Perception of simulated forward and backward motion from optic flow at two different speeds in infants using high-density EEG: a longitudinal study.

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Table of Contents

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Abstract

High-density electroencephalogram (EEG) was used in a longitudinal study in infants at 4-5 months and later at 9-10 months to study brain electrical activity as the participants were presented with simulated forward and backward motion from optic flow at two different speeds, with a static inter-stimulus between each motion condition. The aim of the research was to investigate the evoked and oscillatory brain responses to the motion stimuli in infants, with particular attention directed at the N2 component, as well as to the oscillatory activity recorded in the occipital and parietal regions of the brain. The results showed a main effect of direction, indicating that infants had faster processing times for forward than the backward optic flow, as shown by longer latencies for the latter condition. Further, low speed was more easily processed than high speed, for both directions, but only by the older infants. Lower amplitudes were recorded for the older infants, and it was found that speed affected amplitude for backward motion only, with high speed displaying higher amplitudes, regardless of age. Additionally, direction affected amplitude for low speed only, with forward motion displaying higher amplitudes. Finally, observation of the oscillatory activity revealed theta- and alpha- desynchronizations at both ages when the TSEs for the motion conditions were compared to the static condition, with synchronizations being recorded for the static condition. However, no decrease in low-frequency activity was registered at the second testing, contrary to the expectations. It was concluded that the infant brain specializes and becomes more sensitive to visual motion stimuli as it matures.

1.0 Introduction

J.J. Gibson was the first to investigate the importance of optic flow as a way to navigating the environment, and other researchers have progressively defined optic flow as the streaming pattern of visual information that results from an observer's own motion (Gibson, 1966, 1979). The perception of optic flow informs the individual about his or her own motion, and it allows to perceive the movement of objects in relation to that individual's perspective. In turn, this awareness of space and motion helps employ important maneuvers that are fundamental to adaptive movement. In fact, the perception of optic flow contributes to obstacle-avoidance, maintenance of balance (Bruggeman & Warren, 2010), and head and eye movement (Agyei, Holth, Van der Weel, & Van der Meer, 2015). Optic flow perception is fundamental in aiding navigation and avoiding obstacles or danger. Research has suggested that optic flow processing in infants is associated with increased experience with self-produced locomotion (Van der Meer, Fallet & Van der Weel, 2008), a concept that lays the premises for formulating specific questions analyzing the processing of visual motion in infants at various stages of their motor development. Many studies over the years have investigated the brain's processing of optic flow in infants, yet more research is still needed to explore how optic flow affects the perception of object motion and self-motion in 3D space. As suggested by Gibson (1979), the basic ability in avoiding danger develops even before locomotion in both rhesus monkeys and infants. In young infants for example, the ability to anticipate an oncoming object and expectations of collisions can be observed by a timed response represented by eye-blinks and/or tilting of the head backwards (Van der Meer, Svantesson, & Van der Weel, 2012). These early reactions have been observed in pre-locomotor infants as young as 3-6 weeks (Bower, Broughton & Moore, 1970), while infants as young as 5 months have been shown to be responsive to radial flow patterns simulating collisions (Kayed &

Van der Meer, 2000, 2007; Schmuckler, 1997). Understanding visual motion processing in infancy, and more specifically, how infants' brains are able to process the change of position relative to the environment encourages further research.

The perception of movement is believed to originate in the middle temporal area (V5/MT), which is part of the dorsal pathway of the visual cortex (Kandel, Schwartz, Jessell, Siegelbaum & Hudspeth, 2013; Probst, Plendl, Paulus, Wist, & Scherg, 1993), a claim that is further supported by evidence of visual motion perception disruption upon application of TMS (transcranial magnetic stimulation) over the V5/MT area (Sack, Kohler, Linden, Goebel & Muckli, 2006). Over the years, an elegant and non-invasive technique known as electroencephalography (EEG), has been a favored testing method for its particularly high temporal resolution (in the order of milliseconds). Thus, it comes with no surprise that EEG techniques have established themselves as common techniques to test and establish the neural correlates behind motion perception (Agyei et al., 2015; Agyei, Van der Weel, & Van der Meer, 2016). Particularly, EEG recordings of visual evoked potentials (VEP) have been found in relation to the processing of visual stimuli and, more specifically, VEP are thought to be related to the activity of cortical neurons in response to changes (Brecelj, 2003). Specifically, there are two areas in the occipital/parietal cortices that have been singled out as being involved in the processing of visual information: the ventral stream, assumed to be primarily involved in object recognition (Kandel, et al., 2013; Milner & Goodale, 2008), and the dorsal stream, which appears to play a central role in the visual processing of movement, particularly of speed and direction (Creem & Proffitt, 2001; Kandel et al., 2013). The area of the dorsal stream that is particularly interesting within the context of this research project is the dorsal medial superior temporal (dMST) area, whose direct implication with optic flow has been

6

previously identified, both in humans (Greenlee, 2000) and in rhesus and macaque monkeys (Duffy & Wurtz, 1997; Liu & Newsome, 2005; Xu, Wallisch, & Bradley, 2014). In addition to the dMST area, another area that seems to be substantially involved in the perception of optic flow is found within the V5/MT complex (Morrone et al., 2000). This area is sensitive to only certain types of optic flow, namely circular and radial motion (Morrone et al., 2000).

Studies of the VEP waveforms recorded with EEG show a negativity component, known as N2 or N200, during visual motion processing, which is assumed to originate in the visual motor area. The N2 reflects the peak latency (expressed in milliseconds) at which the underlying neuronal population reacts to visual motion stimuli (Heinrich, 2007). A focus on the dorsal visual stream in conjunction with studies of the VEP waveforms in this area have revealed negativity peaks at about 150-200 ms for adults (Probst et al., 1993) and 180-220 ms in 8-month-old infants (Van der Meer et al., 2008). Additionally, the N2 is also referred to as the main component of visual motion processing, and it is localized in the occipital-temporal region, as confirmed by several other imaging techniques, including fMRI and PET (Chawla, Phillips, Buechel, Edwards & Friston, 1998; Dupont, Orban, De Bruyn, Verbruggen & Mortelmans, 1994). The N2 component is often preceded by the P1 positivity, with the N2 representing both the motion component of the visual stimulus, as well as responses to temporal luminance modulations (Anderson et al., 1993; Heinrich, 2007; Kubova, Kuba, Hubacek & Vit, 1990; Mauer & Bach, 2003). In addition to analyzing the VEP waveforms, time-frequency analysis is another technique that has gained ground within the realm of visual motion processing, and which focuses on the oscillatory underlying neuronal activity recorded with EEG. Oscillations in the brain differ widely among them in frequency, with each group reflecting a functionally diverse cognitive and physiological process. The oscillatory

activity has been grouped into the delta-band (1-4 Hz), theta-band (4-7 Hz), alpha-band (7-13 Hz), beta-band (13-30 Hz), and gamma-band (30-150 Hz) (Buzsaki, 2004). Brain oscillatory activity is extrapolated from EEG recordings through time-frequency analysis, where only the events that are time-locked (but not phase-locked) to the onset of the stimulus are kept after the data averaging. The changes in the time-spectrum evolution (TSE) can indicate either an event-related synchronization (ERS, increase in amplitude/power) or desynchronization (ERD, decrease in amplitude/power), which suggest an increase in synchrony of neuronal populations in the former, and a decrease in synchrony of the neuronal population in the latter (Pfurtscheller & Lopes da Silva, 1999). Studies have indicated that infants tend to display an array of theta-band oscillations, which is an indication of brain immaturity (Pfurtscheller, Neuper, & Mohl, 1994; Pfurtscheller & Lopes da Silva, 1999). The presence of these low-frequency oscillations is expected to diminish as the brain matures, and be consequently replaced with higher frequency alpha-band oscillations when infants are around 1 year of age (Agyei et al., 2016; Stroganova, Orekhova, & Posikera, 1999). Moreover, infant studies have shown that visual motion stimuli elicit theta-band activity when motion stimuli are presented in contrast to static stimuli (Agyei et al., 2016, Agyei et al., 2015; Van der Meer et al., 2008).

As exemplified in the literature above, it is assumed that motion perception follows a developmental pathway that is positively correlated with age. Numerous studies have shown that the visual detection of motion stimuli is refined with experience, which is evident in differences in recordings between pre-locomotor and mobile infants (Van der Weel & Van der Meer, 2009). For instance, looming experiments suggest that anticipation of collision is increasingly more sensitive as infants grow older, as represented by marked theta oscillations on EEG scalp

recordings, which is indicative of attentional mechanisms supporting visual processing (Van der Weel & Van der Meer, 2009). Furthermore, a longitudinal infant study conducted by Agyei et al. (2015), found that latency responses to an optic flow paradigm are sensitive to age increase, where 12-month-old infants with locomotor experience displayed shorter latencies compared to 4-month-olds without self-locomotion experience. The latter study, among others, highlights the important role that visual perception has on the development of navigational skills, which are adaptive to the environment, as shown by their dependency on experience. And it is particularly this experience with self-locomotion that seems to be involved in the functional processing of optic flow (Van der Meer et al., 2008). Nevertheless, despite functional processing of optic flow being associated to experience with self-locomotion, there is evidence that even very young infants, with no experience in self-locomotion, display the functional premises to process structured optic flow (Agyei et al., 2015). And it is this claim which prompts research to continue to look into the developing brains of the very youngest, not just to establish developmental trajectories when compared to the older infants, but also to understand the underlying biological processes that are innate and independent of experience.

The present study was carried out to investigate the differences in perception of visual ego-motion at two different speeds and directions, in a longitudinal design that compared pre-locomotor to mobile infants. Specifically, high-density EEG applied to an experimental design testing infants at both 4-5 and 9-10 months of age, was used to investigate how the visual system processes simulated forward and backward ego-motion down a road at two different speeds. Both VEP and time-frequency analyses were employed to the study of brain activity, enabling an understanding of responses of cortical neurons to afferent activity (Van der Meer et al., 2008), as

well as of the oscillatory activity of underlying cortical neuronal populations (Pfurtscheller & Lopes da Silva, 1999). It was hypothesized that very young infants without previous experience with self-locomotion would display longer N2 latencies compared to when the infants had become mobile at the age of 9-10 months (Agyei et al., 2015). It was expected that no difference would be found in latencies in response to forward and backward visual motion presented at two different speeds for the pre-locomotor infants. However, because of their experience with mobility, we expected locomotor infants to show shorter N2 latencies for forward compared to backward optic flow, indicating a faster response to forward visual ego-motion (Agyei et al., 2015; Van der Meer et al., 2008). It was possible that 9/10-month-old infants would also be able to distinguish between different speeds (Vilhelmsen et al., 2015b). Finally, it was expected that a decrease in low frequency activity would be observed as the infants became older; specifically, a decrease in low-frequency theta activity was expected from the first to the second testing session, with an increase in alpha- and beta- frequency activity in the older infants, a typical sign of brain maturation (Agyei et al., 2015; Agyei et al., 2016).

2.0 Methods

2.1 Participants

Fourteen full-term, normally developing infants were recruited for this study. This study had a longitudinal design, with the infants being tested at 4-5 months and consecutively at 9-10 months. For the first testing, the mean age was 18 weeks (SD=5.0), and none of the infants had experience with self-locomotion. In the second testing, the mean age was 42 weeks (SD=3.6), and all infants had experience with independent crawling or a mix of scooting and crawling, pulling to stand or walking with assistance. Electroencephalography is a non-invasive experimental measure that does not pose risks to the health of the participant. The Norwegian Regional Ethics Committee and the Norwegian Data Services for the Social Sciences approved the study. Parents of the infants who participated in this experiment signed an informed consent before the study began and had the right to withdraw from the testing session at any point in time.
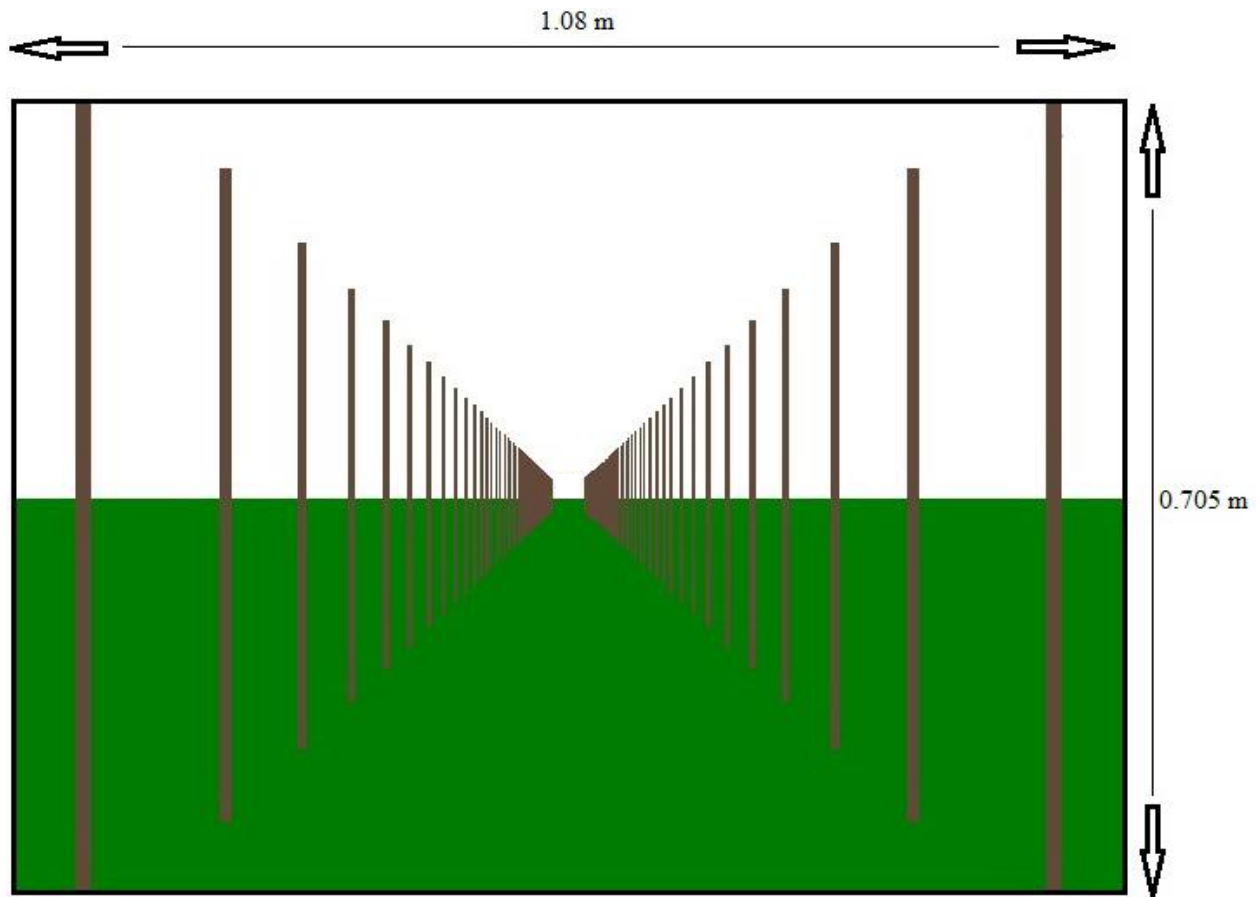
2.2 Experimental stimuli and paradigm

Figure 1. *Screen shot of optic flow stimulus simulating forward ego-motion.*

The stimuli were generated by E-Prime software (Psychological Software Tools, Inc.) and mirror-reversed projected onto a white screen (1.08 m x 0.705 m) by an ASK M2 projector with a refresh rate of 60 Hz, and an image resolution of 593 pixels per meter. The infants were seated approximately 80 cm from the screen so that the projected image had a visual angle of 68° horizontal by 47° vertical.

The stimulus consisted of simulated vehicle driving at two different speeds, referred to as low and high speed. Those were set at 25 km/h and 50 km/h, for low speed and high speed respectively. In addition, both forward and backward motion were simulated. The image on the screen consisted of several poles which appeared small at the center of the screen and grew in size

as they moved outwards, so as to simulate forward motion (see Figure 1). Participants were also exposed to the reversed motion condition, which had similar properties as the forward motion condition except that the poles appeared at the outer edges of the screen and moved inwards. Finally, the inter-stimulus interval (ISI) was created by showing a static stimulus consisting of the same number of poles as in the preceding trial; this condition did not simulate motion, but instead the poles remained in their fixed position for the duration of the trial. This procedure allowed to eliminate differences in luminance between the motion conditions and the static condition. The order of presentation of the four motion conditions (low-speed forward, low-speed backward, high-speed forward, high-speed backward) was random, with a static condition being intercalated between presentations of each of the four motion conditions in order to prevent motion adaptation. The motion and the static control trials lasted 1500 ms each. The experiment ran from 10 to 20 trials for each of the four motion conditions (mean=52, SD=8.4), and four times as many trials for the static control condition (mean=53, SD=8.5). The experiment lasted about three to five minutes.

2.3 Data acquisition

The electroencephalography (EEG) data were recorded using a Geodesic Sensor Net (GSN) 200 (Tucker, 1993). The net consists of 128 Ag/AgCl sensors evenly distributed over the head. The EEG signal was amplified using a high-input EGI amplifier at maximum impedance of 50 kΩ to ensure ideal signal-to-noise ration. The amplified signals were then recorded with Net Station on a Macintosh computer with a sampling rate of 500 Hz. The use of a Tobii X50 camera was employed to track the gaze of the infants. The eye-movement data were processed by ClearView software connected to a HP computer. Additionally, two cameras set at the corners of the screen in front of the infant recorded digital videos of the entire procedure, allowing the

experimenters to track the behavior of the infants. All the recorded data were then stored for offline analyses.

2.4 Procedure

Upon their arrival at the lab and prior to the experiment, the parents of the infants signed the informed consent form. The infants were then allotted some time to familiarize themselves with the new environment and the experimenters. Enough time was offered for the infants to be fed and changed. Meanwhile, an assistant took a measurement of the infant's head circumference to match the right GSN 200 net size. The net was immersed in an electrolyte saline solution to optimize conductivity of the electrical signal, and then placed on the infant's head. While the infant sat on the parent's lap, soap bubbles as well as noisy toys were used to distract the infant from the net mounting procedure. Once the net was placed on the infant's head, pictures were taken, and then the infant was immediately brought to the dimly lit experimental room. While the infant was seated on a secured car seat placed in front of the projection screen, the experimental assistant team went in the computer room to operate the necessary software required for the experiment. The experimental room and the control room were separated by a soundproof window. The signal of the electrodes was checked, and their contact to the scalp improved if required. An assistant was present in the experimental room throughout the duration of the session to assure the infant's focused gaze was maintained on the screen. In addition, one parent remained with the infant in the experimental room to avoid any potential distress that his or her absence might cause.

The experimental session began after calibration of the infant gaze with the Tobii X50 camera. The session began with the optic flow experiment, followed by two other visual motion experiments on looming and occlusion. A session was paused whenever the infant became bored or fussy, and efforts on the part of the assistant and parent were made to regain the infant's

attention. The experiment was terminated early in case the infant showed signs of distress which impeded a useful data collection.

2.5 Data Analysis

Brain Data Analysis

EEG data analysis was carried out with BESA 6.0 and BESA statistics 2.0 (Brain Electrical Source Analysis, BESA GmbH). The preliminary phase of the analysis consisted in segmenting the EEG recordings with the Net Station software and exporting the data as raw files for the offline analysis. The VEP data was segmented into epochs from -200 to 800 ms, with baseline definition of -200-0 ms. Slow drift in the data was removed by setting the filters to 1.6 Hz low cut-off (high band-pass), 60 Hz high-cut off (low band-pass), with the notch filter set at 50 Hz to remove line interference. During the scan for artifacts, the trials and epochs with amplitudes over 200 μV, gradients over 75 μV/sample and signals below 0.01 μV were excluded from further analysis. Additionally, physiological artefacts such as eye blinking, horizontal and vertical eye movements, amongst others, were corrected through semi-automatic artefact corrections using pre-set filters specifically designed to eliminate these types of artefacts from the brain activity of interest (Berg and Scherg, 1994; Ille, Berg and Scherg, 2002). The average number of accepted motion trials for infants were 52 (SD=7, range=43-66) and 52 (SD=9.9, range=42-74), at 4-5 months and 9-10 months respectively. The static condition had an average number of accepted trials of 53 (SD=6.8, range=44-65), and of 53 (SD=10.2, range=35-74) for infants at 4-5 and 9-10 months, respectively. There was an even distribution of trials across the four motion conditions.

VEP Analysis

VEP analysis was carried out using individual averages that were interpolated to the standard 81-electrode configuration of the reference-free (10-10) electrode system. Each infant's average was then combined into a grand average for each testing session. The VEP waveforms gave a time frame from which it was possible to identify the N2 component at different electrode sites. The above component was identified using 3D spherical spline whole-head voltage maps of EEG scalp signal distributions that highlighted the occipito-parietal areas where the maximum N2 activity of the most dominant VEP waveform was found. The peak latency and amplitude values of the individual averages were recorded. The peak latencies were measured as the latencies between the stimulus onset and the peak of each N2 component. The peak amplitudes were measured as the maximum amplitude of the N2 component relative to the pre-stimulus baseline.

Time-Frequency Analysis

In addition to VEP, a time-frequency analysis was performed. The analysis, which transforms the time-domain signal into the time-frequency domain by complex de-modulation (Papp & Ktonas 1977), was carried on using multiple source dipoles that model the activity of the brain areas of interest, in this case the visual and parietal cortices. However, surface electrodes, in addition to the oscillatory activity measured at scalp level, also pick up interfering brain signals from neighboring sources. This effect is due to the widespread focal brain activity that occurs in accordance with the nature of the dipole fields, as well as the smearing effect of brain volume in EEG. Therefore, an optimal separation of the focal brain activity was obtained by applying a source montage (Scherg & Berg, 1991; Scherg, Ille, Bornfleth & Berg, 2002). The VEP source montage consisted of 17 sources that provided information about brain activity of the occipital/parietal areas, in addition to some residual activity in other areas. The sources that were further analyzed

included (with Talairach coordinates, Talaraich & Tournoux, 1988) the visual cortex lateral left (VClL), x=-45.2, y=-57.2, z=6.5, the visual cortex lateral right (VClR), x=45.2, y=-57.2, z=6.5, the parietal midline (PM), x=0.0, y=-72.3, z=37.0, and the visual cortex vertical midline (VCvM), x=0.0, y=-84.9, z=-14.3.
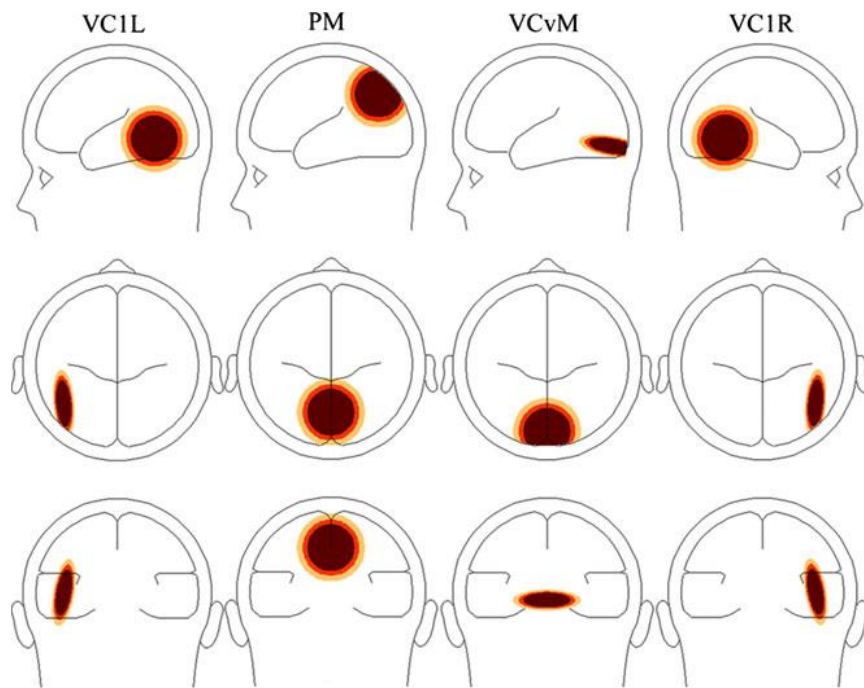

Figure 2. *The head models show the associated cortical areas VClL, PM, VCvM, and VClR (in order from left to right). The colored spot indicates the estimated source activity of the brain region assumed to be active.*

These sources were selected because they are believed to be most active in the visual processing of motion stimuli (Probst et al., 1993; Van der Weel & Van der Meer, 2009). The analysis through these sources was possible with the usage of a 4-shell ellipsoidal head model (Berg & Scherg, 1994; Hoechstetter et al., 2004), created for each of the infants, which transformed the data from electrode level to source montage dipoles. The artefact-corrected coordinate files

17

were also attached. Additionally, the bone thickness and conductivity were adjusted to 3.0 mm and 0.02 σ respectively, as suggested for infant data analysis (Grieve, Emerson, Fifer, Isler, & Stark, 2003). evolution (TSE) displays, showing the change in amplitudes over time, were set to frequency cut-offs of 2 – 40 Hz, and frequency and time sampling were set at 1 Hz, 50 ms. The settings for filters were set at 1.6 low cut-off (high band-pass), and 40 Hz high-cut off (low band-pass). Each TSE plot for each participant was tested for significance by performing a bootstrapping method, with significance for α set at 0.05. TSE displays only showed the induced oscillatory brain activity, which was achieved by removing the signals from the averaged evoked responses before calculating TSEs. Comparisons between the motion condition and the static inter-stimulus condition were also calculated. BESA statistics 2.0 (BESA GmbH) was used to conduct a series of unpaired and paired samples t-tests. Paired samples t-tests were carried out for each testing session to test for significant differences between motion conditions, as well as to look for significant differences in the motion vs static condition, in the time-frequency domain. 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 is lower than the values of condition 2 a negative cluster is found, which shows the direction of the statistical effect. The multiple comparisons problem was avoided by the systematic application in the statistical tests of a series of permutation tests and data clustering (Bullmore et al., 1999; Ernst, 2004; Maris & Oostenveld, 2007). The number of permutations was 16384, with the frequency ranges and epochs equaling those used in the time-frequency analysis. Unpaired t-tests were carried out between first and second testing to check for significant differences between each of the motion conditions, as well as the static inter-stimulus

control condition. The number of permutations was 100000, and frequency ranges and epochs were maintained as stated earlier.

3.0 Results

3.1 VEP responses

      Four posterior electrodes were selected. These electrodes were selected from the grand average that showed the highest N2 amplitude values in the low speed forward condition, and were further analyzed. For the young infants, the electrodes Iz, O9, O10, and Oz were selected. When the infants were older, the electrodes Iz, O9, Oz, and P3 were selected (Figure 3). Two separate repeated-measures ANOVA's were used to analyze the latency and amplitude of the VEPs. The latency and amplitude values used in the ANOVA analysis belonged to the electrode that had the highest N2 amplitude in the low forward condition, with each participant having a different selected electrode.
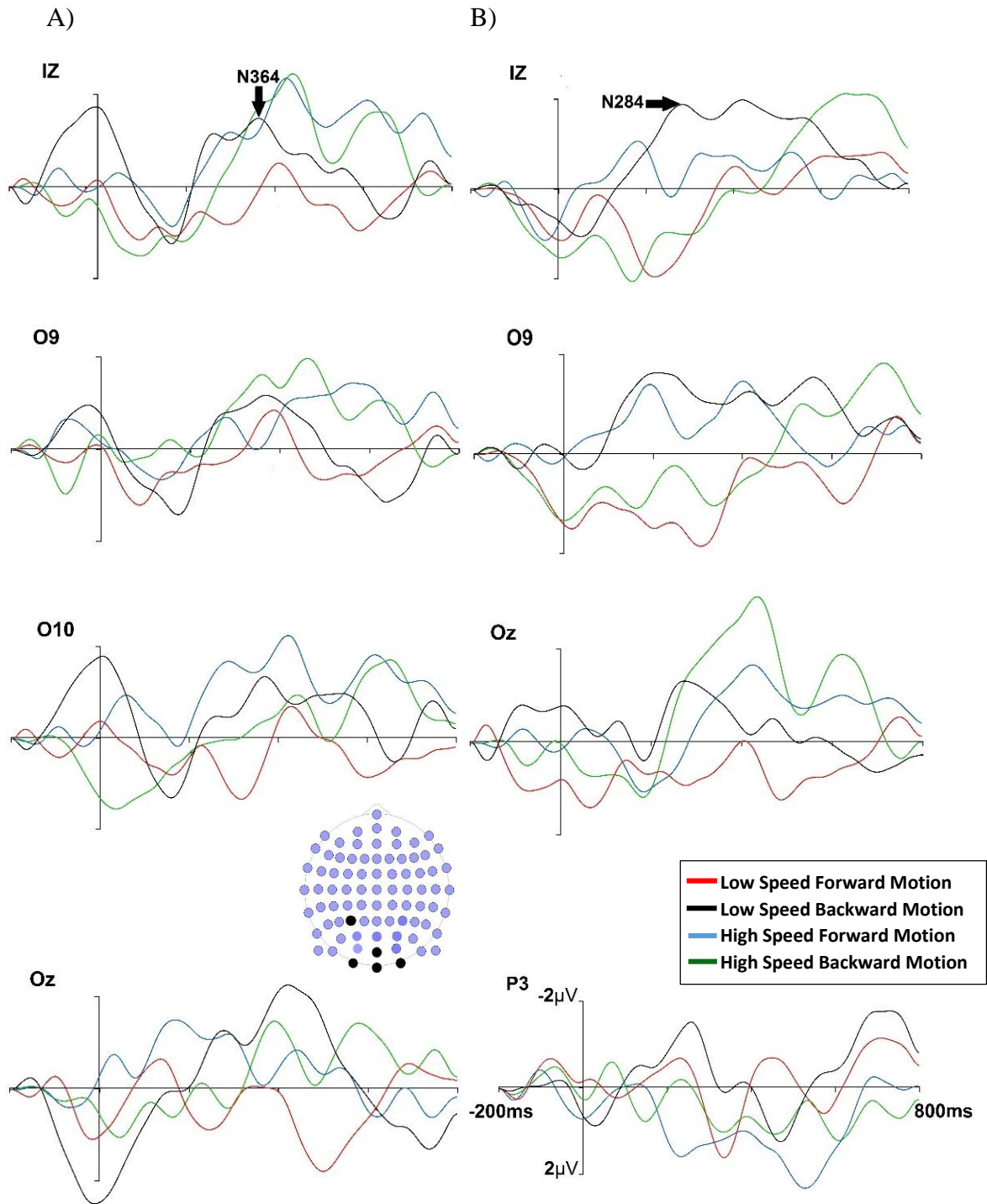
Figure 3. *Grand average VEPs for infants at 4-5 months (A) and at 9-10 months (B). The low speed forward motion waveform is highlighted in black, the low speed backward motion in red, the high speed forward motion in blue, and the high speed backward motion in green. The N2 peak for latency is indicated by the*

arrows on the electrode Iz for both age groups. Scalp localization for the selected electrodes is shown on the head model down the left column (up), with the black circles indicating the selected electrodes Iz, O9, O10, Oz, and P3 (from top to nose bottom, left to right).
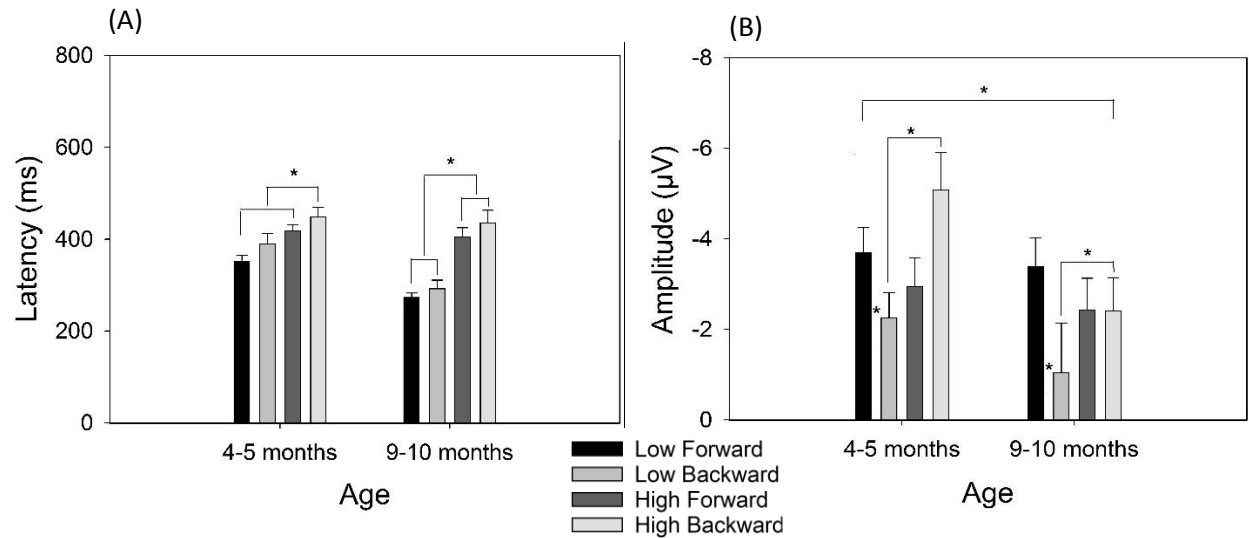

Figure 4. (A) *Group mean peak latencies (with error bars) and (B) group mean peak amplitudes (with error bars) for infants at 4-5 and 9-10 months of age. *Significant at p < 0.05.*

Repeated measures ANOVAs were run separately for peak latency and peak amplitude. Within-subjects factors were speed (low, high), motion direction (forward, backward) and the age at testing (4-5 months, 9-10 months).

The N2 component at the first testing session had a mean peak latency value of 352 ms (SD=47) for low forward motion, with 391 ms (SD=82), 418 ms (SD=45), and 449 ms (SD=77), for low backward, high forward, and high backward motion, respectively. The N2 component at the second testing session had a mean peak latency value of 273 ms (SD=35) for low forward motion, with 292 ms (SD=68), 406 ms (SD=69), and 436 ms (SD=100), for low backward, high forward, and high backward motion, respectively.

For latency, a significant two-way interaction, $F(1,13)=6.10$, $p<0.05$, was found between speed and age. This finding shows that speed had an effect on latency, but only for the older infants,

where low speed forward and backward motions had significantly lower latencies than high speed forward and backward motions (Figure 4A). For the older infants, the mean N2 latency was 421 ms for the high speeds and 282 ms for the low speeds, regardless of direction.

Additionally, for latency, a main effect of direction was found, $F(1,13)=5.57$, $p<0.05$, indicating that at both ages and irrespective of speed, infants displayed significantly shorter latencies for forward than for backward motion. The mean N2 latency value for forward motion was 363 ms, while that for backward motion was 392 ms.

Finally, for latency, a main effect of age was found, $F(1,13)=13.03$, $p<0.005$, indicating that age had directly affected latencies. The mean N2 latency value for the 4/5-month-olds was 403 ms, while that for the 9/10-month-olds was 352.

For amplitude, the N2 component for the younger infants had a mean peak value of -3.70 µV (SD=2.09) for low forward motion, with values of -2.27 µV (SD=2.05), -2.96 µV (SD=2.32), and -5.08 µV (SD=3.07) for low backward, high forward, and high backward motion, respectively. The N2 component in the 9/10-month-olds had a mean peak value of -3.39 µV (SD=2.36) for low forward motion, with values of -1.05 µV (SD=4.08), -2.44 µV (SD=2.58), and -2.42 µV (SD=2.72) for low backward, high forward, and high backward, respectively.

For amplitude, a significant two-way interaction of speed and direction was found, $F(1,13)=10.78$, $p<0.05$. Further post-hoc t-tests suggested that, regardless of age, speed had an effect on amplitude for backward motion only, with high speed displaying significantly higher amplitude. Additionally, direction affected amplitude in low speed only, with forward motion displaying significantly higher amplitude (see Figure 4B).

Finally, for amplitude a significant main effect of age was reported, $F(1,13)= 6.94$, $p<0.05$, where higher amplitudes were associated with younger age. The mean amplitude value for 4-5 month-old infants was higher than that for 9-10 month-old infants.
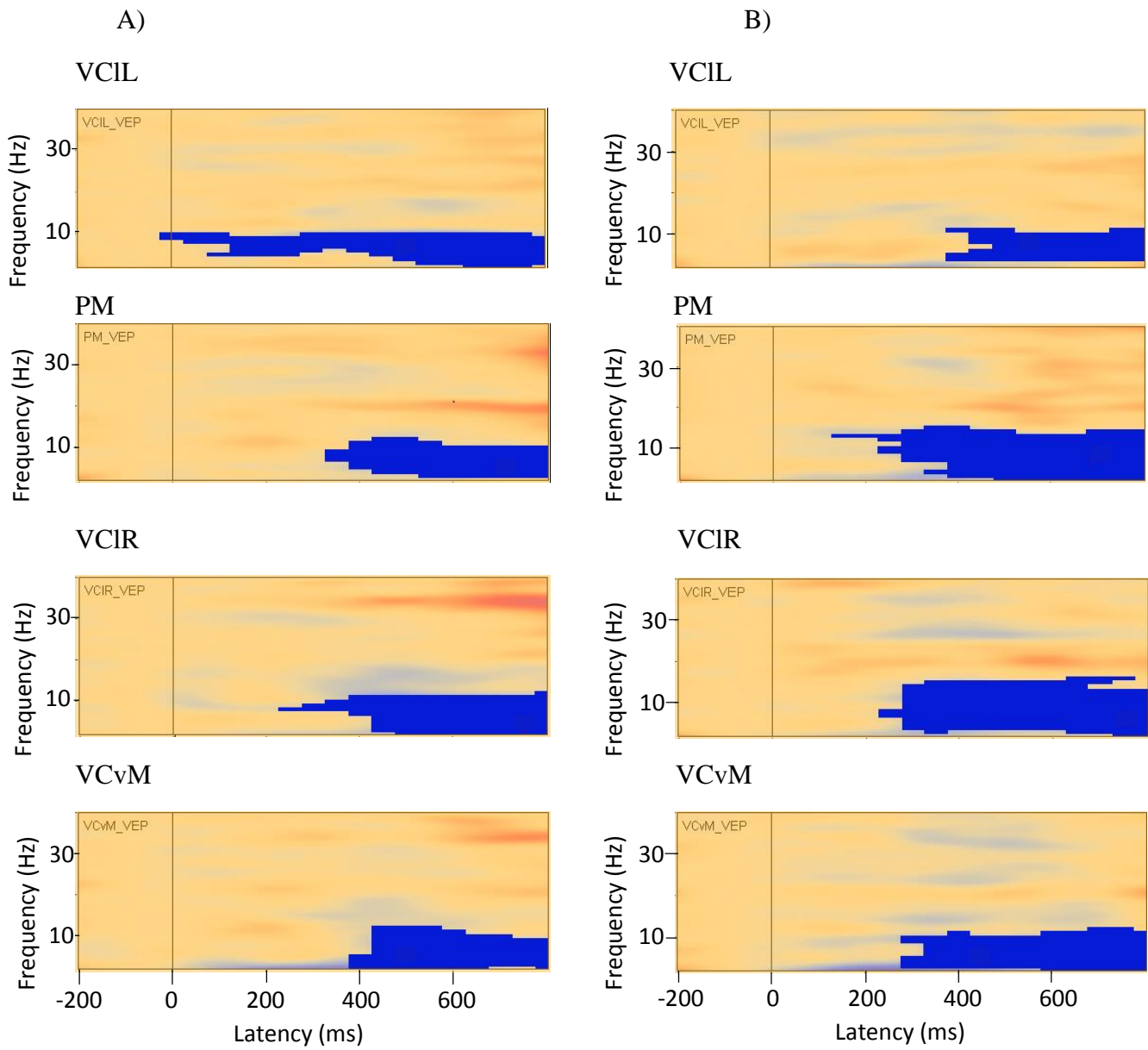
3.2 Time-Frequency analysis

Figure 5. *TSE averaged plots of significant data clusters from the visual areas of interest when the combined motion conditions were compared to the static condition in infants at 4-5 months (A) and at 9–10 months (B). VClL, PM, VCvM, and VClR represent visual areas. Blue colors represent negative clusters while red colors represent positive clusters. Low-frequency theta activity dominates the visual areas of interest and is indicated by the blue clusters. The stimulus onset is indicated by the vertical black line, starting at 0 ms, with epoch set from -200 ms to 800 ms.*

A permutation test was carried out on the averaged TSEs of each participant, comparing the combined motion conditions to the static condition, results showed significant differences indicating that infants at both 4-5 months (Fig. 5A) and 9-10 (Fig. 5B) months perceived a difference between the motion and the static condition (Figure 5).

The results showed significant negative (blue) clusters in sources PM, VClR, and VClL for the 4-5 month-old infants, and in sources PM, VCvM, and VClR for the 9-10 month-old infants, indicating that the combined motion conditions had significantly lower amplitudes than the static condition. The significant visual areas show cluster activity that dominates the low, theta frequency-bands in both groups, with partial alpha-frequency representation in both groups. T-tests were also run for each separate motion condition (i.e. low vs high speed, forward vs backward) but no significant differences were found between them. When the two testing sessions were compared for the combined motion conditions, no significant difference was found, indicating that the older infants did not show a decrease in low-frequency band activity and increase in higher-frequency activity. Furthermore, diffused high-frequency event-related synchronizations were found in the younger compared to the older infants. The negative cluster distribution over time seemed to equal in both groups, with the exception of visual area of interest VClL for the younger infants, which displayed a much longer temporal distribution.
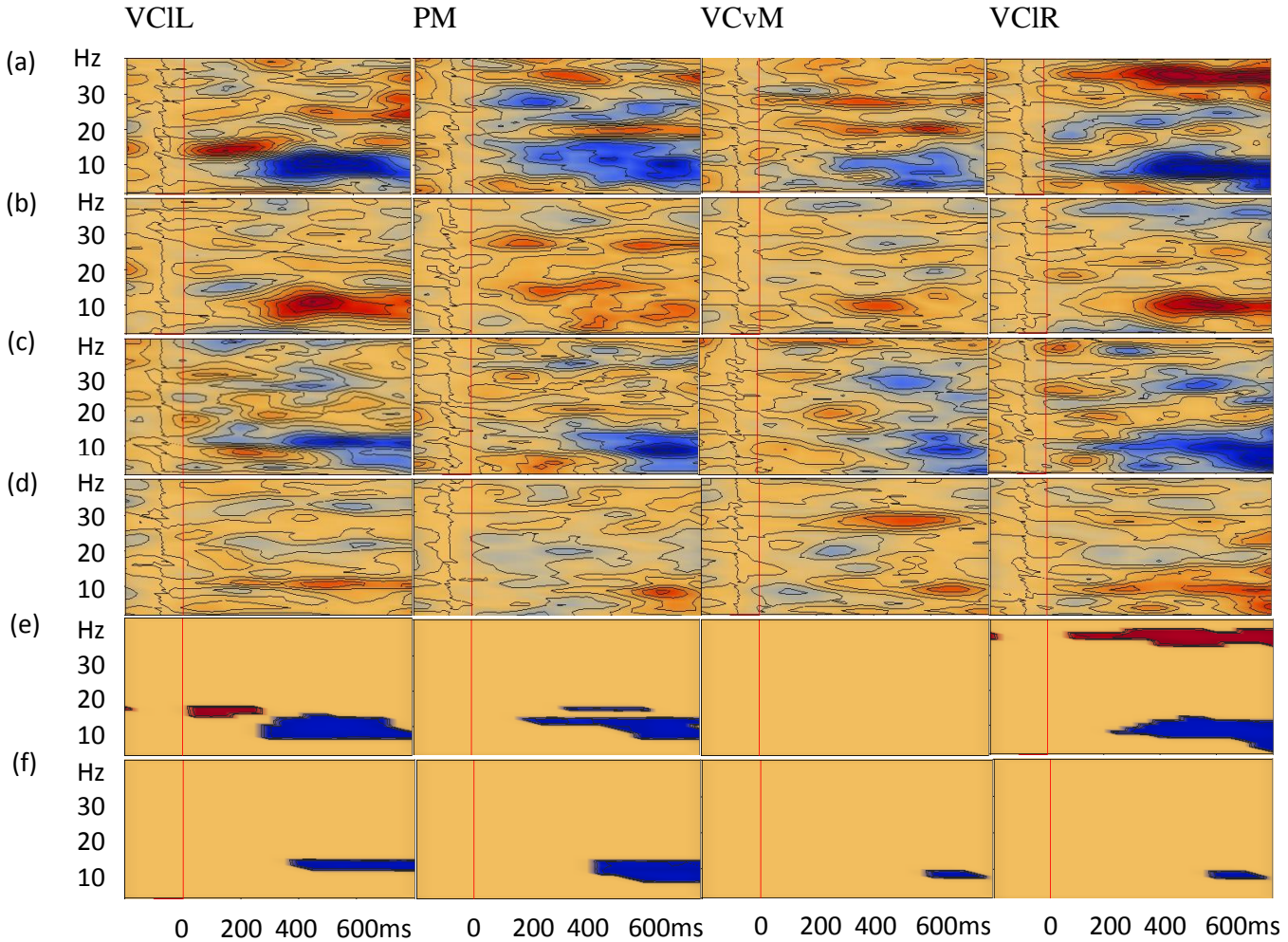
Figure 6. *TSE maps show the combined motion condition's response in the typical infant at 4-5 months (a)*

and at 9-10 months (c). The static non-flow condition responses are shown for the typical 4-5 month old

infant (b) as well as for the 9-10 month old (d). Additionally, the TSE probability maps (p<0.05) for the

typical 4-5 month old (e) and the 9-10 month-old (f) show the comparison between the combined motion

condition and the static non-flow condition. In the plots representing combined motion (a, c), the blue

clusters show event-related desynchronizations, with the bulk of the ERD being concentrated in the theta-

frequency range. Red clusters representing event-related synchronizations are present more so in the 4-5

month old typical infant (a) compared to the 9-10 month-old one (c). A decrease in amplitude, indicated by

the blue clusters, is shown at both testing sessions for the combined motion condition (a, c) compared to

the static (b, d) condition. Significant increase in amplitude (e) is shown at the first testing, in alpha-, beta-

, and gamma-frequencies, compared to the second testing (f). The stimulus onset is represented by a red line at time 0, with an epoch extending from -200 to 800 ms.

TSE maps show the typical 4-5 month-old infant displaying significant desynchronizations in the theta- and alpha-band frequencies. Additionally, at this age there were significant yet sporadic increases in amplitudes, especially in the alpha- beta- and gamma-band frequencies during the motion conditions (Figure 6a), while showing remarkably lower frequency synchronizations, mostly concentrated in the alpha- and beta-band frequencies, during the static condition (Figure 6b). The typical 9-10 month-old, interestingly, displayed desynchronizations in the theta- and alpha-band frequencies during the motion conditions (Figure 6c), while displaying somewhat less consistent synchronizations during the static condition, compared to the typical infant at first testing. The synchronized activity during the static condition was mostly present in the alpha- and beta-band frequencies (Figure 6d). Overall, as apparent in Figure 6 e and f, the TSE plots for the 4-5 month-old infant show more synchronized activity during the motion condition than the 9-10 month-old infant, as well as more widespread and varying desynchronizations.

4.0 Discussion

In this study, high-density EEG was used in 4- to 5-month-old and 9-10 month-old infants to investigate VEP's and TSE's for ecological forward and backward optic flow at two different speeds. Specifically, the goal was to investigate differences in brain processing of the motion conditions, as well as differences and developmental trajectories in brain processing at two different ages.

The VEP analysis showed a significant two-way interaction of speed and age where 9-10 month-old infants displayed shorter N2 latencies in both directions at low speed, compared to high speed. This marked difference in N2 latencies between the two speeds is indicative of brain maturation. In fact, infants go through rapid brain development during their first two years of life, as it is highlighted by the progressive myelination of cerebral fibers and growth of white matter during this time (Dubois et al., 2014). Particularly, it is during the first year of life that myelination of axonal fibers contributes to increasing the volume of white matter (Kandel et al., 2013). Myelin is a fatty sheet that wraps around the axonal fibers, leading the electrical impulses to travel down the axons at higher speeds. This results in higher rates at which the post-synaptic potentials travel from one neuron to the next, leading to increased speed of communication among neurons (Kandel et al., 2013). This increase in myelination might have contributed to the older infants having shorter N2 latencies at low speeds compared to when they were younger.

Furthermore, dendritic and synaptic proliferation increase throughout the first two years of life, reaching a peak growth between 8 months and 2 years, especially in the primary visual cortex (Klaver, Marcar, & Martin, 2011; Loenneker et al., 2010). It is suggested that the dorsal visual pathway reaches functional maturity much later than the ventral visual pathway (Klaver et al.,

2011), and it is perhaps this delay that reflects the N2 latency differences between the younger and older infants.

Additionally, evidence suggests that, with an increase in self-motion experience, perception of optic flow becomes increasingly more accurate and efficient (Agyei et al., 2015; Anderson et al., 2001). At 9-10 months of age, which is when the second testing occurred, all of the infants had experience with self-locomotion, which mostly consisted of commando crawling and/or assisted walking. This experience with self-locomotion, along with normal neurophysiological developments, contributed to the acquisition of faster visual processing, as expressed by shorter latencies in processing optic flow in both directions at low speed, compared to high speed. In addition, as found in previous studies with adults (Vilhelmsen et al., 2015a) and infants (Vilhelmsen et al., 2015b), N2 peak latencies were shorter for optic flow perception at low speeds compared to higher speeds. These results reflect those of the present study, where the 9-10 month-old infants displayed shorter N2 peak latencies at low speeds. From the evidence it can be concluded that the brain seems to be more attuned to processing optic flow stimuli at low speeds rather than high speeds, and this finding is consistent with the literature (Vilhelmsen et al., 2015b).

The significant main effect of age was probably due to the underlying significant interaction involving speed and age, such that the really low latencies at 9-10 months for the low speed in both directions caused an artificial main effect of age. When comparing the latencies between testing sessions for high speed forward and high speed backward motion, there was not a significant decrease with age.

The results also showed a difference in N2 peak latencies for direction. It seemed that, independent of age and speed, the infants were able to detect forward motion faster than backward motion, with shorter latencies for the former motion condition. These results are corroborated by

findings of a previous optic flow study by Agyei and colleagues (2015), which looked at the perception of forward and reversed optic flow, and found that 11-12 month-old infants displayed shorter N2 peak latencies for forward optic flow. Thus, Agyei et al.'s (2015) findings and others (Gilmore, Hou, Pettet, & Norcia, 2007) support the idea that brain responses are faster for forward rather than backward motion. Additionally, the reported shorter N2 latencies for the forward direction seem consistent with experience-related developmental theories (Agyei et al., 2016; Dahl et al., 2013). In fact, since the older infants in Agyei et al.'s (2015) study had some experience with self-locomotion at the time of testing, it could be possible that forward motion is more easily processed than backward motion, since moving forward is a type of motion infants are accustomed to when experimenting with self-locomotion. A study by Van der Meer and colleagues (2008) suggests that the perception of optic flow becomes functional only when infants acquire self-locomotor experience like crawling. The highlighted importance of self-locomotor experience corroborates other findings, where real-world interactions of body and environment aided the development of visually-guided behavior, a finding that is relevant in both humans (James & Swain, 2011) and animals (Held & Hein, 1963). However, it is also probable that the propensity for easier forward processing could be related to the possible presence of human cortical motion mechanisms that are most sensitive to radial expansion (mimicking forward motion) than contraction (backward), and that seem to develop around the age of 4 months (Shirai et al., 2009). And it is in these latter findings that support is found for the direction effect evident even within the youngest infants in the present study, where changes in locomotion are preceded by changes in the perception of optic flow. One study in particular suggests that perhaps developmental changes in some aspects of visual perception might precede and even promote the emergence of related motor actions like crawling and/or walking (Shirai & Imura, 2014).

Higher amplitudes were also recorded in the 4-5 month-olds compared to the 9-10 month-olds. The lower activation values of the older infants could suggest a thicker skull, which could limit the amount of spread of electrical activity, resulting in lower signals recorded at the scalp (Grieve et al., 2003). However, since it has been suggested that higher amplitudes result from a larger number of neurons firing in synchrony (Pfurtscheller & Lopes Da Silva, 1999), these larger activation signals could be the result of larger areas of neuronal activation. This finding could be observed in a very young brain, like that of the infants of the first testing, whose cortical areas are still going through specialization, therefore resulting in larger activation areas (Agyei et al., 2015; Agyei et al., 2016; Van der Meer et al., 2008).

The results showed higher amplitude values for forward rather than backward motion at low speed, at both testing sessions. As previously mentioned, high amplitude values indicate that more neurons are firing in synchrony, thus suggesting that more of them are attuned to a particular motion condition (Pfurtscheller & Lopes Da Silva, 1999). Since more neurons fired in synchrony in response to forward motion, this result seemed to indicate that most neurons in the motion sensitive area are attuned to forward direction. Therefore, it is plausible that forward motion processing might require fewer cognitive resources than backward motion, since the former is a type of ego-motion that is more commonly experienced (Shirai et al., 2009).

Lower amplitude values were recorded for backward motion at low speed compared to high speed, during both testing sessions. Lower amplitude may reflect a relatively lower number of synchronously active neurons upon presentation of the motion stimuli. Since amplitudes of brain electrical waveforms represent the synchronous activity of excited neurons, it is assumed that lower amplitudes may reflect less synchronous signals elicited by neurons in small and more specialized cortical areas (Pfurtscheller et al., 1994; Pfurtscheller & Lopes da Silva, 1999). Thus,

lower amplitude could indicate that infants processed backward motion at low speed more easily than at high speed, suggesting that the relatively high speeds used in this experiment were perhaps considered by the infants to be more complex than the lower speeds.

In addition to the VEPs, the differences in induced activities were also analyzed. When comparing the motion conditions to the static non-flow condition at both 4-5 months and 9-10 months, it appeared that low-frequency oscillations were present in the form of desynchronizations at both points in time. ERD activity was found mainly in theta-bands, particularly in sources PM, VClR, and VClL for the 4/5-month-olds, and in sources PM, VCvM, and VClR for the 9-10 month-olds. ERD activity was also found in alpha-bands, but only in some participants at both testing sessions. This result is corroborated by previous findings (Agyei et al., 2015; Agyei et al., 2016), where the desynchronizations in response to the motion stimuli indicate an activation of visual processing, as some neurons go from a synchronized firing state (high amplitude) to an activated state, where some neurons from a given population react to the new visual stimuli by firing differently than their neighbors, and therefore become desynchronized. The induced change in the theta-band frequencies of the motion and static conditions can be explained as a sign of immaturity typical of an infant brain, where recorded EEG activity is dominated by low-frequency activity of higher amplitudes (Pfurtscheller, Neuper, & Mohl, 1994). TSEs plots also revealed higher amplitude activity in low and high frequencies for motion and static condition in 4-5 month-olds, and mainly in the static condition in the 9-10 month-old infants. These present findings are in contrast with previous studies (Agyei et al., 2015; Agyei et al., 2016), where synchronized activity was mainly found in the older infants (8-10 months of age), and tended to be found at higher frequencies, particularly in the alpha-band range. The findings by Agyei et al. (2015, 2016) along with others (Agyei et al., 2016; Van der Meer et al., 2008) support the idea that infant brain

maturation leads to a shift in neuronal coupling, resulting in the evolution from mainly slow, ineffective low-frequency ERDs, to faster and more efficient high-frequency ERSs.

Results showed no differences between oscillatory activity in response to visual motion when the average TSEs for the 4-5 month olds and 9-10 month-olds were compared, which does not corroborate previous research outcomes (Agyei et al., 2015; Agyei et al., 2016). It was expected that a decrease in desynchronized low-frequency oscillations would occur between the first and second testing, with the older infants displaying desynchronized higher-frequency oscillations, preferably in the alpha-band frequency. Previous studies have shown that a decrease in theta-frequency desynchronization activity, replaced by higher alpha-band desynchronizations is a sign of brain maturation (Pfurtscheller et al., 1994; Pfurtscheller & Lopes da Silva, 1999). Specifically, slowly oscillating neuronal assemblies contain large number of neurons, while fast oscillating neuronal assemblies contain a smaller number. Since the amplitude of oscillation is believed to be proportional to the number of synchronized neuronal firings, it can be inferred that theta-band frequencies (5-8 Hz) involve a larger number of neurons than the faster oscillating alpha-band frequencies (9-13 Hz). Thus, the involvement of many neurons in response to a visual stimulus implicates that the occipital/parietal areas is not yet specialized, and therefore require a larger portion of the neuronal assembly in order to process such stimuli. The gradual transition from low-band frequencies to high-band frequencies suggests that the brain undergoes maturation, where the activation of the visual area involves the activation of fewer but more specialized neurons (Agyei et al., 2015; Pfurtscheller & Lopes d Silva, 1999). The result of this study, however, does not show a decrease in low-frequency desynchronizations with age, which could indicate that the stimuli presented to the infants required a higher degree of specialization of the visual areas. Since the visual motion stimuli mimicking forward and backward ego-motion were set at 25 km/h and 50

km/h for low and high speed respectively, it is plausible to assume that the speeds were too high for the infants to differentiate. In previous studies, Agyei and colleagues (2015, 2016) found similarities in the distribution of desynchronized theta-band oscillations between young and older infants (up to 1 year of age) in the random motion condition, perhaps highlighting the fact that, unlike typical motion such as forward optic flow, random motion is naturally uncommon and therefore more difficult to process, especially in subjects still undergoing a great deal of brain maturation.

In conclusion, a significant difference was found in latencies between low and high speed at the second testing, with lower N2 peak latencies for low speed, indicating that older infants were better at processing stimuli at low speed compared to high speeds. Additionally, infants at both ages perceived the forward direction more easily than the backward direction, suggesting an experience-based learning. Amplitude trends also highlighted a developmental trajectory, with older infants presenting smaller amplitudes, a result possibly suggesting increased skull thickness following age increase.

Oscillatory activity showed that infants from both group distinguished between combined motion stimuli and static non-flow stimuli, as indicated by low-frequency desynchronizations during the combined motion condition. However, no developmental trajectory was highlighted by the findings, showing no decrease in low-frequency theta desynchronizations as the infants became older. Further research is needed in the infant demographic to gain a preliminary understanding of how real life-events are perceived. This in turn, would promote further research efforts addressing developmental disorders (Yamasaki et al., 2011), and how difficulties with optic flow perception might be related to such disorders.

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