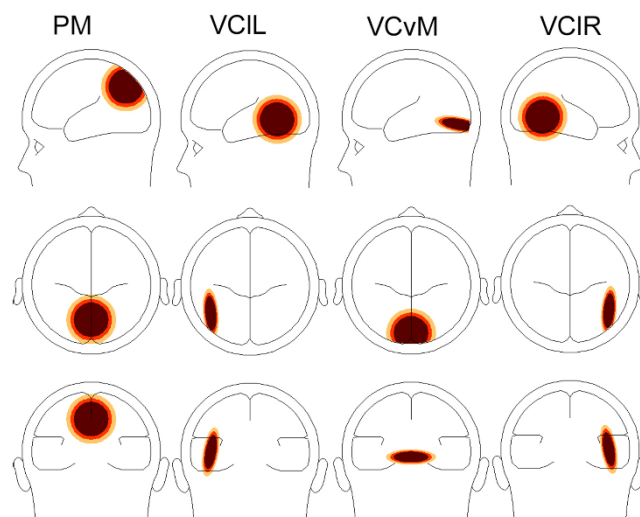


Figure 2. Head model of associated brain regions with approximate Talairach coordinates⁵²: visual cortex lateral left (VCIL), $x=-45.2$, $y=-57.2$, $z=6.5$; parietal midline (PM), $x=0.0$, $y=-72.3$, $z=37.0$; visual cortex vertical midline (VCvM), $x=0.0$, $y=-84.9$, $z=-14.3$; and visual cortex lateral right

(VCIR), $x=45.2$, $y=-57.2$, $z=6.5$. The signal magnitude reflects the estimated source activity in the related brain region if one brain region is active.

2.5.3 Time-frequency analyses in brain space

In addition to peak analysis of VEP components, a time-frequency analysis was carried out, which represents changes in amplitude over time (TSE, temporal spectral evolution). These plots were generated from the single trials by averaging spectral density amplitudes over trials such that each displayed graph plotted the spectral amplitude density of one montage channel over time and frequency that were normalized to the baseline for each frequency (Hoechstetter et al., 2004; Pfurtscheller et al., 1994, 1996). The time-domain signal was transformed into the time-frequency domain by complex demodulation (Papp & Ktonas, 1976). A predefined four-shell ellipsoidal head model (Berg & Scherg, 1994; Hoechstetter et al., 2004) was created for each participant and used to transform data from electrode level to source montage dipoles. The wide distribution of focal brain activity at scalp surfaces due to the nature of dipole fields and the smearing effect of volume conduction in EEG means that scalp waveforms have mixed contributions from underlying brain sources. Thus, measuring oscillatory activity on scalp surface electrodes may not be ideal. Optimal separation of brain activity was therefore achieved using source montages derived from a multiple source model where source waveforms separated different brain activities (Berg & Scherg, 1991). A VEP montage was used to map areas of particular interest (i.e., occipital and parietal sources; see Figure 2), as these areas are found to be active when motion stimuli are presented (Probst et al., 1993; Zeki et al., 1991). As recommended for recording infant EEG, bone thickness was adjusted to 3 mm and conductivity to 0.02σ (Grieve, Emerson, Fifer, Isler, & Stark, 2003; BESA, GmbH information), while for the adult participants bone thickness was set to 7 mm and conductivity was at 0.0042σ . TSE displays were set from 2–40 Hz, and frequency and time sample were set at 1 Hz and 50 ms, while filters were set at 1.6 Hz low cutoff (high-pass) and 40 Hz high cutoff (low-pass).

Averaged waveforms were removed before computing TSEs, and amplitude (μV) was used as the unit of measurement. The static interstimulus interval was used as the control condition, and its TSE was computed separately. Epochs were averaged from 200 ms prior to stimulus onset through 800 ms poststimulus with a baseline period from -100 to 0 ms. Further statistical comparisons of TSEs (changes in amplitude from baseline to particular time-frequency sampling points) between motion conditions and the static nonflow condition for each participant were performed to compute probability maps to test for significant differences in the TSEs when comparing conditions separately for each individual participant. Such an approach permitted the observation of significantly dominant oscillatory activities across the visual areas of interest for each participant in each testing session. Here, Bonferroni procedure and permutation tests as described by Simes (1986) and Auranen (2002) were used and applied to each set of time samples belonging to one frequency bin so as to correct for multiple testing.

Paired samples t tests were conducted in BESA Statistics 2.0 (BESA, GmbH) to test for significant differences between conditions in the time-frequency domain. BESA Statistics uses a combination of permutation testing and data clustering (Bullmore et al., 1999; Ernst, 2004; Maris & Oostenveld, 2007) to avoid the multiple comparisons problem. First, data clusters that show a significant effect between conditions are defined. Then, the clusters are put through several permutations and a new t test is computed for each permutation and a new cluster value is found. The significance of the initial cluster value is determined based on this new distribution. If the values of Condition 1 are lower than the values of Condition 2, a negative cluster is found that shows the direction of the statistical effect. There were 32,768 permutations for each t test, with frequency ranges and epochs the same as in the time-frequency analysis.

3 RESULTS

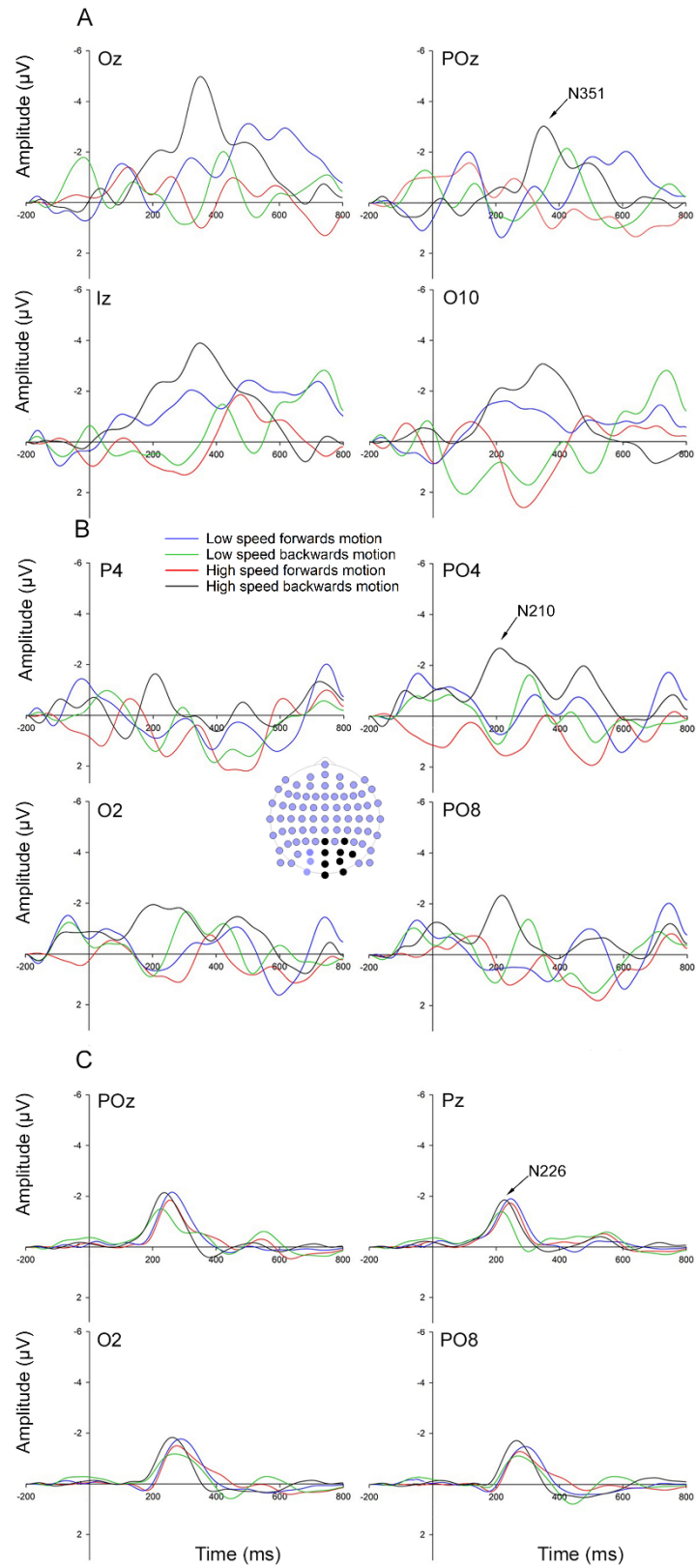


Figure 3. Grand average waveforms in infants at 4-5 months (A), infants at 8-11 months (B), and in adults (C). Epoch is from -200 to 800 ms. The head drawing (nose up) shows scalp locations of the 81 standard electrodes with the electrodes of interest indicated with filled black circles (from top to bottom and left to right): Pz, P4, POz, PO4, PO8, Oz, O2, Iz, and O10. Arrows show peak latency for the low speed forwards visual motion in the three groups.

3.1 VEP responses

Based on grand-averaged waveforms, four electrodes were chosen for each participant group. The latency of the grand-averaged N2 peak was identified and used as a guide to identify the individual N2 components for each participant. This was done using the electrode that showed the highest amplitude in the low speed forward motion condition for the three groups. The peak amplitude and peak latency were recorded and further analyzed. For the 4- to 5-month-old infants, electrodes POz, Oz, Iz, and O10 were chosen, while electrodes P4, PO4, O2, and PO8 were chosen for the 8- to 11-month-old infants. For adults, electrodes POz, Pz, O2, and PO8 were chosen (see Figure 3). Infants at 4–5 months contributed on average 42 motion trials ($SD = 4$), infants at 8–11 months contributed on average 50 motion trials ($SD = 12$), and adults provided on average 292 motion trials ($SD = 6$).

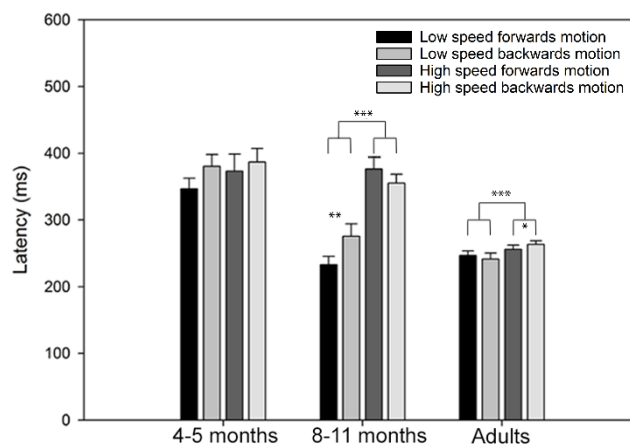


Figure 4. Mean latencies (with SEs) in infants and adults for simulated forwards and backwards motion at low and high speed. * Significant at $p < 0.05$. ** Significant at $p < 0.01$. *** Significant at $p < 0.001$.

Mean peak latencies (ms) were for infants at 4–5 months: 347 ($SD = 61$) for low speed forward motion, 380 ($SD = 69$) for low speed backward motion, 373 ($SD = 99$) for high speed forward motion, and 387 ($SD = 79$) for high speed backward motion. For infants at 8–11 months, the corresponding latencies were 239 ($SD = 52$) for low speed forward motion, 314 ($SD = 64$) for low speed backward motion, 376 ($SD = 75$) for high speed forward motion, and 355 ($SD = 51$) for high speed backward motion. For the adults, latencies were 247 ($SD = 27$) for low speed forward motion, 241 ($SD = 35$) for low speed backward motion, 256 ($SD = 25$) for high speed forward motion, and 264 ($SD = 20$) for high speed backward motion.

Repeated measures analysis of variance (ANOVA) tested for differences in N2 peak latencies with speed (low, high) and direction (forward, backward) as within-subject factors and age (4–5 months, 8–11 months, adults) as between-subjects factor. For N2 peak latency, the results showed a significant main effect of age, $F(2, 42) = 38.71$, $p < 0.001$, indicating that latency decreased with age. A significant interaction was found between age and speed, $F(2, 42) = 15.92$, $p < 0.001$, suggesting that, irrespective of direction of visual motion, latencies for low speed were significantly shorter than latencies for high speed, but only for the older infants and the adults. In addition, latencies for low speed were significantly longer for the young infants than for the older infants, $p < 0.001$, while latencies for both speeds were significantly longer for infants at 4–5 months than for adults, $p < 0.001$. Further post hoc analyses showed that the 8- to 11-month-old infants were able to differentiate between forward and backward motion, with shorter latencies for the forward motion condition ($p < 0.01$), but only for the low speed. Finally, a significant difference between forward and backward motion was found in response to high speed in adults,

$p < 0.05$, showing that, for the high speed, visual motion latencies were higher for backward compared to forward visual motion.

3.2 Time-frequency responses

A time-frequency analysis was carried out for the motion conditions and the static nonflow condition for all participants individually. The visual motion conditions were compared to one another in each of the three groups separately, but no significant differences between speeds or directions were found. All the motion conditions were therefore collapsed into one motion condition and compared with the static nonflow condition. Infants showed theta and alpha activity and adults showed beta activity in response to visual motion (Figure 5).

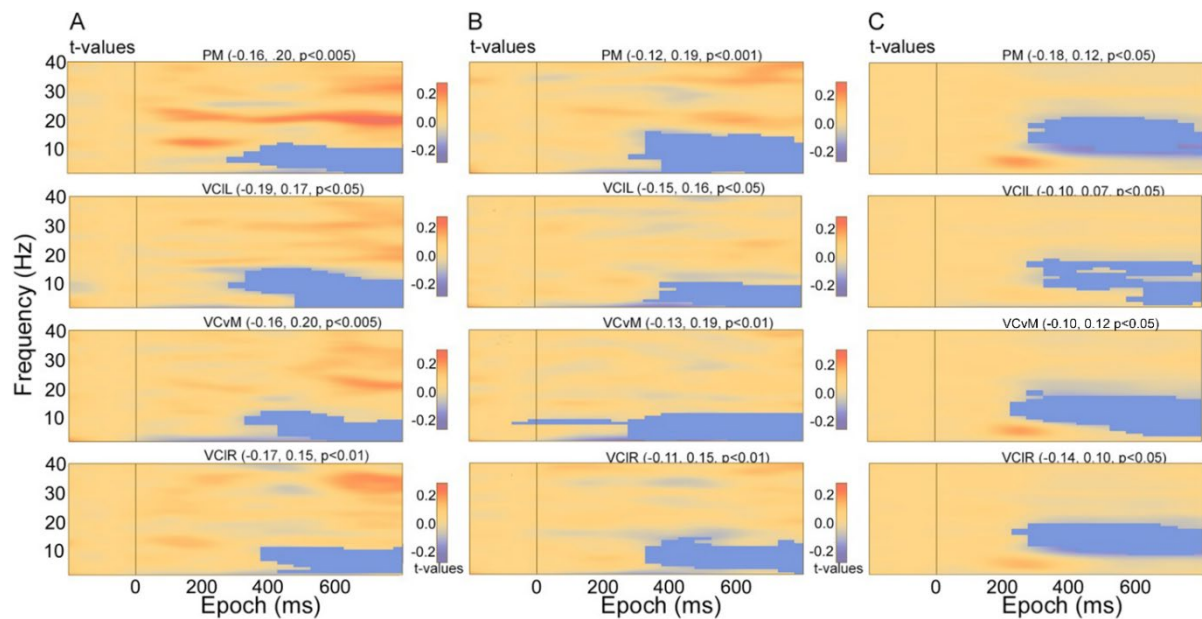


Figure 5. Visualization of averaged clusters in the four visual sources of interest. Averaged activity in infants at 4-5 months (A), infants at 8-11 months (B), and adults (C), when the combined motion conditions were compared with the static non-flow condition. Blue colours indicate negative clusters, i.e., when the visual motion conditions had lower values than the static non-flow condition. These results display clusters of significant differences, showing low frequency theta and alpha desynchronizations in all sources in the 4- to 5-month-old and 8- to 11-month-old infants. Adults displayed beta-band oscillations in all sources.

Similar activation in all infants was found in response to visual motion, where they showed a decrease in amplitude in the theta and alpha bands. Adults also showed a decrease in amplitude in response to the motion conditions, but in the beta band. In response to the static condition, infants showed an increase in amplitude in the theta and alpha bands. Adults showed increased amplitude in the beta band in response to the static condition (Figure 6f). Figure 6g–i shows probability maps in visual motion conditions. Infants at 4–5 months showed significant differences ($p < 0.05$) between the motion conditions compared to the baseline in the theta and alpha bands. At 8–11 months, infants showed similar significant differences ($p < 0.05$) between the visual motion conditions compared to the baseline. Significant differences ($p < 0.05$) between visual motion and the static condition were found in adults, which showed a decrease in amplitude in the beta band.

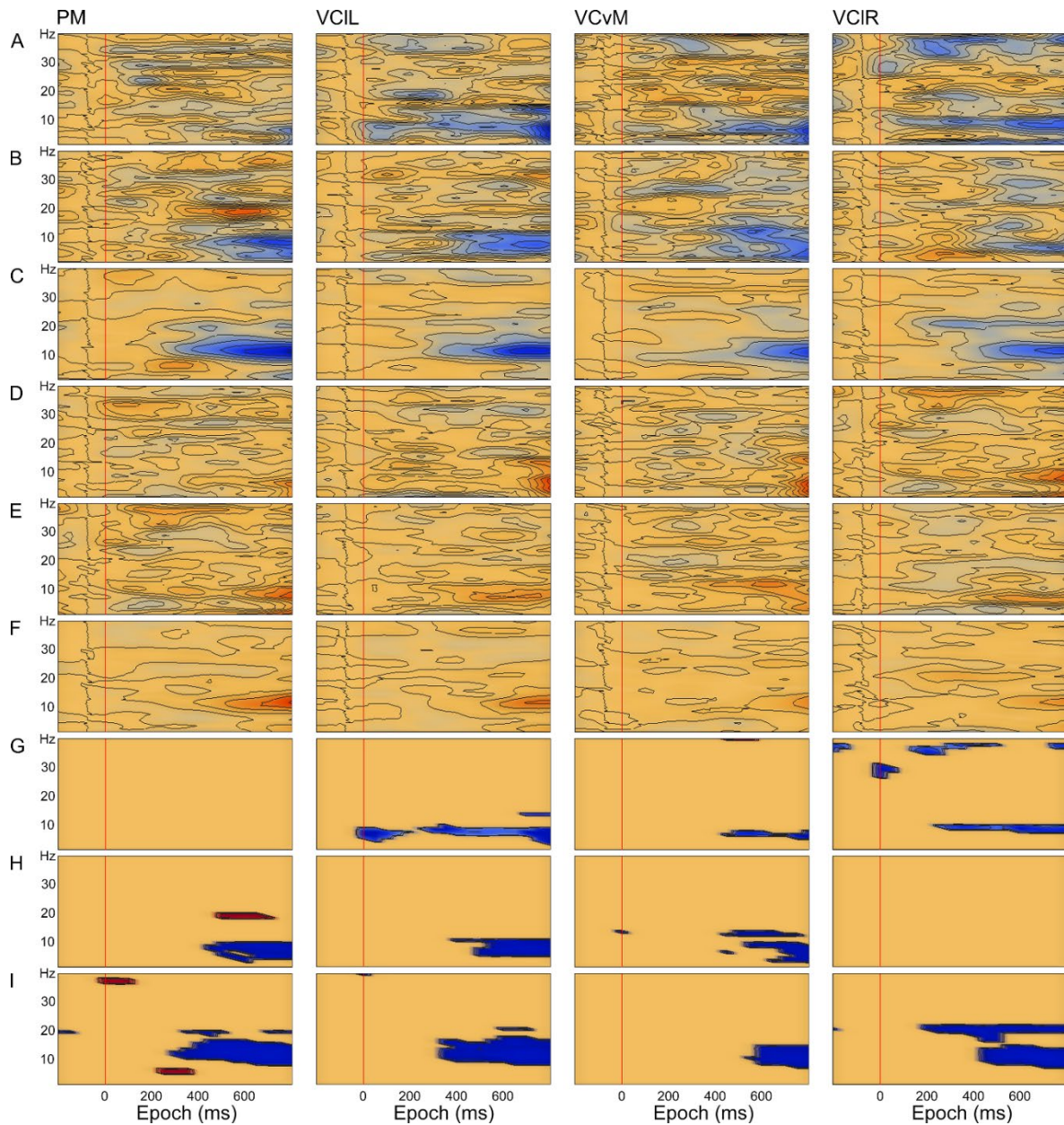


Figure 6. TSE displays of visual motion conditions in the four sources investigated in the 4- to 5-month-old infants (A), in the 8- to 11-month-old infants (B), and in the adults (C) in three typical participants from each group. In infants, theta-alpha activity could be observed in response to the visual motion conditions. Infants showed theta- and alpha-band synchronisations, while adults showed beta-band synchronisation. TSE displays for the static condition in the four sources are shown for 4- to 5-month-old infants (D), 8- to 11-month-old infants (E), and adults (F). All three groups showed synchronized activities in the static condition in the same frequency bands as in the motion conditions. Infants at 4-5 months and at 8-11 months showed synchronised activity in the theta and alpha bands. Adults showed synchronized beta band activity in response to the static condition.

Probability maps showed significant ($p < 0.05$) theta and alpha activity in 4- to 5-month-olds (G), and in 8- to 11-month-olds (H) compared to baseline. Adults (I) showed significant ($p < 0.05$) beta activity compared to the baseline. Stimulus onset is marked with a vertical red line at 0 ms. Epoch is from -200 ms to 800 ms with baseline from -100 ms to 0 ms.

4 DISCUSSION

An EEG study was carried out to investigate responses of infants (4–5 months and 8–11 months) and adults to differences between speed and direction in optic flow. Both motion-onset VEPs and changes in oscillations in TSEs were used to investigate differences between the three age groups and how infants develop visual motion perception through optic flow during the first year of life. N2 component of visual motion investigated changes in latency, while time-frequency analyses investigated changes in oscillations in response to visual motion processing. The younger infants did not differentiate between visual motion speeds and directions, and they had the longest latencies in all visual motion conditions. On the other hand, the older infants displayed significantly shorter latencies for low speed compared to high speed and showed shorter latencies in response to forward motion compared to backward motion at the low speed. Both infant groups showed similar latencies in response to high speed (Figure 4).

The improvement in the infants' visual motion perception from 4–5 months to 8–11 months could be related to increasing maturity of visual pathways during the first year of life (Agyei et al., 2016b; Van der Meer et al., 2008). An increase in glucose metabolic rate occurs in the posterior and temporal areas of infants at this age (Chugani, Müller, & Chugani, 1996), which leads to more available energy for neuronal transmission and processing. Axonal pruning during early development leads to more efficient network connections (Lebel, Walker, Leemans, Phillips, & Beaulieu, 2008; Stepanyants, Hof, & Chklovskii, 2002). Infants show peak synaptogenesis especially in the primary visual cortex between 4–6 months, with rapid formation and overproduction of cortical synapses reported during the first 2 years of life (Casey, Giedd, & Thomas, 2000). In addition, white matter myelination increases with experience (Fields, 2008) and increases from infancy until adulthood (Mukherjee et al., 2002). These developments in functional networks could have resulted in improved processing speeds of visual motion in older infants as observed in the present study.

Previous studies have revealed infants' ability to detect directional differences in radial motion at 3 months (Braddick, Birtles, Wattam-Bell, & Atkinson, 2005; Shirai et al., 2006). The ability to perceive speed differences has also been shown at around 3 months, but only at fairly low speeds between 2.7 and 5.5°/s (Shirai et al., 2008). Even though the 8- to 11-month-old infants in the present study showed shorter latencies for low speed than the younger infants, no particular improvements in latencies with age when processing high speed were found (Figure 4). Thus, the absence of a fully myelinated system in the younger infants might have slowed down information transmission (Braddick, Atkinson, & Wattam-Bell, 2003). Long response times have been argued to be a result of less specialized neuronal networks (Dubois, Hertz-Pannier, Dehaene-Lambertz, Cointepas, & Le Bihan, 2006; Howard et al., 1996; Johnson, 2000). Similar findings have been reported in earlier studies (Agyei et al., 2015; Agyei, Van der Weel, & Van der Meer, 2016a), where it was shown that infants at 3–4 months could not differentiate between structured forward and backward visual motion, while 11- to 12-month-old infants could. In the present study, older infants differentiated between forward and backward visual motion at low speed but not the younger infants. None of the infants in the current study were able to differentiate between direction of visual motion at high speed. These findings suggest that perception of lower speeds likely develops earlier than that of higher speeds. Some findings from other studies (Hadad, Schwartz, Maurer, & Lewis, 2015; Meier & Giaschi, 2014) have reported that the development of perception of higher speeds might occur earlier in infants. However, compared to the current study, these studies have often used different types of stimuli (e.g., rotating or translational random dot kinematograms), making a direct comparison difficult.

A magnetoencephalography (MEG) study (Kawakami et al., 2002) of speeds up to 500°/s reported different latency responses depending on the speeds presented. They found that for speeds ranging from 0.4–100°/s, higher latencies were observed in response to lower speeds. However, speeds above 100°/s showed latency responses increasing as speeds increased, which is similar to findings in the present paper considering that the high speed we used may be

considered analogous to speeds over 100°/s, albeit more complex than display speeds expressed in degrees/second. The speeds used by several other studies have been much lower than 100°/s (Hadad et al., 2015; Joshi & Falkenberg, 2015; Meier & Giaschi, 2014), and they report findings similar to the MEG study (Kawakami et al., 2002) for speeds from 0.4–100°/s. In addition, Hadad et al. (2015) argued that speeds that fall outside the optimal range for infants might develop more slowly. It might thus be that the relatively high speeds used in the current study fall outside the optimal perceptual range and were therefore more difficult for the infants to perceive, leading to such high latencies in response to the high speed. Earlier studies investigating motion perception in infants and adults (Agyei et al., 2015; Gilmore et al., 2004; Van der Meer et al., 2008) argue that infant development is closely linked to their ability to move on their own. The older infants in the present study had started to crawl and, in some cases, could walk upright with the aid of a parent or a steady surface. James and Swain (2011) found that experience with self-produced locomotion leads to a closer link between perception and action in the developing brain. Active exploration of the environment is shown to improve the visual system (Gilmore et al., 2004). The older infants' locomotor experience through crawling and/or walking might have contributed to an improvement in perceiving visual motion information. Evidence of the importance of self-produced locomotion for visual perception was also shown in an experiment by Held and Hein (1963). They demonstrated that kittens that only passively experienced visual motion without being given the opportunity for self-produced locomotion did not have a normal development of visually guided behavior. Adequate brain responses to differences in optic flow have been found to appear around the end of the first year of life (Agyei et al., 2015). Results from previous studies (Kawakami et al., 2002; Vilhelmsen et al., 2015) indicate that higher speeds result in higher latencies. The present results corroborate these previous studies, where infants at 8–11 months showed longer latencies in response to the high speed. A reason for the increase in latencies may be lack of experience with such high speeds as used in the current study. Together with the increased experience that the older infants have with self-produced locomotion,

expansion-sensitive neural mechanisms in the brain might have been developed in these infants, leading to improved processing of high speeds at this age. The current results suggest that, before 1 year of age, infants are capable of detecting both speed and directional differences in response to ecological visual motion, but that the dorsal stream involved in processing optic flow may not yet be developed enough to discriminate between high speeds efficiently. Since perception of optic flow has been linked to areas such as the hMT/V5 and the MST of the dorsal stream (Duffy & Wurtz, 1997; Yu et al., 2010), the current results may indicate an immature dorsal pathway that likely affected the ability to properly differentiate the highest speed in the older infants.

It was found that adults had the shortest latencies in all visual motion conditions and showed significantly shorter latencies in response to the low-speed condition compared to the high-speed condition. An adult-level response to visual motion has been shown not to occur until 16–18 years (Hadad et al., 2015; Joshi & Falkenberg, 2015). It is therefore not surprising that infants at 8–11 months displayed such long latencies and were unable to differentiate between directions at the high speed. Adults were able to separate between the high and low speeds, and they showed the shortest latencies in response to the lowest speed compared to the two infant groups. Short latencies are common for young adults (18–30 years) compared to younger participants who tend to show longer latencies in response to visual motion onset (Langrova, Kuba, Kremlacek, Kubova, & Vit, 2006; Van der Meer et al., 2008; Vilhelmsen et al., 2015).

The present findings show that adults differentiated between forward and backward visual motion. From a life-span developmental perspective, it has been argued that increased latencies in response to visual motion reflect slower information processing (Langrova et al., 2006; Van der Meer et al., 2008). The increased latencies in response to the high speeds presented in the current study might be due to the increased amount of information contained in the high-speed condition and, as a result, the participants may have perceived it as more complex than the lower speed. At the higher speed, the adult participants showed longer latencies in response to backward compared to forward visual motion, showing that at high speeds adults seem to have a harder

time separating between the two motion directions. This might indicate a lack of experience with backward visual motion at such high speeds, as experience has been shown to affect latencies in response to motion stimuli (Mukherjee et al., 2002).

Time-frequency analyses showed differences between the groups when comparing all motion conditions to the nonflow static condition. Infants both at 4–5 months and at 8–11 months showed oscillatory activities in the theta and alpha bands, while adults showed beta-band activities. The participants' responses to visual motion were seen as induced desynchronized activity in all the visual sources (Figure 5). Previous studies investigating responses to visual motion in parietal and occipital areas have found similar EEG activities in both infants and adults (Agyei et al., 2016a; Van der Meer et al., 2008). These studies attributed these activities to active processing of visual motion.

Amplitude in oscillations reflects the number of synchronously firing neurons, where slower oscillations in cell assemblies would indicate more neurons firing in synchrony compared to faster oscillating cell assemblies (Elul, 1972; Pfurtscheller, 1992; Pfurtscheller & Lopes Da Silva, 1999; Singer, 1993). Infants tend to display low frequencies in response to visual motion (Agyei et al., 2016a; Stroganova, Orekhova, & Posikera, 1999). Such low-frequency ERD activity in response to sensorimotor stimuli has been interpreted as a sign of immaturity in infants (Carmeli, Knyazeva, Innocenti, & De Feo, 2005; Orekhova et al., 2006; Van der Meer et al., 2008). This was seen in the current study where both infant groups showed low-frequency activity, seen as theta and alpha activity, in response to visual motion.

Behavioral studies have shown that perception of both direction and speed develops during the first year of life (Adolph, Vereijken, & Denny, 2008; Agyei et al., 2015; Berger & Adolph, 2007; Braddick & Atkinson, 2009; Gunn et al., 2002; Van der Meer, Ramstad, & Van der Weel, 2008) and is closely linked to infants' interaction with the environment (James & Swain, 2011).

Evidence from EEG studies also shows that infants' oscillatory activities in response to visual stimuli develop from lower to higher frequencies and are linked to visual experience from 7 to 11

months of age (Orekhova et al., 2006; Stroganova et al., 1999). Both infant groups showed the same theta- and alpha-band oscillations in response to visual motion, which might indicate an inadequate experience of the real world as simulated by the present study. Both the low and high speeds in this study are well above adult walking or running speeds, which are not commonly experienced by infants. These results may indicate that infants at 8–11 months may not have enough experience with such high speeds. Further studies will display lower speeds using the same optic flow paradigm to investigate if infants are more sensitive to more ecologically lower speeds.

Beta-band oscillations found in adults may indicate a fully developed visual perception system, as reported by several other studies (Babiloni et al., 2002; Neuper, Wörtz, & Pfurtscheller, 2006; Pfurtscheller et al., 1994; Van der Meer et al., 2008). Similar results were also found in adults using similar speeds as the current study, but without the inclusion of direction of motion (Vilhelmsen et al., 2015). The present study showed that adults display relatively short latencies in response to visual motion, which might indicate that they have little difficulty with the speeds and the directions presented to them in the present study.

Induced synchronizations were observed in response to the static condition in all groups, in contrast to the motion condition where induced desynchronizations were observed as a result of active processing of visual motion (Figure 6). Underlying neuronal cell assemblies therefore fired in synchrony during the static condition, but in response to radial motion the cells fired in desynchrony. Synchronized activity in response to visual motion is thought to reflect nonactive or resting neuronal assemblies (Pfurtscheller, 1992; Pfurtscheller et al., 1996). These oscillatory activities are common in response to sensorimotor stimuli (Neuper et al., 2006) and have been argued to reflect a preparation for information processing (Pfurtscheller, 1992). All groups displayed this synchronized activity in response to static nonflow.

In conclusion, this study has shown the effects of perception of motion speed and direction in the infant and adult brain. Latency results indicated that infants at 4–5 months were not able to

differentiate between any of the visual motion conditions, whereas infants at 8–11 months were able to differentiate between the low and high speed and between forward and backward visual motion at the low speed. Adults showed the shortest latencies in response to both motion speeds and directions. White matter myelination, improvements of synaptic connections, and increased experience with self-produced locomotion were proposed as possible reasons behind the observed development in infants during the first year of life. Time-frequency analyses revealed that both infant groups showed induced desynchronizations at low frequencies in response to visual motion, a reflection of a visual system yet to fully develop to adequately process high motion speed. Adults displayed consistent high-frequency EEG rhythms, which indicates a developed and mature visual system.

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