

**A high-density EEG study of looming related brain activity in
young infants**

by

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Summary

As infants get more mobile from the second half of the first year of life the ability to perceive and efficiently respond to colliding objects becomes increasingly important. It is suggested that this ability develops as part of a specialization process as infants get more experienced with self-produced locomotion. The aim of this study was to investigate brain electrical activity in infants aged 5-6 months, 8-9 months and 10-11 months. The infants were presented with a looming stimulus approaching on a direct collision course under three different accelerations. Brain electrical activity was investigated by source analysis. A three-dipole model of the visual areas O1, Oz and O2 was fitted around peak looming VEP activity at these sites, providing source waveforms (SWF) as a measure of activity in these areas. Start time, duration and amplitudes of the source waveforms were analyzed on a trial by trial basis. The infants seemed not to distinguish between the three looming conditions. There were significant differences between the three dipoles for start time, duration and amplitudes, indicating that the looming stimuli were processed differently in these areas. Visual Cortex radial Left (VCrL) and Visual Cortex radial Right (VCrR) showed the most prominent activity, with activity in these dipoles starting first and lasting for the longest period of time. Also, amplitudes were higher in these dipoles, indicating more cortical activity. However, a pattern of decreasing processing time with age was observed for VCrL and VCrR, which supports earlier findings of a developmental trend for decreasing processing time within the first year of life. Presumably this is due to better control over self-produced locomotion and increased specialization in the developing infant brain. Whether this decreasing brain activity in infants' perception of looming correlates with behavioural changes should be investigated to get a better understanding of the developing brain and behaviour.

1. Introduction

When we move around in the world we are dependent on information from our surroundings in order to change to an appropriate direction when approaching a destination, avoid bumping into objects and avoid being hit by other moving objects. Such actions involve prospective control, i.e. control of movement in relation to perception of forthcoming events. Our interaction with the environment involves a complex system where action, perception and cognition are tightly coupled together (von Hofsten, 2004, 2007; Lee, 1998). Gibson (1979) states that the information we need for perception of self movement and motion in the environment is available from the optical flow field. Smooth pursuit eye movement is seen as an indicator of prospective control and this ability seems to develop within the first three months in human infants (von Hofsten, 2007; von Hofsten and Rosander, 1997; Shea and Aslin, 1990). Perception of motion becomes increasingly important as infants become more mobile in the second half of their first year. From a perception-action point of view infants are active participants in learning about themselves and the environment, and they provide through their own actions, e.g. crawling which emerges between 6 and 9 months, some of the experience necessary for further growth and development (Bertenthal, Campos and Kermoian, 1994).

According to Johnson (2000), traditional views on brain and behaviour see behaviour as a result of brain growth and maturation, i.e. behaviour emerges due to physical development of the brain. Johnson (2000) suggested an interactive specialization framework for postnatal functional cortical development and argued that postnatal brain development can be analyzed in terms of the differential specialization of multiple coactive pathways. Further, he hypothesized that differential specialization occurring between and within brain pathways may result in patterns and temporal dynamics of the neural basis of behaviour in infants that differ from those observed in adults. Shortly after birth a cortical region may respond to a wide variety of visual stimuli. With development the same region may only be activated by certain components of these stimuli. This specialization process may be related to the concept of tuning of response properties of single neurons. In addition the specialization process facilitates speed of processing for the stimuli on which it becomes specialized (Johnson, 2000). For example, Pascalis, De Haan and Nelson (2002) report that 6-month-old infants process the faces of humans and monkeys in the same way, while in 9-month-old infants and adults human face stimuli produce different patterns of activation from monkeys. These

findings suggest that cortical processing of faces becomes more specialized throughout development (Johnson, 2000).

Studies of ERPs in infants have indicated that for word learning (Neville, Mills and Lawson, 1992) and face processing (De Haan, Oliver and Johnson, 1998) there is increasing localization of processing of a stimulus class with age and experience in which a larger area of the scalp shows a stimulus specific effect in younger infants than in older ones. This indicates that stimulus processing activates a smaller part of the cortex with age and that this is part of an increasing specialization (Johnson, 2000).

Numerous studies have been carried out for the purpose of deciding which cortical areas are involved in visual processing and the perception of motion. An area with cells specialized to process visual motion located at the posterior bank of the superior temporal sulcus and in the middle temporal area (MT), subsequently named V5, was first discovered in monkeys (Zeki, 1974) providing a foundation for a theory of functional specialization (Zeki, 1978; 2004). Evidence for a human equivalent of this area comes from imaging studies in human adults (for a review see Born and Bradley, 2005) using PET (Cunningham, Deiber, Frackowick, Friston, Kennard, Lammertsma, Lueck, Romaya and Zeki, 1990; Zeki, Watson, Lueck, Friston, Kennard and Frackowiak, 1991), fMRI (ffytche, Howseman, Edwards, Sandeman and Zeki, 2000; Sunaert, Van Hecke, Marchal and Orban, 1999; Tootell, Repas, Kwong, Malach, Born, Brady, Rosen and Belliveau 1995) and MEG (Uuitsalo, Virsu, Salenius, Näsänen and Hari, 1997). In humans this area is referred to as V5/ MT complex (MT+). Impaired motion perception has been found in patients with brain lesions that include the MT area (Zeki, 2004, 1991) and has been demonstrated using TMS in healthy subjects (Sack, Kohler, Linden, Goebel and Muckli, 2006). Other motion-sensitive areas that have been identified are V1 and hV3a (e.g. Dupont, De Bruyn, Vandenberghe, Rosier, Michiels, Marchal, Mortelmans and Orban, 1998; Smith, Greenlee, Singh, Kraemer and Hennig, 1998; Sunaert et al., 1999; Tootell, Mendola, Hadjikhani, Ledden, Liu, Reppas, Sereno and Dale, 1997).

Visual information from the retina is thought to reach area V5/ MT+ mainly via two parallel pathways in adults. The primary visual pathway projects via the lateral geniculate nucleus (LGN) to V1, V2 and then V5. Another pathway projects to V5/ MT+ via superior colliculus (SC) and pulvinar (e.g. Callaway, 2005; ffytche, Guy and Zeki, 1995; Schneider and Kastener, 2005; Schoenfield, Heinze and Woldorff, 2002) or via LGN (Sincich, Park, Wohlgenuth and Horton, 2004). The pathway via SC is functioning for fast moving stimuli as

signals from fast speed motion input has shown to reach V5 before V1 (ffytche et al., 1995). Findings indicate that this pathway dominates the immature visual motion processing in neonates (e.g. Atkinson, 2000; Rosander, Nyström, Gredebäck and von Hofsten, 2007). It is suggested that a functional cortical pathway involving the V5/ MT+ develops from this subcortical pathway and is functioning from 5 months of age (Rosander et al., 2007; Wattam-Bell, 1991). Information in the primary visual cortex is widely believed to be processed in two parallel interconnected pathways, the dorsal (movement) and ventral (object recognition) streams (Goodale and Milner, 1992).

Neuroimaging techniques are normally not used for studying the brains of healthy infants due to unknown risk to the developing brain (Johnson, De Haan, Oliver, Smith, Hatzakis, Tucker and Csibra, 2001) so less is known about the V5 area/ MT+ in infants and how it develops. A feasible method for studying the neural basis of behaviour in the developing brain is analysis of event related potentials (ERPs) recorded from the scalp (Johnson, 2000). Electroencephalography (EEG) with a high-density geodesic sensor net gives improved spatial resolution (Tucker, 1993) and provides a method for studying both the time course and spatial distribution of functional activity within the cortex (Johnson, 2000). The interpretability of the recorded EEG data is limited by the ambiguity of relating a surface signal to a particular brain region, thus a brain electrical source analysis (BESA) may be applied to create a discrete multiple source model which can be used as a source montage to transform the recorded data from sensor level into brain source space (Hoechstetter, Bornfleth, Weckesser Ille, Berg and Scherg, 2004).

ERP signals (event related potentials) represent transient changes in the brain's electrical activity and can be considered as post-synaptic (dendritic) responses of main pyramidal neurons, time- and phase-locked to a particular event (Pfurtscheller and Da Silva, 1999). The N2 component in visual motion ERPs (VEP) has been identified in relation to area MT+ in humans (Probst, Plendl, Paulus, Wist and Scherg, 1993). In infants this component has been recognized from two months of age (Lippé, Roy, Percehet and Lassonde, 2007) with longer latency than in adults thought to reflect a slower processing (e.g. Pascalis et al., 2002; Van der Meer, Fallet and Van der Weel, 2008), although infants have shown adult values of N2 already from 7 – 12 months of age (Lippé et al., 2007).

VEP studies (EEG) using different age groups and different visual stimuli have observed that infants process motion stimuli different than older children and adults and that the development is non-linear with a rapid decrease in latencies and increase in amplitudes

within the first two years (e.g. Brecelj, 2003; Coch, Skendzel, Grossi and Neville, 2005; Pascalis et al., 2002; Hamer and Norcia, 1994; Hammarrenger, Leporé, Lippé, Labrosse and Guillemot, 2003; Hollants-Gilhuijs, De Munck, Kubova, Van Royen and Spekrijse, 2000; Langrová, Kuba, Kremláček, Kubová and Vít, 2006; Lippé et al., 2007; Van der Meer et al., 2008; Webb, Long and Nelson, 2005). Different occipital brain regions displayed coherent U-shaped patterns indicating that the regions followed the same developmental pattern with a turning point from 7 to 24 months corresponding with a period of low coherence from 3 – 23 months (Lippé et al., 2007).

Postnatal improvements in the maturation of synapses and myelination should lead to decreases in information processing speed during the first year of life (Grieve, Emerson, Fifer, Isler and Stark, 2003; Webb et al., 2005). Synaptic pruning may also be responsible for the tuning of specific functions and myelination (Picton and Taylor, 2007). It has been reported that synaptogenesis starts earlier in the visual cortex than in other brain regions (Huttenlocher and De Court, 1987) and that synaptic density reaches a peak between 9 – 15 months of age (Huttenlocher and Dabholkar, 1997). This implicates several synaptic changes until 24 months of age and could account for reduced efficiency of processing in this period of development (Lippé et al., 2007). Also, inter-baby variability has shown to be much greater than the variability in adult subjects (Thierry, 2005).

In a study of optic flow Van der Meer et al. (2008) reported that N2 had shorter latency in coherent motion both in adults and infants compared to random non-flow and that infants displayed longer latencies and higher amplitudes than adults. It has been observed that infants who are more experienced with self-produced locomotion, e.g. crawling, also are more sensitive to patterns of optic flow (Bell and Fox, 1996, 1997; Berthenthal et al. 1994; Van der Meer et al., 2008).

The ability to perceive motion and to respond with appropriate action is of fundamental importance to the organism (Webb et al., 2005). The nervous system of animals and humans must extract and process information from the environment for the purpose of a quick and accurate response to looming danger, i.e. an object on a direct collision course providing an expanding image on the retina (Schiff, Caviness and Gibson, 1962). Defensive responses to a looming stimulus were first investigated in monkeys and avoidance reactions were observed in the behaviour of both monkey infants and adults (Schiff et al., 1962). Neurons responding specifically to approaching objects have been found in the locust (Hatsopoulos, Gabbiani and Laurent, 1995; Rind and Simmons, 1997), the pigeon (Sun and

Frost, 1998) and in human adults (Dougherty, Koch, Brewer, Fischer, Modersitzki and Wandell, 2003; Holliday and Meese, 2005). The human visual system is shown to be specialized for detecting and responding to approaching (looming) motion (Holliday and Meese, 2005; Morrone, Tosetti, Montanaro, Fiorentini, Cioni and Burr, 2000).

Behavioural studies of human infants show that blinking as a defensive response to optical collision is precisely timed to the time to collision of the approaching object (Kayed and Van der Meer, 2000, 2007). Sensitivity to expansion has been discovered in infants from a very early age (Shirai, Kanazawa and Yamaguchi, 2004; Yonas, Pettersen and Lockman, 1979). Visual motion activates both cells sensitive to the spatiotemporal (coherent motion) and temporal characteristics (flicker) (Rosander et al., 2007). Sunaert et al. (1999) found that response to coherent motion is weak in V1 and strong in MT+, whereas the opposite was found for flicker. Van der Weel and Van der Meer (2009) investigated brain electrical responses to a looming stimulus in a cross-sectional design in 5- to 11-month-old infants and found a developmental trend in which the youngest infants had longer processing times than the older infants suggesting established neural networks for the processing of impending collision in older infants with crawling experience. In an unpublished Master's thesis, Svantesson (2010) investigated VEP activity in the same infants at 5 – 6 months and at 12 – 13 months and reported that VEP activity in the youngest infants started earlier in the looming sequence and had a longer duration. Brain activity was also found to propagate from occipital areas to parietal areas with age.

In collision judgments, the timing aspect in particular is crucial. fMRI studies in adults have reported neural activity in left inferior parietal cortex, left ventral pre-motor cortex and left sensorimotor cortex (Assmus, Marchall, Ritzl, Noth, Zilles and Fink, 2003; Coull, Vidal, Goulon, Nazarian and Craig, 2008; Field and Wann, 2005), indicating that these areas may be involved in temporal prediction. In a study of attention to motion, Pavlova, Birbaumer and Sokolov (2006) found left hemisphere MEG response in the parieto-occipital region.

Measured psychophysically, motion sensitivity has been found to develop asymmetrically in the left and right visual half fields during childhood, where children showed more difficulty in detection of motion in the left than the right half-field (Hollants-Gilhuijs, Ruijter and Spekreijse, 1998). A VEP/ MRI study found that N2 is generated by extrastriate activity and that motion stimuli are not equivalently processed in the two cerebral hemispheres with a hemispheric lateralization in all adult subjects but does not support a hemispheric predominance in children (Hollants-Gilhuijs et al., 2000). VEP analysis of

human infants presented with a looming stimulus (Van der Weel and Van der Meer, 2009) revealed localised activity in the visual cortex especially in the two dipoles localised laterally left and right. The left dipole showed a significant effect for start time and duration. The evidence taken together suggests a left hemispheric dominance in motion perception in infants.

The aim of the current study was to investigate brain electrical activity (i.e. SWFs) in three infant age groups with different crawling/ self-locomotion experience when presented with a looming stimulus that approached on a direct collision course under three different accelerations.

2.Method

2.1 Participants

A total of 22 babies in three different age groups were recruited from birth announcements in a local newspaper and tested. For the babies to be included in the analyses a minimum of three trials for each looming condition had to be performed. Two of the babies were excluded because they were born preterm and five babies were excluded because the total number of trials performed was too few or the data were too contaminated by artefacts. 15 babies were included in the final analyses, 5 in each age group.

The youngest group was 5 – 6 months old and five babies (three boys) were analyzed. Mean age was 26 weeks (SD = 2.7). Five infants (four boys) of 8 – 9 months participated. Mean age was 37.4 weeks (SD = 0.5). In the eldest age group five infants (two boys) of 10 – 11 months participated. Mean age was 46 weeks (SD = 1.7). The two youngest age-groups were not yet capable of self-produced locomotion, while the eldest babies had some crawling experience.

According to parental report all the babies were healthy, full-term and born without any serious complications. The parents understood that they could withdraw at any time during the experiment and they gave their informed consent in writing before the experiment started. The study has been approved by the Norwegian Regional Ethics Committee and the Norwegian Data Services for the Social Sciences.

2.2 Stimuli

The infants were visually paying attention to a looming stimulus (Van der Weel and Van der Meer, 2009), generated with E-Prime (Psychological Software Tool Inc.) and mirror

reversed projected onto a wide screen by an ASK M2 projector. The stimulus simulated an object that came from far away on a direct collision course and approached the subject with a constant acceleration.

The stimulus object was a flat, black circle, with four coloured inner circles in red, green, blue and yellow shown on a light background. The radius of the inner circles was 1/3 of the radius of the outer circle. The entire object constantly rotated on its centre with an angular velocity of 300 degrees per second. After one second the rotating circle started to approach the subject under one of three different accelerations as the circle grew. Actual duration for the stimulus was 2 s (fast), 3 s (medium) and 4 s (slow). In acceleration this corresponded to 21.1 m/s^2 , 9.4 m/s^2 and 5.3 m/s^2 , respectively. Before the circle started to grow its diameter was 6.5 cm and it had a visual angle of 5° . When it “exploded” the projection was 350 cm with a visual angularity of 131° . The three conditions were presented in random order and the inter-trial interval was 1 s (see Figure 1).

2.3 Equipment/ apparatus

The Geodesic Sensor Net 200 (GSN) (Tucker, 1993) for infants consisting of 128 Ag/AgCl sponge sensors/ electrodes for even distribution across the scalp was used for recording of the EEG activity. The vertex electrode (Cz) served as a reference. The electrical potentials were amplified 1000x according to the impedance measured before onset of the experiment, and recorded with Net Station software on a MacIntosh computer. All electrode impedances were kept under 50 k Ω as recommended to ensure an optimal signal-to-noise ratio (Ferree, Luu, Russell and Tucker, 2000; Picton, Bentin, Berg, Donchin, Hillyard and Johnson, 2000.) The sampling rate was 500 Hz. Low-pass filter was set to 100 Hz and high-pass filter to 0.1 Hz. The data were segmented and stored on hard disk for off-line analyses.

Corneal reflection was detected with Tobii (50Hz) infrared eye tracker so that the eye movements during the experiment were recorded and could be processed with ClearView (version 2.2.0) on an HP computer. The infants were also filmed with a digital video camera so the experimenters could monitor overall looking behaviour during the experiment, and if necessary, use the data for off-line analyses.

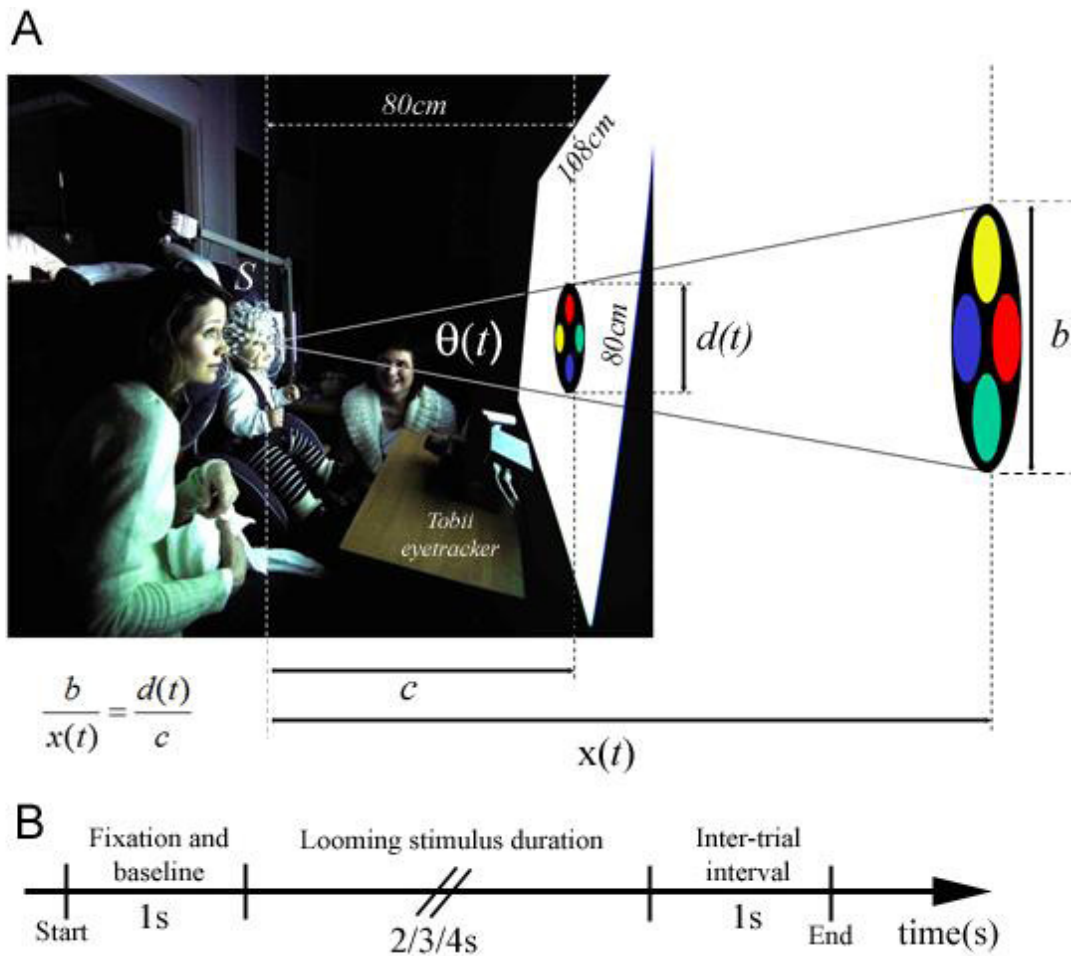


Figure 1: Experimental setup (and diagram of stimulus configuration) (A) and the stimuli sequence shown in a timeline (B). The infants were shown a sequence of a looming stimulus simulating an object approaching from far away lasting 2, 3 and 4 s under three different constant accelerations (21.1, 9.4, and 5.3 m/s²). As the virtual object approached the infants' eyes, the image on the screen grew and eventually filled the whole screen before it stopped.

2.4 Procedure

The infant's head was measured to find the right size of net which was then prepared in a saline electrolyte solution to help the electrodes to connect with the scalp. The infant was seated on the parent's lap and the baby was distracted with soap bubbles and toys while the net was placed on the baby's head. After the net was mounted the infant was seated in a baby car seat in front of a projection screen (108 x 70 cm) with a distance of approximately 80 cm from the screen so most of the infant's visual field was covered by the stimulus and its gaze made an angle of 90° when looking at the horizontal centre of the screen.

During the whole experiment one parent and one assistant were sitting on either side of the baby for the purpose of helping the baby focus on the screen and to avoid distress

caused by a missing parent. The net was connected to an amplifier and the impedance was measured. When there was insufficient contact with the scalp the electrodes were corrected with use of saline electrolyte or by repositioning them to improve contact. Computers for stimulus generation and recording were operated from a control room, divided from the experimental room by a window. A two-point eye calibrating procedure for infants was performed and the experiment started immediately after this calibration.

Number of trials completed by the infants varied. When believed to be necessary, short breaks were taken. The experiment was ended when the infant did not show any more interest in the stimulus, or showed signs of fussiness. The infants performed the looming experiment usually after an optic flow experiment (Van der Meer et al., 2008) lasting for about 8 minutes and right before an occlusion experiment (Van der Meer, Holth and Van der Weel, 2008) run from an E-Prime computer, and the EEG-data were saved and stored on a NetStation computer for offline analyses. Afterwards there was a short debriefing with baby and parent.

2.5 EEG data analyses

The EEG recordings were segmented by NetStation and exported to BESA for analyses. All data analyses were carried out using the software program Brain Electrical Source Analysis (BESA) version 5.1. The procedure was the same for all participants. Notch filter was set to 50.0 Hz. Low cut-off (high band pass) filter was set to 1.6 Hz to avoid slow drift in the data and a high cut-off filter was set to 20 Hz. The EEG data were inspected for artefacts and poor recordings. Bad channels and trials contaminated with artefacts were decided by visual inspection and excluded from further analyses.

A total of 372 trials were analyzed. On average the youngest infants contributed with 24 (SD = 7) trials, the infants aged 8 – 9 months with 25 (SD = 4) and the eldest infants with 26 (SD = 5) trials more or less equally distributed over the three looming conditions.

2.6 Single trial VEP analyses and Source analyses (SWF)

Each infant's raw EEG recordings of signals from the 128 electrodes were visually inspected on a trial by trial basis. Based on earlier VEP studies (Di Russo, Martinez, Sereno, Pitzalis and Hillyard, 2001), prominent VEPs at the electrode sites O1, Oz and O2 were identified in the reference free channel distribution and marked at the N2 peak for further analyses.

In addition, a 3D map of build-up and decline of voltage activity in the visual cortex over time was generated and used as a second criterion in determining the VEP peaks (Figure 2).

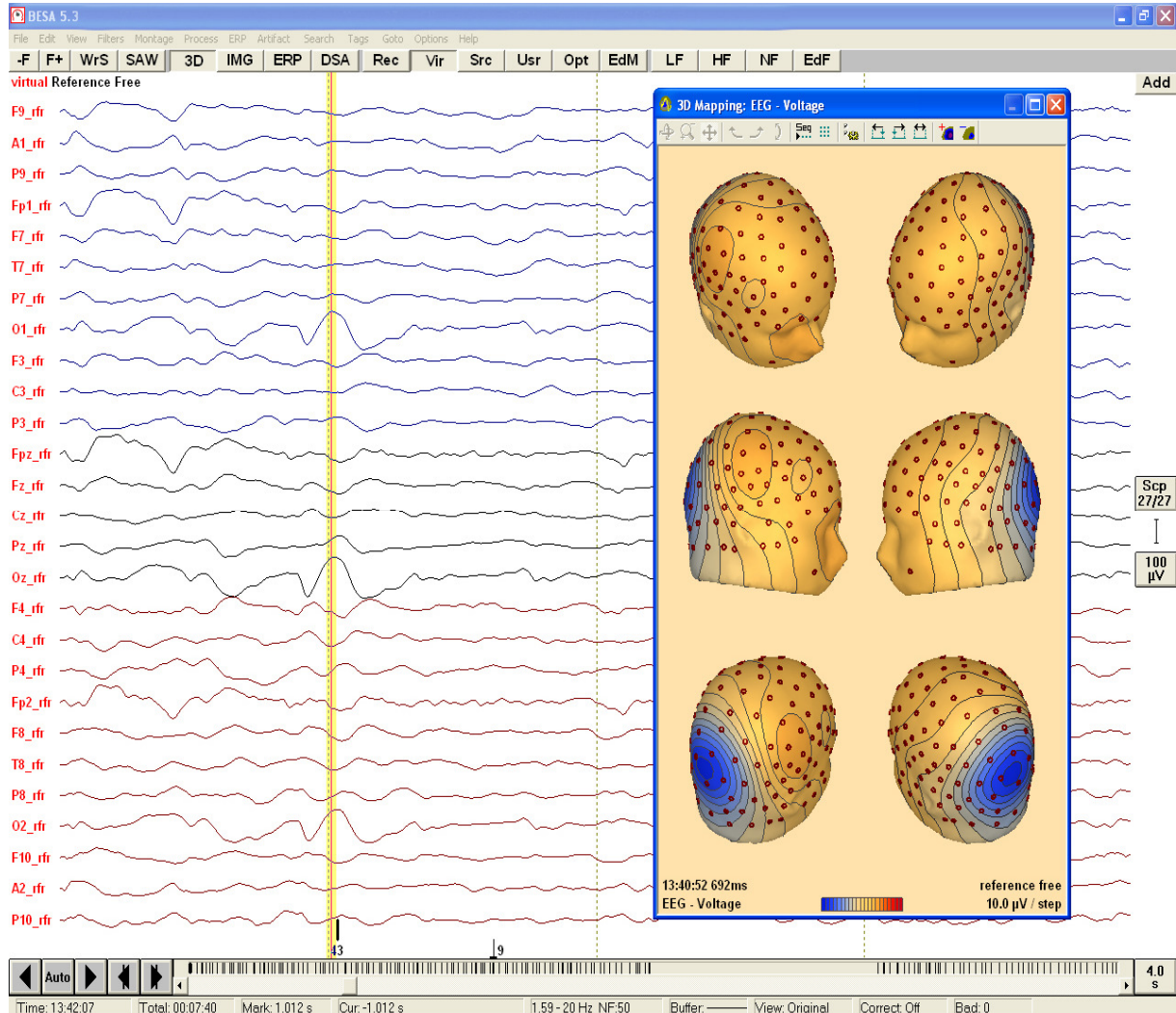


Figure 2: Visual evoked potentials at electrode sites O1, Oz and O2, viewed reference free in the raw EEG recording for one infant in the 5 – 6 month old group in a 3s looming trial. VEP peak is marked with a vertical yellow line. Voltage distribution of the VEP in the occipital area is shown in a 3D map.

The BESA algorithm estimates the location and the orientation of multiple equivalent dipolar sources (Scherg, Ille, Bornfleth, and Berg, 2002). This is based on a calculation of the scalp distribution that would be obtained for a given dipole model and comparing the location and orientation with the original VEP distribution (Scherg, 1990). The areas of interest are the areas believed to be most active during processing of visual motion and supposedly covering V1 and the V5/ MT+ (e.g. Zeki, 2004). These areas were included as three dipoles, visual

cortex radial left (VCrL), visual cortex radial right (VCrR) and visual cortex vertical midline (VCvM), in a predefined surrogate source model (Scherg et al., 2002) consisting of the standard 10 – 20 sites O1, Oz and O2. This model serves as a virtual source montage where the raw EEG data are transformed into brain source space (Hoechstetter, Bornfleth, Weckesser, Ille, Berg and Scherg, 2004; Scherg et al., 2002). A four-shell spherical model was included to account for the varying conductivity of the brain, the cerebrospinal fluid (CSF), the skull and the scalp (Berg and Scherg, 1994). Dipoles at the O1, Oz and O2 sites were fitted around peak looming VEP activity, providing source waveforms (SWF) of the modelled brain regions as a measure of the activities in these visual areas on a trial by trial basis. The SWF for each dipole and trial were visually inspected and the amplitude and time as measures of activity from the first positive to the first negative peak were decided so that averages for each baby and group could be computed and further analyzed (see Figure 3).

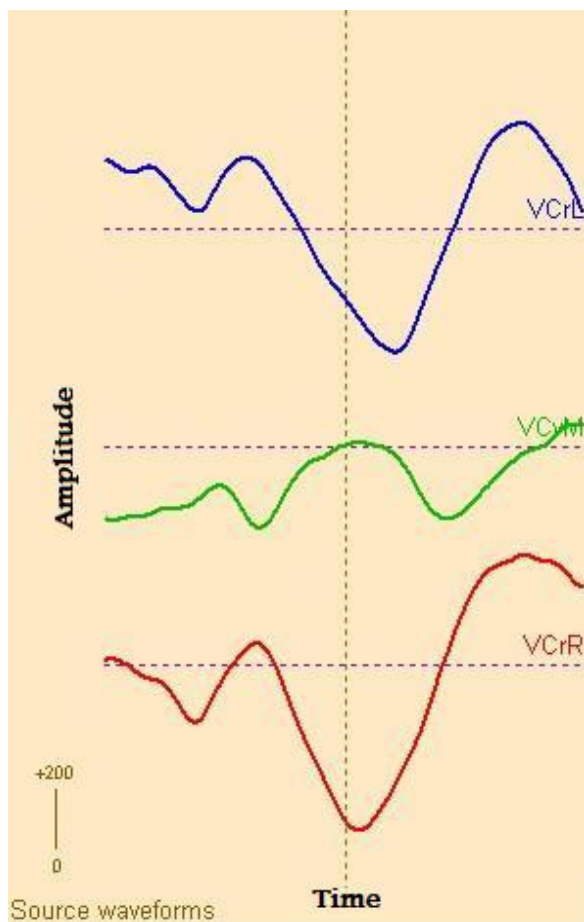


Figure 3: Source waveforms for dipole activity in VCrL, VCvM and VCrR in a 3s looming trial. The vertical dotted line represents the VEP peak, i.e. the N2 component, from activity in areas O1, Oz and O2 as marked in the raw EEG recording.

3.Results

Looming-related VEP activity in the occipital areas O1, Oz and O2 was translated into brain source space and the dipole activity was analyzed trial by trial from the source waveforms. Measures of dipole activity were start time, duration and amplitude. Overall, the source waveforms (SWF) were quite similar in appearance for the babies in all the groups. Dipole visual cortex radial left (VcRl) and dipole visual cortex radial right (VcRr) often showed symmetrical synchronized activity while visual cortex vertical midline (VcVm) displayed a different pattern. Dipole VcVm was oriented in another direction and was in general less pronounced than dipoles VcRl and VcRr.

3.1 SWF start activity

The start time was measured relative to the N2/ VEP peak. Related to the VEP peak the left visual dipole, VcRl, became active first, 84 ms (SD = 15) before the N2 peaked, averaged across looms and groups. The right visual dipole, VcRr, started next, on average 77 ms (SD = 18) before the peak and eventually the middle dipole, VcVm, became active at 72 ms (SD = 21) before the peak.

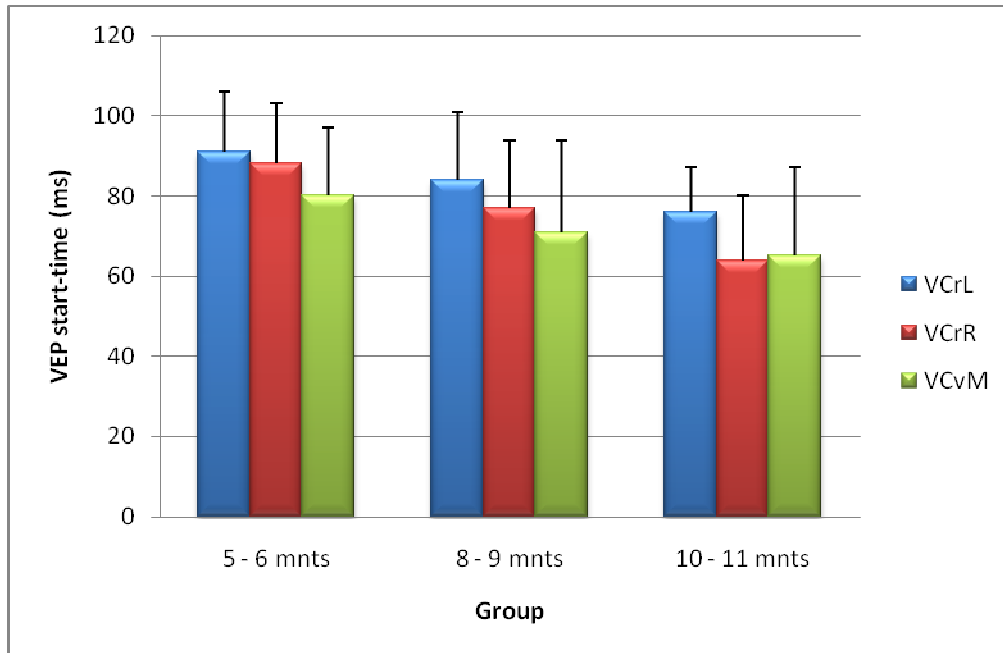


Figure 4: Start time and SD bars for the dipoles VcRl, VcVm and VcRr before the N2 peaks for the three age groups. With age, all dipoles started later in relation to the VEP/ N2 peak.

The averages for start time distributed over the three dipoles showed a tendency towards decreasing start time with age (see Figure 4). Averages for the three looms displayed little distinction between the looming conditions within the groups, but the averages showed a developmental trend for start time when comparing these across looms and dipoles for the three groups. For VEP activity the youngest group performed an average start time of 87 ms (SD = 16), the 8-9 months-old infants had a start time of 77 ms (SD = 19) and start time in the eldest group was 69 ms (SD = 17).

A repeated measure ANOVA was performed on start time with group (5-6, 8-9, 10-11 months) as between subjects factor and loom (2, 3, 4s) and dipole (VCrL, VCrR, VCvM) as within subjects factors. The ANOVA revealed a significant main effect of dipole $F(2, 24) = 8.09, p < 0.005$, indicating that there are differences in the start time activity between the three dipoles and with VCrL becoming active first, followed by VCrR and then VCvM. There were no significant main effects of loom or group, nor were there any significant interaction effects.

A follow-up post hoc test using Bonferroni correction revealed significant differences between VCrL and VCrR ($p < 0.05$), and between VCrL and VCvM ($p < 0.05$), while the start times for VCrR and VCvM were not significantly different.

3.2 SWF duration

The duration of the dipoles was measured as the SWF activity from the first positive to the first negative peak for VCrL and VCrR, and from the first negative to the first positive peak for VCvM, i.e. from the build-up of VEP activity until it started to decline. VCrL lasted for the longest time with a mean value of 100 ms (SD = 15), while VCrR had a mean duration of 94 ms (SD = 15). VCvM was the shortest dipole with a mean of 83 ms (SD = 19) (see Figure 5). The duration means were subject averages across looms and groups.

The VEP durations computed for each dipole and across looms within the groups tended to be shorter for the two eldest infant groups for both VCrL and VCrR. No pattern for the infants distinguishing between the looms was seen in the average data.

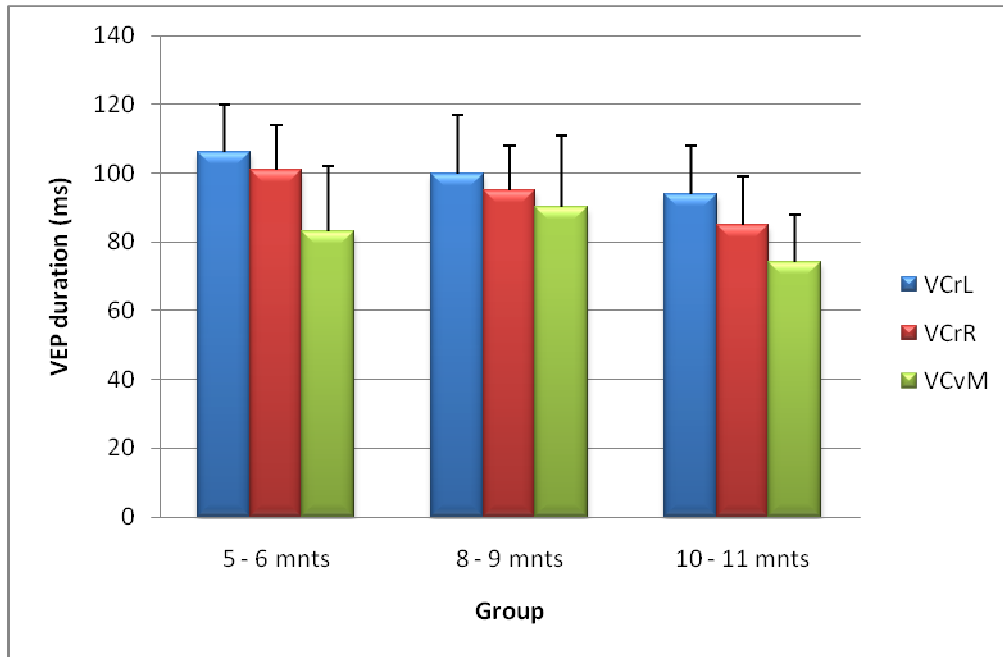


Figure 5: VEP durations and SD for VcRl, VcVm and VcRr for 5-6, 8-9 and 10-11 months-old infants. Duration of VcRl and VcRr decreased with age, while VcVm lasted for a longer period in 8-9 month-olds than in the younger and older infant groups.

The repeated measures ANOVA carried out to measure duration with group (5-6, 8-9, 10-11 months) as between subjects factor and dipole (VcRl, VcVm, VcRr) and loom (2, 3, 4s) as within subjects factors found a main effect of dipole, $F(2, 24) = 26.58, p < 0.001$. This indicates significant differences in the duration of VcRl, VcRr and VcVm with VcRl lasting for the longest period of time, followed by VcRr and then VcVm. There was no significant main effect for loom or group, nor were there any significant interaction effects.

Post hoc tests using Bonferroni correction showed that both VcRl and VcRr lasted significantly longer than VcVm ($p < 0.001$ and $p < 0.005$, respectively), although they did not differ significantly from each other.

3.3 SWF amplitudes

The radial dipoles VcRl and VcRr had slightly different amplitudes being 512 nA (SD = 174) and 515 nA (SD = 224), respectively. VcVm had a mean amplitude value of 351 nA (SD = 120). The averages were computed across looms and groups.

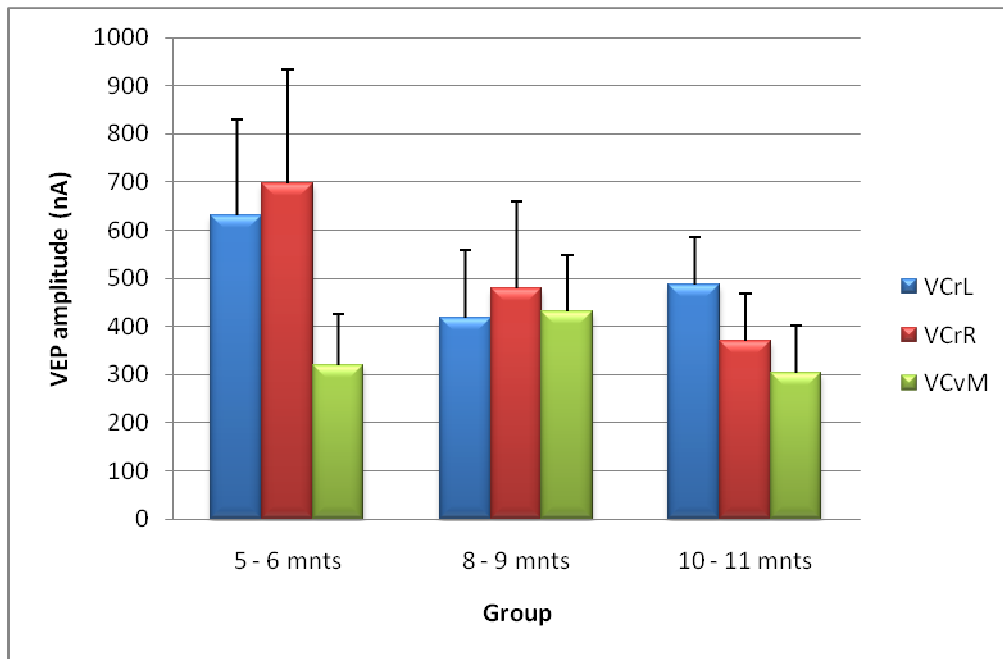


Figure 6: VEP amplitude and SD bars for VCrL, VCvM and VCrR for 5-6, 8-9 and 10-11 months-old infants. Amplitudes for VCrR decrease with age. Amplitudes for VCrL decrease in the 8-9 month-olds and then increase. VCvM amplitudes increase in the 8-9 month-olds and then decrease.

A 3 (group: 5-6, 8-9, 10-11 months) x 3 (dipole: VCrL, VCvM, VCrR) x 3 (loom: 2, 3, 4s) repeated measures ANOVA for amplitude yielded again a main effect of dipole, $F(2, 24) = 6.48, p < 0.01$. The result indicates that the strength of the activity in the three dipoles is significantly different, with VCrR and VCrL being the dipoles with most activity and VCvM being weaker. No significant main effects for either loom or group were found, but there was a significant interaction effect of dipole and group for amplitude, $F(4, 24) = 2.90, p < 0.05$. This indicates that there are differences in the strength of dipole activity as a function of age and further that dipole activity decreases with increasing age.

Subsequent post hoc tests using Bonferroni correction revealed that VCvM had significantly lower amplitude than both dipole VCrL ($p < 0.005$) and VCrR ($p < 0.05$). Amplitudes in dipoles VCrL and VCrR were not significantly different (see Figure 6).

The ANOVA results indicate that the left and right visual dipoles are more dominant than the middle (midline) dipole. VCrL and VCrR were the most prominent dipoles as the SWF activity started earlier related to the VEP/ N2 peak, lasted for a longer period of time and had significantly larger amplitudes than VCvM.

4. Discussion

Bertenthal et al. (1994) argued that there is a close relationship between action and brain development in infancy when they showed that the emergence of crawling and the degree of experience is followed by significant cognitive and behavioural changes. In an attempt to get a better understanding of the developing brain and behaviour this study has investigated brain activity, i.e. characteristics of the source waveforms, in three visual dipoles on a trial by trial basis, in infants aged 5 – 6 months, 8 – 9 months and 10 – 11 months. The infants were presented with a looming stimulus approaching on a direct collision course under three different accelerations.

4.1 The looming stimuli

The infants were presented with a looming stimulus approaching on a direct collision course under three different accelerations. This study did not find any significant differences between the three looming conditions, implying that for the SWF characteristics start time, duration and amplitude the infants did not differentiate between the fast, medium and slow looms. Using the same paradigm and tau analysis which essentially investigates how the SWF progresses over time, Van der Weel and Van der Meer (2009) did find evidence that infants could differentiate between fast, medium and slow looms. Thus, straightforward SWF analysis investigating start time, duration and amplitude of the SWF may not be a sufficient method for studying how temporal information is processed in the developing brain.

In a study by ffytche et al. (1995) signals from fast moving stimuli arrived at V5 before V1 in human adults, while signals from slower moving stimuli arrived at V1 first. This phenomenon was referred to as ‘dynamic parallelism’. It might be expected that signals from the fastest moving looms, or perhaps all, reach V5 first in infants because the pathway via SC has shown to function in the neonate (e.g. Atkinson, 2000; Martin, Joeri, Loenneker, Ekatodramis, Vittaco, Hennig and Marcar, 1999; Rosander et al., 2007) and presumably would be the first to develop and function in the same way as in adults. The present study showed that the most prominent activity was in the lateral dipoles supposedly covering area V5/ MT + (e.g. Zeki, 1974) indicating that signals reach V5 first also in infants between 5 and 11 months of age. However, the signals also reach V1 supporting the findings of a parallel processing of different stimulus information (ffytche et al., 1995) from 5 months. More activity in VCrL and VCrR might reflect a stronger response to coherent motion in MT+ as has been found in adults (Sunaert et al., 1999).

4.2 SWF start time

Start time of SWF activity was measured related to the first negative peak for dipoles VCrL and VCrR, and related to the first positive peak for dipole VCvM, i.e. the VEP peak (N2). This SWF characteristic is thought to reflect an aspect of the processing time of the looming stimuli. There was a significant effect of dipole for SWF start time. In relation to the peak SWF activity started first in dipole VCrL at 84 ms followed by activity in dipoles VCrR at 77 ms and VCvM at 72 ms before the N2 peaked. This implicates a parallel processing in the three dipoles with a possibly longer processing time in the left and right visual dipoles as compared to VCvM and may indicate that coherent motion information is mainly processed in these areas in infants from 5 to 11 months of age as has been found in adults (ffytche et al., 1995; Sunaert et al., 1999). Also, earlier start time in VCrL and VCrR might indicate that signals reach area V5/ MT+ from the visual pathway via SC or LGN rather than from the primary visual pathway via V1 (Callaway et al., 2005; ffitche et al., 1995; Rosander et al., 2007; Schneider and Kastener, 2005; Schoenfield et al., 2002; Sincich et al., 2004). Shorter processing time in VCvM might not necessarily contradict that information from the looming stimuli actually are projected via LGN to V1 and then to V5. It could be that the measured electrical activity reflects the processing of several components of the looming stimuli as this probably activates several pathways at the same time (Johnson, 2000) and it is also possible that activity temporarily overlap. Thus, the results might be difficult to compare with research conducted with other types of stimuli.

Post hoc tests revealed significant differences between VCrL and VCrR and also between VCrL and VCvM indicating longer processing time in VCrL. Left hemispheric dominance in motion processing, especially linked to neural activity concerning timing of collision, has been observed in adult data (Assmus et al., 2003; Coull et al., 2008; Field and Wann, 2005; Pavlova et al., 2006) and is suggested from findings in infants from psychophysical data (Hollants-Gilhuijs et al., 1998) and cortical activity (Rosander et al., 2007; Van der Weel and Van der Meer, 2009).

4.3 SWF duration

Source waveform durations for the three dipoles varied from 100 ms for dipole VCrL to 94 ms for VCrR and to 83 ms for VCvM. This indicates that signals from the looming stimulus are processed for a longer period of time in VCrL, followed by VCrR and VCvM. VCrL and VCrR both lasted significantly longer than VCvM. As area V5/ MT+ is located

laterally in visual cortex longer processing time of motion stimuli in the radial dipoles VCrL and VCrR corresponds to previous findings of strong motion-selective responses in these areas in adults (e.g. Morrone et al., 2000; Sunaert et al., 1999).

Irrespective of age, the processing of the looming stimuli seemed to begin earlier and last longer in the occipital region in the left hemisphere. Investigating SWF activity in the three visual dipoles, Van der Weel and Van der Meer (2009) found shorter durations in VCrL specifically. Rosander et al. (2007) reported bilateral activation in the occipital region from 5 months, starting in the left hemisphere. Our results from source analysis support this finding. Also, more similar activity in VCrL and VCrR indicates a more parallel processing in O1 and O2.

4.4 SWF amplitudes

Dipoles VCrL and VCrR had only slightly different amplitudes, 512 and 515 nA respectively, while dipole VCvM had a significantly lower amplitude with a mean value of 351 nA. Average values of dipole strength indicated more neural activity in O1 and O2, than in Oz, since amplitudes are proportional to the number of neuronal elements firing in synchrony (Pfurtscheller et al., 1999). A larger cortical area activated might reflect less specialization in these areas (Huttenlocher, 1990; Johnson, 2000).

If several neural pathways are partially activated, strengthening of existing pathways and pruning of others may result in that a smaller cortical area becomes activated as infants get more experienced with certain stimuli and situations throughout development (Johnson, 2000). Johnson (2000) proposed that competition between neural pathways results in a process of neural selection. For example, more distant pathways are more likely to be extinguished for the 'benefit' of pathways closer by. Increased specialization is thought to be activity dependent and should therefore be seen in the light of behavioural changes (Bertenthal et al., 1994; Johnson, 2000) and movement skills could be closer investigated in relation to brain development.

Processing of fast moving motion has been found to reach V5/ MT+ first suggesting a bypassing of V1 (ffytche et al., 1995) and coherent motion to be processed mainly in the V5/ MT+ area (Sunaert et al., 1999) in adults. Thus, larger amplitudes in VCrL and VCrR might reflect more activity in the V5/ MT+ area in infants aged 5 to 11 months. As mentioned there is evidence that areas in the left occipital hemisphere are more active in the processing of

motion in both adults and infants, especially for processing of timing (Assmus et al., 2003; Coull et al., 2008; Field and Wann, 2005; Van der Weel and Van der Meer, 2009).

We also found an interaction effect of age and amplitude which can be interpreted as evidence for decreasing brain activity in the dipoles with increasing age. This indicates decreasing brain activity in the occipital areas as a function of increased neural specialization presumably reflecting better perceptual skills. Older infants are more experienced with self-produced locomotion and might have developed better capacity for perception of motion. An interactive specialization framework suggests that neural activity becomes more finely tuned as a result of experience with specific stimuli and situations (Johnson, 2000). This would presumably lead to specialized neurons and pathways demanding smaller areas of the cortex to be activated and thereby a decrease in brain activity. From this perspective physiological processes such as myelination and synaptic pruning which has a major role in the developing brain within the first year of life (e.g. Grieve et al., 2003; Huttenlocher, 1990; Lippé et al., 2007) cannot solely account for brain maturation.

4.5 General discussion

The results of this study showed that visual dipoles VCrL and VCrR displayed the most prominent activity in motion processing when analyzing characteristics (i.e. start time, duration and amplitude) of the N2 component translated into brain source space. These characteristics were here associated with processing time and strength of activity in the visual cortex. VCrL and VCvM showed almost synchronized activity indicating parallel activity in area V5/ MT+, although VCrL was the most active dipole in terms of start time. This could indicate a left hemispheric dominance in processing of looming stimuli in infants. An interpretation of more lateral activity considers the location of the V5/ MT+ area which are extrastriate areas closer to cortical motor areas. A bypassing of V1 for fast moving stimuli might reflect better capacity for situations that demands fast action.

A tendency towards decreasing processing time and strength with age was observed in the data and interpreted as a developmental trend. A significant effect of age was not found, but this does not mean that such a difference does not exist. Several studies have reported a rather rapid decrease in latencies, but increase in amplitudes within the first 1 – 2 years of life thought to reflect decreasing processing time and increasing activity (e.g. Svantesson, 2010; Van der Meer et al., 2008; Van der Weel and Van der Meer, 2009; Lippé et al., 2007; Langrová et al., 2006; Webb et al., 2005). This is explained by physiological processes such

as synaptic maturation and myelination (Grieve et al., 2003; Huttenlocher and Dabholkar, 1997; Picton and Taylor, 2007; Webb et al., 2005) and these processes are assumed to be facilitated by the infant's increasing interaction with the environment (Johnson, 2000).

The method in the current study might not have been sufficient for the uncovering of age effects. Also, the looming stimulus consists of several components and this implies activation of several pathways simultaneously which can make it difficult to compare this finding to research conducted with other types of stimuli. Due to the possibility of relatively high inter-baby variability (Thierry, 2005) in the data the same paradigm should be investigated in a longitudinal study within the first year of life and/ or with more babies in each group. One step further for the purpose of getting a better understanding of the relationship between the developing brain and behavior is to investigate a possible correlation between behavioural events and brain activity. Findings from the current study suggest bypassing of the V1 area and asymmetrical processing of looming stimuli in infants aged 5 to 11 months.

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