High-density EEG study of how looming information is processed in the infant brain

by

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Acknowledgements

Summary

Looming images indicate the rapid approach of objects and provide warning information about the impending impact. Prospective control when responding to a looming virtual object approaching on a direct collision course was studied longitudinally in 12 infants aged 3/4 and 11/12 months. Brain electrical recordings (EEG) and different characteristics of the looming-related visual evoked potential (VEP) were explored and compared between the infants at these different ages. The aim of this study was to investigate how infants at this early age process looming stimuli approaching on a direct collision course under three different accelerations. It was also investigated how neural information is processed in the infant brain by applying the General Tau Theory. The results showed that the timing and the duration of the VEP responses differed with age. At the age of 3/4 months, infants showed VEP peaks after the looming virtual objects had hit them. At the age of 11/12 months, on the other hand, infants showed clear looming-related VEP peaks before virtual impact. Further, the application of the General Tau Theory showed that when looming-related information flows inside the neurons in a particular brain region, infants' ability to pick up the flow improves as they mature and get more locomotor experience providing them more veridical information about time-to-collision information. Brain maturation together with a dramatic increase in locomotor experience during the first year of life in infancy could explain the developmental trend in our study. Further studies is needed to investigate brain associated activity with infants' perception of looming motion.

1. Introduction

Detecting imminent collision is challenging to the visual system. As an object moves directly towards the head, the changing size of the retinal image can create motion-in-depth perception (Beverley & Regan, 1979). The visual system can utilize expansion motion to estimate time to collision in order to avoid approaching objects (Lee, 1976). Images that grow in size trigger avoidance reactions in a number of species. Looming images indicate the rapid approach of objects and provide warning information about the impending impact (Maier, Chandrasekaran, & Ghazanfar, 2008). In the animal world, this information about how and when to respond to an approaching danger is crucial in order to survive. The animal needs to gain an estimate of the time remaining before colliding with an approaching object in order to time its reaction appropriately. This could be determined from knowledge of the distance and speed of movement of the approaching object, but there is a more direct way of perceiving time-to-collision (Lee, 1976). In 1976, Lee suggested a strategy stating that the animal could determine the ratio between retinal image size at a given instant and the rate of expansion of the image. As long as the image is not too large and the provided velocity of the object relative to the observer is constant, the particular ratio τ gives an accurate measure of time to collision which is independent of absolute speed or of the size of the object (Lee, 1976; Rind & Simmons, 1999). This strategy was first shown for gannets (Lee & Reddish, 1981), which close their wings just before entering the water during a plunge dive. The timing of wing closure during the dive correlates more closely to a particular value of τ than with other parameters, such as the distance to the water surface.

There are specific neurons in the brain that respond to time to collision. In pigeons, neurons in the dorsal posterior zone of the nucleus rotundus were examined (Wang & Frost, 1992). The result provided evidence that neurons in that particular site were looming-sensitive neurons which was shown by the tight correlation found between the timing of the response made by these neurons and the bird's heart rate. These looming-sensitive neurons are also found in locusts and are known as the lobula giant-movement detector (LGMD) and the descending contralateral-movement detector (DCMD) neurons (Rind & Simmons, 1999). In rhesus monkeys multisensory integration of looming signals were found (Maier et al., 2008; Maier, Neuhoff, Logothetis, & Ghazanfar, 2004). Multisensory integration of auditory and visual looming signals was mediated by interactions between auditory cortex and the superior

temporal sulcus. Gamma-band coherence between these areas increased when activated by looming signals (Maier et al., 2008).

In humans, little has been done to establish how the detection of looming and estimation of time to collision processes are represented in the central nervous system. Visual motion is initially processed in the striate and extrastriate visual areas in the cortex (Moutoussis & Zeki, 2008). Using functional magnetic resonance imaging (fMRI) in human adults between 20 and 40 years old, parts of the brain that are active during time to collision judgments were identified (Coull, Vidal, Goulon, Nazarian, & Craig, 2008; Field & Wann, 2005). An accelerating pattern of optical expansion (looming) is present when an object approaches the point of observation which will produce a strong response in the primary visual cortex. Time to collision specific dorsal-stream activation is found strongest in the left hemisphere, where it straddles the sensorimotor areas of parietal and frontal cortex (Field & Wann, 2005). This sensorimotor response suggests that there was motor preparation in response to an approaching object. Differential activation of the visual areas V1 and V5 which reflects specific visual processing areas for optic-flow and lateral motion, was also observed (Coull et al., 2008; Field & Wann, 2005).

Another study supported the earlier observation that different brain regions support explicit and implicit timing (Billington, Wilkie, Field, & Wann, 2011). At the subcortical levels, a response to looming in human superior colliculus (SC) and thalamic medial pulvinar (mPu) was found to be in line with findings from both locusts and pigeons. Looming stimuli may be more attentionally challenging, thus resulting in tectopulvinar activation given that pulvinar of the thalamus played an important role in attentional modulation and orientation. It was also observed that inhibitory mechanisms in the basal ganglia network were involved in ceasing the ongoing motor behaviour when a looming object was detected (Billington et al., 2011).

Human infants are also in need of neural structures allowing them to judge impending collisions adequately. It is important to note that infants need to judge whether an object is approaching on a collision course and how imminent the collision is. In the 1990s, Johnson reported that infants' visual attention, oculomotor control and neuroanatomical maturation would not appear before approximately 4 to 6 months of age (Johnson, 1990). In addition, Johnson noted that cells in the early maturing Layers 5 and 6 of primary visual cortex (V1) project only to subcortical structures, including the superior colliculus and the basal ganglia, while Layer 2 and 3 eventually project to higher cortical structures including the prefrontal cortex (PFC). Based on Conel's (1967) study, cells in these layers would not be mature to contribute to information

processing until infants are about 4 to 6 months of age. However, in 1988, another study reported that development of the pyramidal cells in cortical Layers 2 and 3 of V1 happens earlier than Conel had reported (Mrzljak, Uylings, Kostovic, & Van Eden, 1988, 1992). Layer 3 cells undergo continued rapid dendritic differentiation as their axons begin establishing connections with target cells in the opposite hemisphere during the late prenatal and neonatal period (Mrzljak et al., 1988). The maturation of cells in Layer 3 is slightly behind that in Layer 5, however, there appears to be sufficient structural maturity in PFC to support information processing in the neonate (Burkhalter, Bernardo, & Charles, 1993).

Infants' perceptions of object looming have been subject to investigation. What infants look at reflects their cognitive development. Studies have demonstrated that young infants are sensitive to looming information by showing avoidance or defensive behaviours such as blinking (Nañez & Yonas, 1994). Studies have also investigated infants' dissociation of expansion from contraction pattern (Náñez, 1988), and the functional implications of the looming displays such as between an approaching object and an approaching aperture (Schmuckler & Li, 1998).

In a behavioural study, infants' defensive blinking in response to a visual looming stimulus approaching on a collision course under different constant velocities and constant accelerations was investigated (Kayed & van der Meer, 2000). It was found that infants used different strategies to time their blink. The youngest infants (5-6months) used a strategy based on visual angle causing them to blink after the end of the virtual object's approach, whereas older infants (6-7 months) used a strategy based on time enabling them to blink before the end of the approach of the visual object. In a longitudinal study conducted by Kayed and van der Meer (2007), the results supported the previous findings. It was observed that infants around the time they became mobile switched timing strategy from a strategy that was based on visual angle to a more sophisticated strategy based on time. These findings showed that with age there is a development in the perceptual system of infants. The switch in strategy from a less useful to a more sophisticated timing strategy enables infants to better time their defensive blinking to impending optical collisions. When investigating which timing strategy preterm infants use to determine when to make the defensive blink (Kayed, Farstad, & van der Meer, 2008), it was observed that out of eight preterm infants at 26 weeks, three infants had problems with the fast, accelerating approaches, blinking at relatively constant values of visual angle irrespective of the approach condition of the virtual object, whereas four infants blinked when the virtual object was a certain time away allowing them to blink in time in all approach conditions. The inability to switch from a timing strategy that is prone to errors to a strategy that enables successful

defensive blinking might reflect a lack of flexibility to interact appropriately with the environment.

Another study investigated whether infants can discriminate between objects approaching on a hit versus a miss path (Schmuckler, Collimore, & Dannemiller, 2007). It was observed that 4- to- 5-month-old infants indeed discriminate hits versus misses, and the discrimination of hits from misses was modified by whether or not the approaching object passed in front of the infants' faces.

The visual system is specialized to detect an expansion in a mixed expansion/contraction display rather than to detect a contraction in such display (Takeuchi, 1997). In a study, the development of asymmetry for the perception of extraction/contraction was examined in 2- to- 3-month-old infants (Shirai & Yamaguchi, 2004). The results showed that infants preferred the target in the expansion search condition, and that this ability emerges at around 3 months of age. This result is different from previous findings (Ball & Tronick, 1971; Náñez, 1988), where it was found that the sensitivity to expansion emerges at about 1 month of age. These differences between the ages may be attributed to the difference of measurement. Shirai and Yamaguchi (2004) used infants' preferential looking (perceptual measurement) as index of infants' sensitivity, whereas the earlier studies used infants' defensive responses (sensory motor measurement). These differences have been explained by a framework regarding the two different visual pathways; i.e., the ventral pathway processing perceptual responses and the dorsal pathway processing sensory motor responses. In addition, it was also suggested that this difference in ages in which the sensitivity to expansion emerges may be explained by such a neural framework (Shirai & Yamaguchi, 2004).

Several psychophysiological and neural data suggest that responses to expansion in 1-month-old infants may be mediated by subcortical pathways. These defensive responses were found in human adults (King, Dykeman, Redgrave, & Dean, 1992). Human adults' defensive responses to a looming stimulus are driven by the subcortical system such as the pathway via the superior colliculus (Billington et al., 2011; King et al., 1992). It is plausible that 1-month-old infants' responses are also driven by the subcortical system because their cortical system is not completely functional yet. The dorsal pathway may not be able to process expansion/contraction motion until about 3 months of age (Shirai & Yamaguchi, 2004), since the projections from the striate cortex to the medial temporal- and medial superior temporal areas (MT/MST) functionally develop during the second and third month of life for a review, see (Banton & Bertenthal, 1997).

Self-locomotion and better control of self-movement are important skills influencing the cognitive level. Studies have reported that infants with hands-and-knees crawling experience, and prelocomotor infants who had experience moving about in "walker" devices showed an increased sensitivity to optic flow (Higgins, Joseph J. Campos, & Kermoian, 1996). Their findings also suggested that locomotor experience plays a role in the sensorimotor processes of detecting optic flow in the visual periphery. Other studies argued that selective responses are due to synaptic maturation and myelination of the visual cortical areas (Webb, Long, & Nelson, 2005).

Development of non-invasive, high-density electroencephalography (EEG) allows the investigation of how information is processed in the infant brain. In a study, EEG was used to study brain electrical activity as a function of perception of structured optic flow and random visual motion in 8-month-old infants (van der Meer, Fallet, & van der Weel, 2008). Significant differences both in amplitudes and latencies of visual evoked potentials for optic flow in brain regions PO3, POz, O1 and Oz versus random visual motion were observed. Both infants and adults showed shorter latencies for optic flow suggesting that it was easier to detect the coherence in the optic flow. Infants showing shorter latencies for optic flow than random visual motion could be an indication of a specialization in the brain that may be related to the locomotor (crawling) experience where they use visual information to navigate (van der Meer et al., 2008). Sensitivity to optic flow significantly increased when infants started crawling (Agyei, Holth, van der Meer, & van der Weel, 2014; Anderson et al., 2001; Bell & Fox, 1996).

Visual evoked potentials (VEPs) have proven to be a great measure in the study of brain development. Parameters including amplitudes and latencies of the response components have been coupled to synaptic transmission and myelination (Scherg & Picton, 1991). In a study using VEP in children aged from 27 days to 5.5 years, as well as in young adults, electrophysiological responses in VEP peaks N70, P100 and N145 were investigated (Lippe, Roy, Perchet, & Lassonde, 2007). Reduced brain specialization was found in the period between 7 and 23 months, as well as an appearance of negative waves (N70 and N145) and decline in P100 amplitudes. From 24 months onward, enhanced synaptic density was observed. An increase in coherence in the occipital interhemispheric and intrahemispheric connections was also found. This increase in coherence may reflect the development of visual networks.

In 1998, Lee introduced the General Tau Theory which provides information on how movements are perceptually and intrinsically guided. According to this theory, all behaviours are thought of as goal-directed actions that involve the closure of gaps between the state a

person or an animal is currently in and the goal state to be achieved through movement (Lee, 1998). Tau is the time before the animal would reach its desired goal, at its current speed of approach. For example, when an object approaches on a collision course, infants can avoid its impending impact appropriately. The exact timing of such avoidance behaviour was hypothesized to involve the variable tau (τ), which provides the temporal measure of the closure of motion gaps at their respective speed of closure (Lee, 1976, 1998). Neurophysiological studies have provided evidence that the nervous system can represent tau. The tau information that is present in the nervous system is in the form of flow of electrical energy in ensembles neurons, which Lee refers to as "neural power" (Lee, 2005). Data collected monkeys' motor cortex and parietal cortex provided evidence that neural activities were related to tau, and that there were neurons in these areas which were significantly related to tau (Maier et al., 2004; Merchant & Georgopoulos, 2006). In pigeons certain population of thalamic neurons within the nucleus rotundus fired consistently at a threshold before collision regardless of velocity or size of the stimuli. The activities of these neurons are related to the relative expansion rate which is equivalent to the variable tau (Sun & Frost, 1998; Wang & Frost, 1992).

A basic concept of the General Tau theory is that the coordination of multiple processes can also be described in terms of gap closure, and this is achieved by tau-coupling wherein two (or more) taus (τs) are coupled and remain at a constant ratio over some time (Lee, 2005). When tau-coupled, the relationship between two τs can be described as

$$\tau_{X\,(t)} = K\tau_{y\,(t)}$$

where K is the coupling constant. The larger the value of K, the longer the duration of the acceleration phase of the movement and the more abrupt the deceleration to the goal. In addition, it has also been suggested that self-regulated and skilled movements generally follow a form of process that is intrinsically guided, referred to as the tau-guide (τ_G) (Lee, 2005):

$$\tau_{X\,(t)} = K\tau_{G\,(t)}$$

When τs are τ_G-coupled, the constant K is related to the speed profile of the gap closure. The strength of tau-coupling, as expressed in percentage, is determined by the proportion of movement data relative to the whole strength of movement segment. The percentage of tau-coupling is accounted for the derived linear regression between tau of the movement gap and the tau guide satisfying a regression r^2 (> 0.95).

In a cross-sectional study using high-density EEG, it was investigated whether event-related theta activity in the infant brain can provide the infant with information for impending collision (van der Weel & van der Meer, 2009). It was reported that infants between 5 and 11 months of age improved with age in terms of extracting and processing information for impending collisions. Looming related brain activity was characterized by theta oscillations in the visual cortex. The temporal dynamics of the source waveform was also analysed, and the result showed that 5- to 7-month-old infants used twice as long to process the looming information than 10- to 11 month-old infants. However, source waveform activity *per se* did not discriminate between slow, medium and fast looms. A tau-coupling analysis was performed on the visual cortex lateral left (VClL) source waveforms. A strong ($r^2 > 0.95$) and long ($> 65\%$) tau-coupling was found in all infants, where the 10-to 11-month-old infants were able to differentiate between the three different loom speeds. The results indicated that the temporal structure that was consistent with that present in the visual looming information was sustained during processing in the more mature infant brain.

In the present study, infants' brain responses to looming danger were studied. Using non-invasive, high-density EEG, looming-related brain responses were investigated in a longitudinal design where infants were tested first at 3 to 4 months and then again at 11 to 12 months. By analysing infants' VEP responses, the aim of the present study was to investigate how infants at this early age process looming stimuli approaching on a direct collision course under three different accelerations. Further, by applying the General Tau Theory (Lee, 1998, 2005), it was also investigated how neural information flows in the infant brain.

2. Materials and methods

2.1 Participants

A total of 15 babies were recruited from local newspaper birth announcements to take part in the experiment which consisted of two testing sessions, one when the babies were 3-4 months old and one when they were 11-12 months old. Three of the babies were excluded. Two of them lost interest in the stimulus early in the first test session, while the other one was not able to come back to the laboratory for the second testing. Twelve (7 boys and 5 girls) babies provided data for the final analyses. At the first test session, babies had a mean age of 15 weeks (SD = 2.7), while they had a mean age of 50 weeks (SD = 2.4) at the second test session. All babies were healthy and full-term infants without any birth complications according to parental report.

Electroencephalogram recording as a psychophysical procedure causes no pain or physical harm to the participant. The parents understood that they were free to withdraw at any time during the experiment and they gave their informed written consent before the experiment began. The study has been approved by the Norwegian Regional Ethics Committee and The Norwegian Data Services for the Social Sciences.

2.2 Apparatus

EEG activity was recorded using a Geodesic Sensor Net 200 (GSN), run by Electrical Geodesic, Inc. System 200.Geodesic sensor net is a device that achieves an even distribution of array sensors across the head surface (Tucker, 1993). It comprises 128 electrodes which were evenly distributed across the scalp. Amplified EEG signals were recorded with Net Station software on a Macintosh computer. All electrode impedance was kept under 50 kΩ as recommended to ensure an optimal signal to-noise ratio (Ferree, Luu, Russell, & Tucker, 2001). The data were stored on hard disk for off-line analyses.

Tobii x50 (Tobii Technology, Stockholm, Sweden) was used to record gaze of both eyes at 50 Hz during the entire session, and was then processed with the accompanying software Clear View on a HP computer. Triggers about the onset and offset of the looming stimuli were communicated from E-prime (Psychology Software Tools, Inc.) onto the EEG recordings of infants' brain electrical activity. The infants were also filmed by two digital video cameras to monitor behaviour during the experiment.

2.3 Stimulus representation

Each infant was shown a sequence of a circular disc image approaching on a direct collision course. The stimulus consisted of a flat, black circle with four coloured (red, green, blue and yellow) inner circles of equal size rotating on its centre with a constant angular velocity of 300º per second (see Figure 1a). Inner circles had a radius that was 1/3 of the radius of the outer circle. The image size on the screen grew as it approached the infant for a duration of 2, 3 and 4 s (see Figure 1b) under three different constant accelerations (21.1, 9.4 and 5.3 m/s^2, respectively). The virtual object was programmed to loom up to the infant's face so that the infant would get a visual collision experience. The initial visual angle of the virtual object was 5º (diameter of 6.5 cm), and it grew to a maximum visual angle of 131º (diameter of 350 cm) where it disappeared from the screen after which the screen went blank for one second.
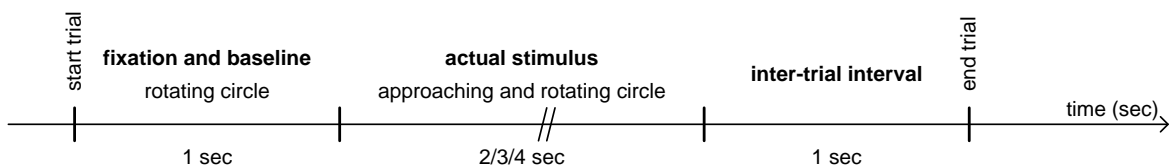
a)
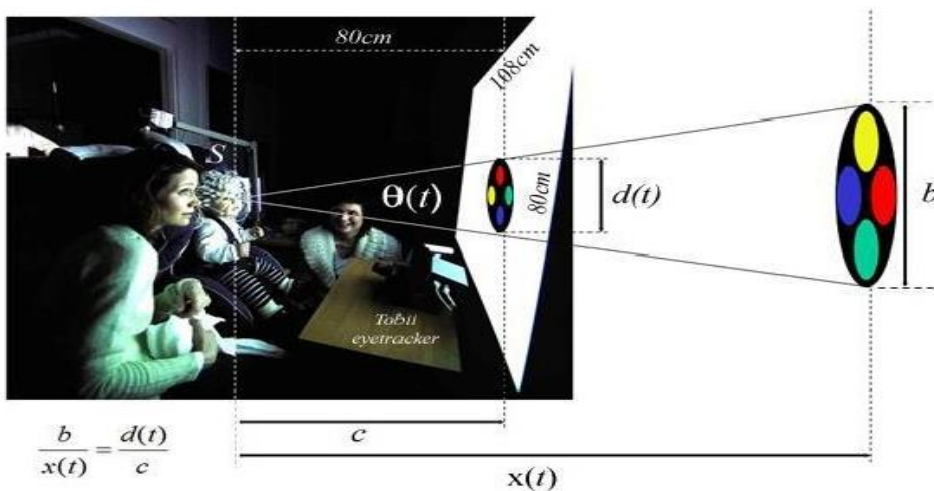
b)

Figure 1 a) The experimental setup and diagram of looming stimulus configuration approaching the infant. During the first session, the infant sat on the parents' lap instead of the baby car seat. **b)** The timeline. Each infant was shown a sequence of randomly presented looming stimuli simulating an approaching object coming from far away and approaching for 2s,3s and 4s under three different constant accelerations (21.1, 9.4 and 5.3 m/s^2, respectively).

As the virtual object approached the infant's eyes, the image on the screen grew, and the loom stopped and disappeared as soon as the image filled the whole screen.

2.4 Procedure

Letters were sent to the parents containing information about the project, followed up by phone calls. Most of the parents were willing to participate in the experiments. Other parents voluntarily contacted the Developmental Neuroscience Laboratory (NTNU, Trondheim) to take part in the research. When the baby arrived at the laboratory with its parent(s), information about the experiment was given, and a consent form was signed. Then the infant's head was measured to find the right size of the net which was then prepared in a saline electrolyte solution. The infant sat on the parent's lap while the electrode net was mounted on the infant's head. After the net was in place, the parent with the baby and an assistant went into the experimental room. In the experimental room, a projection screen (108 cm wide and 70 cm high) was hanging down from the ceiling. The distance between the infant and the screen was 80cm. In the first session at 3-4 months, the infant sat on the parent's lap with an assistant on one side to help the baby keep focusing on the screen. In the second session at 11-12 months, the baby sat in a baby car seat facing the screen, and one of the parents and the assistant were sitting on either side of the infant during the entire experiment.

Before starting the experiment, the net was plugged into an amplifier and the impedance of the electrodes was checked. Electrodes that had an insufficient contact with the scalp were corrected with use of saline electrolyte or by repositioning to improve contact. The infant's eye movements in visual space were calibrated to the Tobii x50 eye camera, and the experiment started immediately after this calibration.

Short pauses were made during the experiment when the infant seemed to have lost interest and was not focusing on the image. When the infant showed no further interest at all or showed distress, the experiment was stopped.

The looming experiment was performed together with an optic flow (van der Meer et al., 2008) and an occlusion experiment, where the looming experiment was usually run immediately after the optic flow experiment, about 5-7 minutes into the session. The looming testing session lasted about 5-7 minutes.

2.5 EEG recording and data analysis

Electroencephalogram (EEG) recordings were used to measure brain electrical activity providing information about the spatial distribution and time course of brain activity in response to the visual looming stimuli that were presented to the infants.

EEG recordings were exported to the software program Brain Electrical Source Analysis (BESA) 5.3 for further analysis. All EEG recordings were segmented by the Net Station software on a Macintosh computer, with a low-pass filter of 100 Hz and a 0.1 Hz high-pass filter. The procedure in BESA was the same for both test sessions. To remove slow drift in the data, notch filter was set to 50 Hz, low cut-off filter (high band pass) was set to 0.5 Hz, and high cut-off filter (low band pass) was set to 30 Hz. The EEG data were inspected for poor recordings, and bad channels as decided by visual inspection were excluded from further analyses.

A trial-by-trial investigation was performed on each infant's raw EEG recordings. The three electrode sites of the visual areas consisting of standard 10-20 sites O1, Oz and O2, and two electrode sites in the parietal areas Pz and P3 were investigated. These particular sites were examined based on anatomical positioning of the brain areas involved in visual processing (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; van der Weel & van der Meer, 2009). The selected electrode sites were fitted with the peak looming VEP activity which provided information about the activity at the selected brain regions as a direct measure of amplitude channel activity (see Figure 2).

Each infant had to have VEP peaks on at least three trials for each of the three looming speeds per test session. A total of 1072 trials were analysed, where on average the 3- to 4-month-olds contributed with 61 (SD = 10) trials and the 11- to 12-month-olds contributed with 36 (SD = 6.6) trials more or less evenly distributed over the three looming conditions.
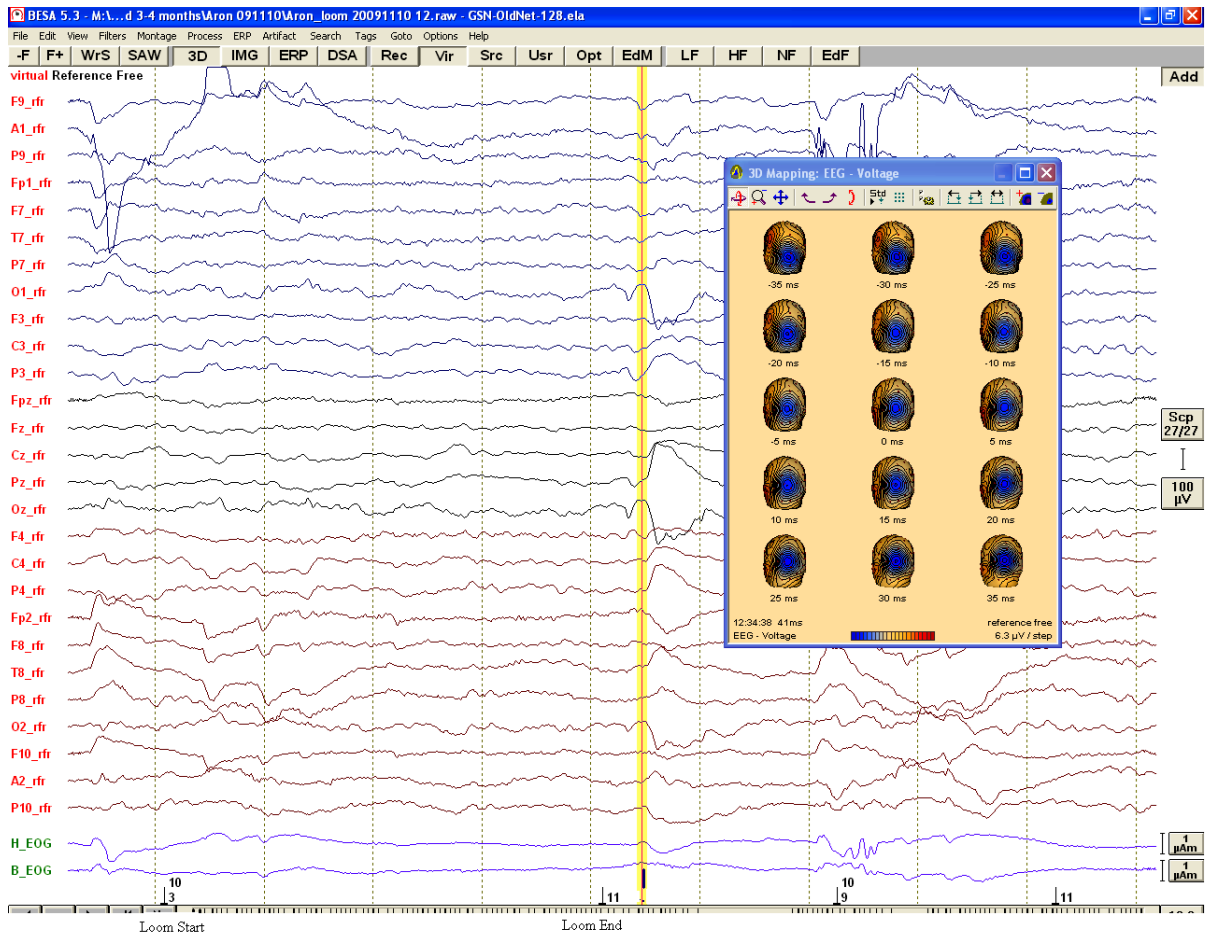
Figure 2 Showing the raw data of EEG recording. The increase in brain electrical activity in areas O1, Oz and O2 is marked by the yellow vertical line. The 3D-mapping also shows the increase in brain electrical activity (a dark blue colour in the occipital areas which was typical in infants at both ages).

2.6 τ_G - guidance analysis

The General Tau Theory (Lee, 1998) was applied to investigate how neural information flows in the infant's brain. The VEP amplitudes were marked (default block -300, 300 µV) and then exported to Generic Tau Server 8.0. The raw data files were Gaussian filtered with a sigma of 5 (50 ms). For each trial, the peak velocity of each VEP was identified at 10 % to avoid dividing by speeds near zero velocity. The VEP activity from the beginning of the amplitude peak (i.e. the increase in neuronal activity in Oz) and its rate of change were plotted against time (Figure 3a). In Figure 3b, τ_{VEP} and τ_G were plotted against time to illustrate the co-variation between these during the looms progression. The gaps between the two taus (τs) can be close simultaneously by keeping the τs of the gaps coupled in a constant ratio, such that

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$\tau_y = K\tau_x$, (where K is a coupling constant). A linear regression analysis (Figure 3c) was run between the two τs to determine the coupling strength between τ_{VEP} and τ_G (as measured by the value of the regression coefficient, r^2). The relative duration of τ-coupling was measured for each trial as the percentage of the movement. It was assumed that the higher the relative duration of τ-coupling the stronger the evidence for τ-coupling (Figure 3d).

$$\tau_G = \frac{\left[(S+T)t^2 - T^2t - ST^2\right]}{\left[(2t(S+T) - T^2\right]}$$ where T is the VEP duration t = 0 and S is the starting value of τ_G
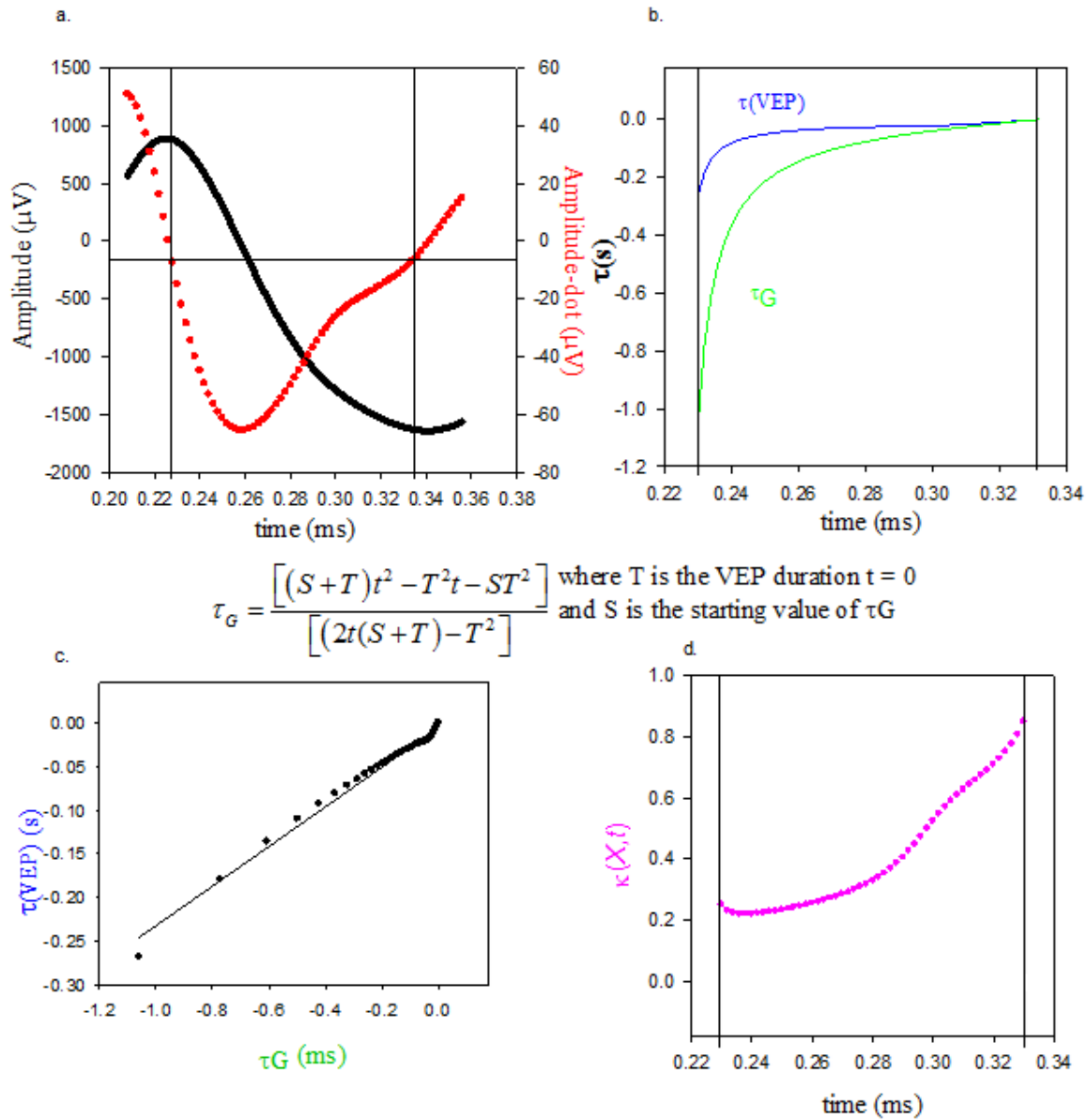
Figure 3 The procedure for analysing tau-coupling. **a)** Shows the VEP activation (and its derivative) against time. **b)** Shows how τ_{VEP} (t) and τ_G (t) co-varied with time. **c)** The τ_{VEP} (t) values were plotted against the corresponding values of τ_G (t). For this particular loom, percentage tau-coupling was 100 %, r^2 of the coupling 0.994, and the regression slope K was 0.210 **d)** Shows the tau-coupling time series κ (X,t) plotted against time. The value of K_{start} was 0.230 and it went smoothly up to K_{end} of 0.853 during the VEP activation.

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3. Results

3.1 VEP responses

Visual Evoked Potentials (VEPs) were found in the EEG readings from all of the tested infants. Looming-related peak VEP activation in both occipital areas O1, Oz, O2 and parietal areas P3 and Pz was indexed on a trial-by-trial basis as the times before the loom would have made contact with the infant, i.e. the time-to-collision (ttc). The three occipital areas showed prominent looming-related peaks in all trials at both ages, whereas the parietal areas did not show consistent looming-related VEP activity in 3/4-month-old infants. As the occipital areas O1, Oz and O2 represented the primary visual processing areas that displayed significant looming responses in both 3/4- and 11/12-month-old infants, the comparative VEP responses between the two age groups were measured in these areas.

The analyses were performed on a total of 375 trials in the first session and 215 trials in the second session where the stimulus was approaching the infant on a direct collision course. On average, each infant contributed 31 (SD = 7) VEPs in the first session and 18 (SD = 7) in the second session. VEP activation at 3/4-months occurred at 0.285s (SD = 0.05) after the virtual collision whereas at 11/12 months the activation occurred at -0.137s (SD = 0.08) before the virtual collision (see Figure 4). A 2 (age: 3/4 months and 11/12 months) x 3 (loom: 2s, 3s, and 4s) repeated measured ANOVA showed that VEP responses at 11/12 months occurred significantly closer to the virtual collision (at ttc= 0) than at 3/4 months [$F_{(1, 11)} = 39.588$, $p < 0.05$].
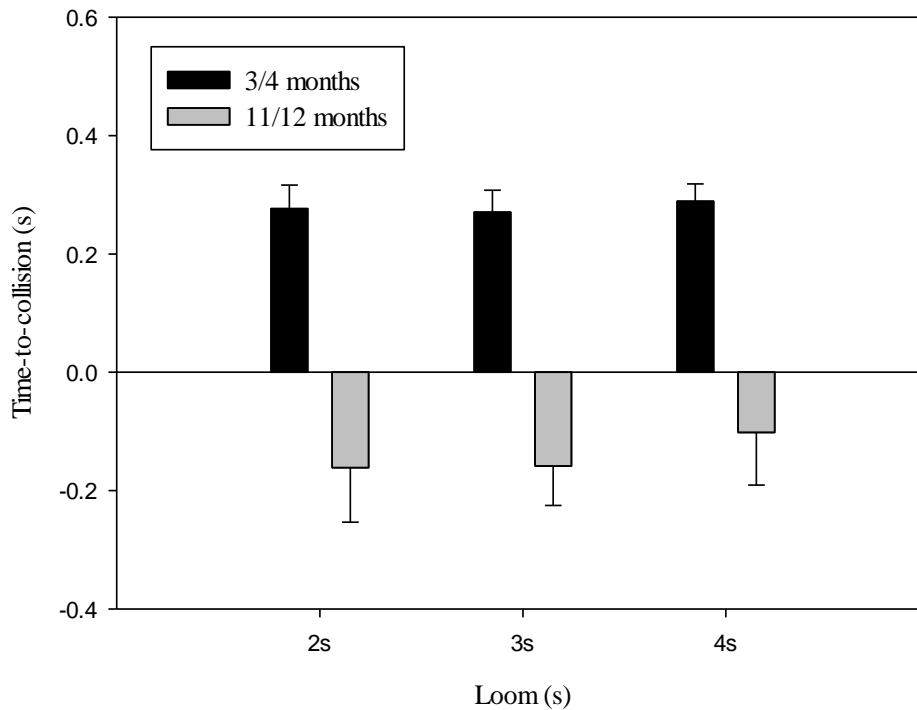
Figure 4 Averaged looming-related peaks for time-to-collision (including SD bars) in the Oz region for the three looms. Infants' at the age of 11/12 months show their responses on average -0.137s before the virtual collision at ttc=0, whereas infants' at 3/4 months show their responses more than 0.400s later and on average 0.285s after the virtual collision.

3.2 VEP duration

It was also observed that infants at the age of 11/12 months had shorter VEP duration (VEP_{end} – VEP_{start}) with respect to the approaching looms. The average VEP duration at 11/12 months was 0.209s (SD = 0.05), while at 3/4 months the average was 0.296s (SD = 0.07) (see Figure 5). Another 2 (age: 3/4 months and 11/12 months) x 3 (loom: 2s, 3s, and 4s) repeated measures ANOVA was performed on averaged VEP duration indicating that the averaged VEP duration at 11/12 months decreased significantly with age [F (1, 11) = 45.199, p< 0.05].
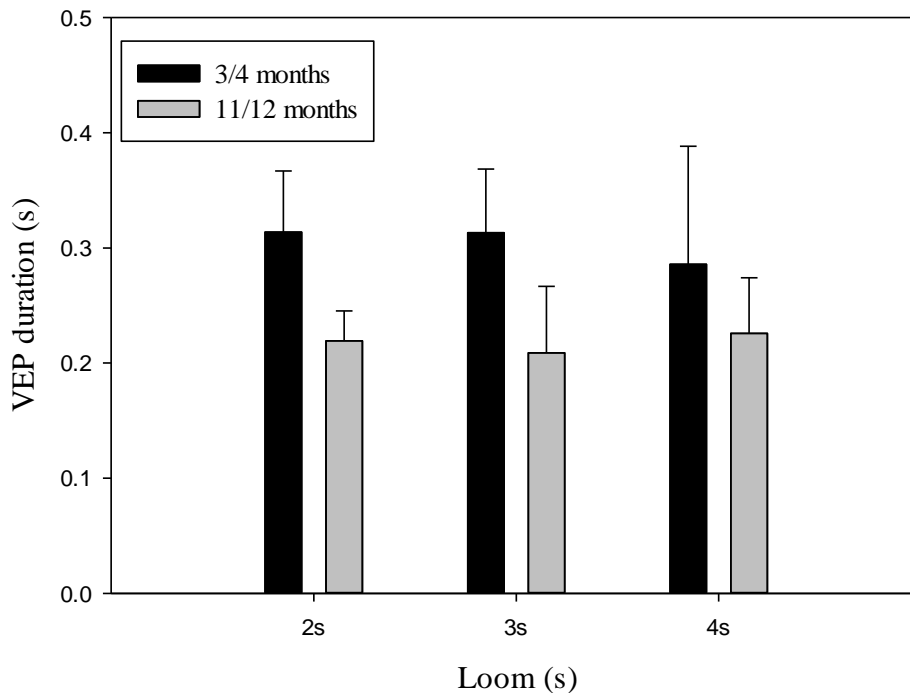
Figure 5 Averaged looming-related VEP durations (including SD bars) for the three looming speeds at the age of 3/4 months and 11/12 months in the Oz region. With age, infants show significantly shorter VEP durations compared to when they were younger for all three looms.

The two ANOVA's indicated that the averaged peak VEP activation for infants at 3/4 months appeared later in the looming sequence and after the loom's virtual collision and had a longer VEP duration as opposed to when they were 11/12 months old. VEP responses for infants 11/12 months occurred before the loom's virtual collision and were of a shorter duration.

3.3 Tau-coupling analysis

Tau-coupling analysis was applied to investigate how neural information is being processed in the infant brain. The tau of the peak-to-peak VEP activity (τ_{VEP}) and the corresponding tau-G (τ_G) in the Oz region were calculated using the general equation: $\tau(x) = x/\dot{x}$.

A total of 600 VEP amplitudes were exported to Generic Tau Server and were used for analysis. Of the 600 trials, 513 trials were 100% tau-coupled (317 trials were from the first testing and 196 trials from the second testing) and were used for further analysis. Each infant contributed an average of 26 trials (SD= 3) in the first session and 16 (SD= 3) in the second session.

In all trials, r^2 values were very high at both ages, giving group mean r^2 values of 0.98 for infants at 3/4 months of age and 0.99 for infants at 11/12 months. The high mean r^2 values and percentages of tau-coupling indicated that τ_{VEP} was strongly coupled onto τ_G allowing the regression slope of the regression line to be a good estimator of the coupling constant K.

Group mean K values were lower than 1 ($K < 1$) for all age groups and all loom speeds (see Figure 6). For infants at 3/4 months K values were as follows: 2s loom: starts at 0.33 (SD= 0.08) and ends at 0.76 (SD=0.04), 3s loom: starts at 0.35 (SD=0.12) and ends at 0.78(SD=0.04), and 4s loom: starts at 0.33 (SD=0.10) and ends at 0.76 (SD=0.05). For the 11/12-month-old infants the mean K values were as follows: 2s loom: starts at 0.44 (SD=0.06) and ends at 0.74 (SD=0.04), 3s loom: starts at 0.46 (SD=0.10) and ends at 0.74 (SD=0.03), and 4s loom: starts at 0.47(SD=0.07) and ends at 0.75 (SD=0.05). K_{start} and K_{end} refer to the first and the last value in the kappa-profile respectively, see Figure 3d.

A 2 (age: 3/4 and 11/12 months) x 3 (loom: 2s, 3s and 4s) repeated measured ANOVA was performed on the averaged K_{start} values, revealing a main effect of age, $F_{(1, 11)} = 10.951$, p <0.05, indicating that the average K_{start} values in infants at 3/4 months were significantly lower than when they were older. No main effect of loom or interaction effect between age and loom was found.

Another 2 (age: 3/4 and 11/12 months) x 3 (loom: 2s, 3s and 4s) repeated measured ANOVA was performed on the averaged difference between K_{start} and K_{end} ($K_{end} - K_{start}$), revealing another main effect of age indicating that infants at 11/12 months had less steep K curves between the start and the end of VEP activation, $F_{(1, 11)} = 9.825$, p < 0.05 than when they were younger. Again, no main effect of loom or an interaction effect was found.
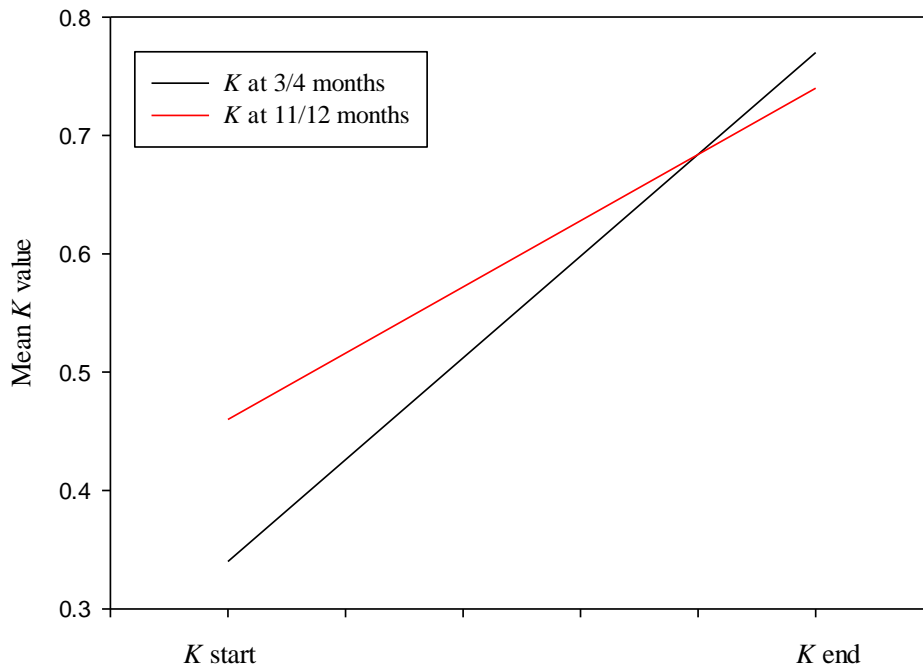
Figure 6 Two variables, τ_{VEP} and τ_G, are coupled in a tau-coupling analysis, where K is the coupling constant. The Figure shows group means of the K values (K_{start} and K_{end}) in the Oz region for infants 3/4 months and 11/12 months. The progression of K values from start to end for the older infants is gentler compared to when they were younger.

4. Discussion

The present longitudinal study was set out to investigate the development of motion processing of a looming object in infants aged 3/4 and 11/12 months. This kind of processing demands a high degree of prospective and visuo-cognitive control. Infants need to extract and process information for impending collision in order to respond adequately. Using high-density EEG, this study investigated infants' brain electrical activity as a function of perception to a looming visual object approaching on a collision course under three accelerations. VEP analyses were explore to investigate any differences and similarities between the two ages.

4.1 VEP Responses

VEP responses on a trial-by-trial basis were found in the EEG readings from all tested infants. By investigating at the looming-related averaged peak VEP activation, infants at the age of 3/4 months showed an average peak VEP at 0.285s after the virtual collision, compared to -0.137s before the virtual collision at the age of 11/12 months. Irrespective of the loom's three different approach conditions, at 3/4 months the average brain response appeared relatively late in the looming phase, after the looming virtual object would have hit the infant's face. At the age of 3/4 months, neural pathways are generally less specialized and may respond to a wide variety of visual stimuli (Johnson, 2000). In addition, when infants are 3/4 months old, the cells in the early maturing Layers 5 and 6 of the primary visual cortex (V1) project only to the subcortical pathways, and cells in Layer 2 and 3 which project to higher cortical structures including the prefrontal cortex (PFC) are not mature yet to contribute to information processing (Conel, 1967). Through development, neural pathways get more specialized and become specifically tuned to certain stimuli, which would lead to a response that is more accurate. At 11/12 months, infants were able to respond -0.137s before the virtual collision, when the object was about to hit the infant's face. Infants at 11/12 months showed a developmental trend showing more accurately timed VEPs responding to the looming object before it hit them.

In the analyzed VEP duration (VEP_{end} - VEP_{start}), infants at 3/4 months had longer mean VEP duration of 87ms compared to at 11/12 months. A peak VEP closer to the virtual collision and of a shorter duration could illustrate an increase in speed and efficiency of visual information processing (Coach, Skendzel, Grossi, & Neville, 2005; van der Weel & van der Meer, 2009). This increase of speed processing in the infant brain can be explained by several mechanisms.

An increase in white matter due to myelination of axons is an important physiological change that is associated with the efficiency of cortical processing (Picton & Taylor, 2007). Myelination of the functioning pathways makes information transmission more rapid and secure. Another important mechanism is synaptic maturation. The synaptic density of the visual cortex reaches its peak at approximately 9-15 months of age (Huttenlocher & Decourten, 1987), and can therefore explain the findings in our data showing that 11/12 months infants' VEP responses took place before virtual collision and were of a shorter duration.

Unlike when they were 3/4 months, infants on their second testing at 11/12 months had developed locomotor abilities, i.e. crawling. Motor activity has been associated with psychological development. Self-produced locomotion and better control of self-movement influence the cognitive level (Higgins et al., 1996). Locomotor experience plays a role in the sensorimotor processes of detecting optic flow in the visual periphery. In addition, increased locomotor experience accompanied by brain development results in more effective processing of motion stimuli (van der Meer et al., 2008). Thus, 11/12-month-old infants' ability to process information about an impending collision may have improved due to increased self-produced locomotor experience.

4.2 Tau-coupling analysis

The coupling constant K was investigated to show how well the looming-related VEPs were coupled to tau-G. Indicated by high percentage of tau-coupling and high r^2 values, evidence were found that τ_{VEP} was strongly coupled with $\tau_{G.}$ The progression of K values from start to end followed as different path in the younger and older infants. 3/4-month-old infants had lower K values at the start towards higher K values at the end, whereas 11/12-month-old had higher K values at the start to slightly lower K values at the end.

This gentler flow of the kappa-profile from start to end during VEP activation could suggest a well-established neural network for impending collision for the older infants. Our results are consistent with another study of infants aged 5/7 months, 8/9 months and 10/11 months responding to looming danger conducted by van der Weel and van der Meer in 2009 where tau-coupling analysis was applied on the visual cortex lateral left (*VCrL*) source waveforms. It has been proposed that 10/11 months infants have well-established neural networks for registering impending collision, but not yet in the 5/7-months-old infants. 8/9-month-old infants displayed an in-between developmental stage as a sign that neural networks are in the process of being

established. 11/12-month-old infants in our study, as well as 10/11-month-old infants in the previous study, had locomotor experience i.e. crawling, and could explain their improved ability to pick up the looming visual information.

With increasing locomotion and brain development, motion stimuli are to be processed more effectively (van der Meer et al., 2008). Bertenthal et al., (1994) have proposed that locomotion is functionally related to the development of infant cognitive behaviours. The crawling infant may develop an understanding of how objects are interrelated in the environment by using environmental landmarks. Kermoian and Campos (1988) reported that infants with 9 or more weeks of hands-and-knees locomotor experience performed at a higher level utilizing an ordinal object permanence scale opposed to infants with less than 4 weeks crawling experience, and speculated that the onset of hands-and-knees locomotion may promote brain maturation (Kermoian & Campos, 1988). The onset of prone progression, especially hands-and-knees crawling, is accompanied by changes in perception, spatial cognition, and social and emotional development (Campos et al., 2000).

Gibson (1979) stated that self-produced locomotion may permit infants to convert effective information variables available in the optical flow field into information useful for prospective control. Locomotor experience facilitates the infant's ability to attend to and use specific portions of the optic array for the various functions involved in locomotion to a destination. Object-search paradigm studies have shown that locomotor infants are better than prelocomotor infants at finding hidden objects (Horobin & Acredolo, 1986).

In a review of infant EEG studies, a type of brain plasticity that occurs with the expectation of a species-wide maturational experience was reported (e.g., crawling) (Greenough & Black, 1992). This plasticity is manifested in synaptic overproduction or blooming prior to the event and pruning of unused synapses with increased experience after the event. In a recent longitudinal study of structured optic flow and random visual motion in infants aged 3/4 months and 11/12 months, findings showed that older infants with active locomotion experience were able to distinguish between the different patterns of the radial motions (Agyei et al., 2014). Self-movements may have led to a relatively faster recruitment and activation of neuronal networks responsible for motion recognition in the older infants.

Base on the view where brain and behavioural development are interdependent, it is possible to argue that 11/12-month-old infants with locomotion experience have the ability to process impending collision more accurately.

4.3 General Discussion

Using high-density electroencepholography, infant brain electrical activity was investigated in a longitudinal design. At the first testing, 3/4-month-old infants had no locomotor experience in the form of crawling, whereas at the second testing at 11/12 months infants had all been crawling for some weeks. Increase in locomotor experience could be one of the underlying causes of the developmental trend found in our study. A growing number of researchers have proposed that locomotor experience is associated with psychological development (Anderson et al., 2001; Bell & Fox, 1996; Campos et al., 2000). In a study, it was suggested that self-locomotion results in changing perspective of the environment that serves to show the infant that egocentric spatial relations do no aid in relocating objects (Acredolo, 1990). From the perspective where brain and behavioural development go hand in hand (Johnson, 2000), it is possible to argue that as 11/12-month-old infants gain better control over their self-produced locomotion, their abilities for sensing looming danger improve.

The tau-coupling analysis gave us evidence of strong ($r^2 > 0.95$) and long ($> 100\%$) tau-coupling in all infants. Previous studies (Svantesson, van der Meer, & van der Weel, 2012; van der Weel & van der Meer, 2009) as well as the present findings suggest that when looming-related information flows inside the neurons in a particular brain region, infants' ability to pick up the flow improves as they mature and get more locomotor experience providing them more veridical information about time-to-collision information.

In conclusion, our study has demonstrated the development of motion processing of a looming object from infants 3/4 months to 11/12 months. Differences in brain activity as observed in VEPs were presented. The study showed clear differences in VEP responses as infants got older, illustrated by a decrease in processing time and VEP peaks closer to the loom's time-to-collision. The study further showed that as infants mature and got locomotor experience, their ability to pick up looming-related information improve. Neurodevelopmental changes coupled with active locomotion, infants in our study were able to show developmental trend in the prediction of an object's time-to-collision. Our research can be used as a diagnostic tool for understanding neural mechanisms underlying infants' ability to perceive visual information.

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