Infants' cortical responses to audiovisual looming studied with high-density EEG

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ABSTRACT

Infants' cortical electrical activity as a function of audiovisual looming perception was investigated using high-density electroencephalogram (EEG). Fourteen infants between the ages of 3 and 4 months participated in the study. The aim was to study how audiovisual looming is processed by the infant brain and what timing strategies infants used to time their brain responses to the approaching audiovisual loom. Analysis was performed on all EEG trials in which a looming-related VEP or AEP peak was detected. Results indicated that infants significantly showed earlier looming-related brain responses to the auditory loom than to the visual loom. The results further showed infants used the less sophisticated visual angle/pitch and velocity timing strategies in timing their looming-related brain responses. Using these strategies resulted in errors in judging the loom's time-to-collision as they are dependent on the approach velocity of the loom. Three infants, however, had developed a more advanced strategy which was based on timing responses to the time-to-collision of the approaching audiovisual loom, but only when timing the collision of the visual loom and not the auditory loom. Furthermore, infants significantly showed looming-related brain responses closer to contact for the faster looms, but no differences in the duration of looming-related VEP and AEP peak responses were detected. When the looming-related peaks at channels Oz (vision) and Cz (audition) were compared, peaks at occipital channel Oz were significantly higher in amplitude for all three loom speeds. In conclusion, it was suggested that audiovisual integration was heavily influenced by infants' spatial attention captured by the visual loom which resulted in looming-related VEPs that occurred relatively late in the looming sequence. Infants' response asymmetry was also suggested to represent an evolutionary bias for survival which prioritizes an early auditory response over that of the visual in audiovisual looming perception. The use of less sophisticated timing strategies showed infants' levels of neural maturity and locomotion experience, two very important factors needed for accurate timing of looming.

1. INTRODUCTION

In our everyday life, we often come into contact with multisensory events that approach us on a direct collision course. In such situations, our ability to accurately time the collision of these looming multisensory stimuli serves a survival value, enabling appropriate action to be taken. Throughout the animal kingdom, different species share this similarity in detecting looming audiovisual stimuli, although differences exist in the behavioral responses used.

It appears primates as well as humans have evolved a bias towards the perception of coherent looming visual and structured sounds and are more likely to show responses to these stimuli than unstructured (noise) sounds and receding visual stimuli. When responding to looming sounds, adults mostly underestimate the approach time of the loom, an adaptive bias which aids us to prepare for a quick escape response (Ghazanfar, Neuhoff, & Logothetis, 2002; Neuhoff, 1998). When an audiovisual looming object is temporarily occluded, the auditory component becomes vital. The ecological benefit of early response to auditory looming component in an audiovisual loom is the enhancement of the visual stimuli when the audiovisual loom is approaching on a direct collision course (Leo, Romei, Freeman, Ladavas, & Driver, 2011) or the direction of our gaze towards the occluded visual loom (Guski, 1992). In such situations, the auditory component serves a warning purpose by creating an urgency which alerts us of an approaching danger (Gordon, Russo, & MacDonald, 2013).

The perception of looming has been widely investigated unimodally in locusts (Rind & Simmons, 1992), pigeons (Sun & Frost, 1998), monkeys (Ghazanfar et al., 2002) and humans (Kayed & van der Meer, 2000; Yonas, Pettersen, & Lockman, 1979), and bimodally in monkeys (Maier, Neuhoff, Logothetis, & Ghazanfar, 2004) and humans (Schiff & Oldak, 1990). These studies have identified different neural regions and specific classes of neurons that are selectively sensitive to the kinematic properties of looming, as well as the perceptual responses displayed towards the loom. Sun and Frost (1998) identified three classes of neurons – tau, rho, and eta, in the nucleus rotundus of the pigeon midbrain that respond to different kinematic properties of looming. Neurons of the first group (tau) always initiate their responses at a fixed time before an object makes a collision. Neurons in the second (rho) and third (eta) groups both initiate their responses earlier in the looming sequence for larger or slower objects, with one distinctive feature – rho neurons have a response threshold after which their responses remain unchanged with different object size and velocity, while eta neurons decrease their responses as the approaching object reaches a particular angular size.

In humans, the cortical visual motion pathway starts with orientation-tuned neurons of layer 4B in area V1. These neurons basically code for the fundamental properties of the visual stimulus such as the speed and direction of movement, and send their projections to higher cortical areas responsible for the processing of complex visual motion – V5/Medial Temporal (MT) area and Medial Superior Temporal (MST) area (Orban et al., 1995). Area MT integrates various orthogonal inputs coming from the primary visual cortex (V1) into a robust perceptual image, which shows the true direction of the object (Andersen, 1997). An adjacent area, MST, receives afferents from MT, and has a dorsal subdivision (MSTd) which has the largest receptive field among all the areas in the visual pathway, and responds to the pattern of motion (Andersen, 1997). Neurons in the MSTd are responsible for coding of more complex movements such as expansion and contraction, rotation and spiral motions (Orban et al., 1995; Tootell et al., 1995; Zeki et al., 1991).

The area MT can be influenced by attentive processes. Treue and Maunsell (1996) demonstrated that attending to a stimulus increases the response patterns of neurons of the area MT. The authors presented two dots within the receptive fields of MT neurons moving in opposite directions with a 180-degree phase difference with one another. They found that when the monkeys switched their attention from one dot to the other, the MT neurons also switched the phase of their activities by nearly 180 degrees.

Unlike the detailed understanding of visual motion processing mechanisms, auditory motion processing is relatively less understood. Lesion studies have identified the deficiencies in the perception of auditory motion when the parietal and insular cortices were ablated (Griffiths et al., 1997). There are close to 10 secondary auditory cortical regions collectively known as the belt areas, that surround about 3 to 4 primary auditory cortical areas (the core) (Oertel & Doupe, 2013), and perform various higher level auditory motion processing. The primary auditory cortical areas (area A1s) receive input from the ventral nucleus of the medial geniculate body (MGB) while the secondary areas receive their inputs primarily from the non-leminiscal divisions of the MGB (Kaas & Hackett, 2000). Area A1 neurons are organized in a tonotopic manner according to the frequencies that best stimulates them, from the rostral to the caudal length, with these neurons responding to the increasing frequency of an auditory stimulus. Some neurons in the primary auditory cortex respond to the loudness of sound, the modulation of loudness, and the rate of frequency modulation (Oertel & Doupe, 2013).

Pitch is that perceptual property of frequency or the period of sound vibrations in the audible frequency range of about 20 Hz to 20 kHz (Tramo, Cariani, Koh, Makris, & Braida, 2005). The pitch of a simple pure tone is the same as its fundamental frequency, that highest frequency for which spectral components of the sound are integer multiples of (Bendor & Wang, 2006). The pitch of ecological sounds may or may not increase with the intensity of the sound source (Neuhoff & McBeath, 1996). The perception of a rising pitch with rising sound source intensity is limited in the range of 30 to 5k Hz, with a higher periodicity evoking a higher pitch (Krumbholz, Patterson, & Pressnitzer, 2000). Pitch perception however is not limited to the regularity of the sound but also to its spectral properties (Bizley & Walker, 2010). At the neural level, pitch perception is mostly a cortical function. The subcortical structures involved in the processing of auditory stimuli also code for some form of sound periodicity (Bizley & Walker, 2010), but do not invariantly process pitch, which occurs higher up the auditory pathway. Even though the processing of pitch has been shown to be a function of the lateral Heschl's gyrus (HG) (Patterson, Uppenkamp, Johnsrude, & Griffiths, 2002), an area anterolateral to the primary auditory cortex (Bendor & Wang, 2006), the location of pitch processing can also be influenced by the sound type (Hall & Plack, 2007) and its spectral content (Nelken et al., 2004).

Humans use the dynamic pitch changes as a cue for the perception of loudness of a sound as it approaches them. In a behavioral study, Neuhoff and colleagues (1999) found a relationship between rising frequency sounds and the perception of loudness. This difference in loudness of sounds of increasing pitch was only observed when the pitch was changing dynamically. The opposite was found for sounds with static frequency – sounds with discrete changes in frequency (Neuhoff, McBeath, & Wanzie, 1999). This result suggests dynamic but not static changes in pitch were inducing the perception of loudness of sounds. Rising frequency sounds, even when sound intensity is held constant is enough to create the looming experience of an approaching sound source. When the intensity is ignored, the pitch changes of the sound alone create the loudness perceived by subjects (Ghazanfar & Maier, 2009; Neuhoff et al., 1999).

Infants have been reported to respond to looming as early as a few weeks after birth (Nanez, 1988; Yonas et al., 1979), with accurate timing of the collision of a visual loom shown to develop gradually through infancy (Kayed & van der Meer, 2007). Infants start to respond to looming audiovisual stimulus when they begin to perceive synchrony in multimodal events.

Synchronous presentation of two unimodal stimuli from the same location usually results in an enhancement of any one of these stimuli through multisensory integration (Stein, London, Wilkinson, & Price, 1996; Stein & Meredith, 1993). Throughout infancy, the perception of audiovisual synchrony is a rather gradual process (Lewkowicz, 1996), with age influencing how much synchrony is perceived (Morrongiello, Fenwick, & Nutley, 1998) and how it aids in the timing of a collision. At about 5 months old, infants can easily detect the synchrony in audiovisual events by showing a habituation towards matched as opposed to unmatched audiovisual stimuli (Pickens, 1994; Schiff, Benasich, & Bornstein, 1989; Walker-Andrews & Lennon, 1985). Audiovisual synchrony has also been shown in fMRI studies to improve the activation of low-level visual and auditory cortices through the enhancement of connections between the calcarine sulcus and the ventral occipitotemporal cortex, and also connections between the Helschl's gyrus and the planum temporale (Lewis & Noppeney, 2010).

Earlier studies in multisensory perception have suggested a hierarchical model of cross-modal processing, where early sensory cortices were responsible for processing unimodal stimuli, with multisensory processing the reserve of higher association cortical areas such as the superior temporal sulcus (STS), ventral intraparietal area, and regions in the frontal cortex (Beauchamp, Lee, Argall, & Martin, 2004; Calvert, Campbell, & Brammer, 2000; Stein & Meredith, 1993). Accumulating evidence now challenges this classical view, and shows that multisensory integration occurs even earlier down the cortical pathway in the early sensory cortices (Ghazanfar & Schroeder, 2006). Recent studies with fMRI have suggested a bilateral enhancement of primary auditory and visual cortices together with the STS that occurs superaddictively in response to audiovisual looming (Tyll et al., 2013). Auditory-visual multisensory interactions have also been shown to occur even earlier in time post-stimulus at primary as well as secondary sensory cortices (Cappe, Thelen, Romei, Thut, & Murray, 2012; Giard & Peronnet, 1999; Molholm et al., 2002).

Integration of looming signals has been found to be selective, where multisensory static, and non-looming signals did not induce any enhancement in target detection or reaction time compared to the reduction in reaction time observed with multisensory looming signals (Cappe, Thut, Romei, & Murraya, 2009). Using rhesus monkeys (Mucaca mulatta), Ghazanfar and Maier (2009) found that monkeys showed a strong attention bias towards a sound source with rising frequency compared with a source with falling frequency. The monkeys in their experiment responded to the rising pitch of the sound as a salient indicator

of looming sound source and displayed the right behaviorally adaptive response in that particular direction. When the sound was paired with visual looms, the monkeys were able to pair sound source of rising frequency with looming visual stimulus by showing longer habituation compared to receding frequency and receding visual loom pairs. The rising pitch of the looming sound mimicked an ecologically salient threat which caught the attention of the monkeys as compared to the less threatening receding visual loom paired with a falling frequency sound. Maier et al. (2004) using a similar paradigm, found monkeys to integrate bimodal looming signals by showing a strong attentional bias towards synchronous audiovisual looming sources compared to the asynchronous looming sources.

It has now been established that adults as well as infants use the variables present in the looming information to guide brain responses or make defensive blinks, before the loom makes a virtual collision. In these studies, subjects were found to use the loom's angle, pitch, approach velocity, and the time remaining to a collision to time their responses – neurally (van der Meer, Svantesson, & van der Weel, 2013) and behaviorally (Kayed & van der Meer, 2000; Neuhoff et al., 1999; Schiff & Oldak, 1990). In responding to visual and auditory looming stimuli, participants based their responses on the relative changes occurring in these variables just before the looming stimulus 'collided' with them, indicating the presence of prospective information used in estimating time-to-collision (Kayed & van der Meer, 2000; McLeod & Ross, 1983; Rosenblum, Carello, & Pastore, 1987; Schiff & Oldak, 1990; van der Meer et al., 2013)

As a looming visual object approaches with constant velocity, the angle subtended by the edges of the object on the retina and its angular velocity would grow non-linearly, while the time remaining before a collision decreases linearly (Fotowat & Gabbiani, 2011). This would mean infants' responses would be heavily influenced by the approach velocity and they would be making late responses with faster approaching looms. When the pitch of a looming sound is used to time its arrival, response underestimation would be influenced by how much the pitch increases. Changes of pitch which are slow and delicate would result in lower underestimations than faster and higher changes. In a recent study, Gordon et al. (2013) demonstrated the influence of pitch of sound sources on time to arrival judgments. Subjects were presented with nine one-octave sound sources with frequencies ranging from 40 Hz to 20 kHz under three different velocities – 35 km/h (low), 70 km/h (moderate) and 140 km/h (fast). As was expected, subjects underestimated the time to arrival of all nine sound sources

in the experiment, with the greatest underestimation observed for sound sources of frequencies between 350 Hz and 5 kHz. The authors argued that the higher underestimation found for this frequency range could mean the heavy reliance on the sound's spectral cues in judging the collision time of the sound.

The visual angle, pitch and angular velocity of the audiovisual loom are considered the less sophisticated strategies, as they are dependent on the approach velocity of the loom, and are prone to errors when used to estimate the loom's time-to-collision (Kayed & van der Meer, 2000; Schiff & Oldak, 1990). For these strategies to work, approach velocity must be slow. As velocity increases, the threshold of response decreases linearly, lying very close to the time-to-collision which creates a problem for a behavioral response (Kayed & van der Meer, 2000).

A more sophisticated timing strategy that is independent of the approach velocity is based on the time-to-collision of the loom. Infants using this strategy would show brain responses at a specific time before the loom makes a collision (van der Meer et al., 2013).

Kayed and van der Meer (2000; 2007), in a series of cross-sectional and longitudinal experiments found infant's age as a major influencing factor in the choice of a timing strategy. According to the study, infants switch from the less sophisticated visual angle and velocity strategies to the more sophisticated time strategy based on the loom's time-to-collision. This, the authors suggest, was due to maturation as infants begin to explore their environment through locomotion. Recently, van der Meer et al. (2013) found infants within the age of 5/6 months mostly used the angle of the visual loom to time their VEP related brain responses. These infants switched at around one year of age to using a strategy based on time, by initiating their VEP responses at a specific time before the loom makes a virtual collision.

When a looming audiovisual stimulus approaches on a direct collision course, infants must use the information available in the loom to accurately time their responses. This study aims to investigate 3- to 4-month-old infants' cortical responses to a looming audiovisual stimulus approaching under three different accelerations. Timing strategies infants used to time their brain responses when perceiving the audiovisual looms were also investigated. Infants' cortical evoked potentials in the visual and auditory cortices were recorded using high-density electroencephalography.

2. METHODS

2. 1. Participants

A total of 18 babies were recruited for the present study. Four of the babies were eventually excluded from the final sample. One baby could not complete the experiment, while three provided trials that were too few to be included in the final analysis. 14 babies (8 boys) provided data for the final sample and were all of the age of 3/4 months with a mean age of 13.6 weeks (SD = 1.7)

All babies used in this experiment were healthy, as determined by a parental report. One baby was born 3 weeks before term but no cognitive or physical deficits were reported. None of the babies had developed any sophisticated form of locomotion at the time of testing. None were crawling and only one could roll over by himself. Almost all had at least one episode of rolling over accidentally from stomach to back.

The babies for this study were recruited through an advertisement in the local birth announcement newspaper and through a simple snowball technique. Students and other workers in the Department of Psychology who recently had a baby were invited to participate in the study. Parents of the newborn babies recruited through newspaper advertisements were contacted through the post and notified about the research. Those who were willing to participate were then enrolled in the study. Parents of the babies participating in the experiment were given a brief introduction on electroencephalography and all their concerns satisfied before the testing began. Electroencephalography (EEG) as a psychological procedure is non-invasive and causes no harm to participants. All parents signed an informed consent before the commencement of the experiment and were free to withdraw at any point of the study.

One parent was always present with the baby during the entire experiment and was allowed to interrupt whenever necessary and for whatever reason. Since 3/4 month-old babies are too young to sit in the experimental chair, they sat on their parent's lap with their chests firmly supported throughout the experiment, (see Figure 1).

This study was approved by the Norwegian Regional Ethics Committee and the Norwegian Data Services for the Social Sciences. All testing was carried out at the Developmental Neuroscience laboratory.

2.2 Equipment/Apparatus

The experiment was conducted in a testing room, which was separated by a transparent glass partition from a recording room. The glass partition facilitated communications between the experimenter in the testing room and two assistants in the recording room during testing.

A white projector screen, 108 cm wide and 80 cm high hung in front of the baby who sat on the parent's lap in a chair 80 cm away from it (see Figure 1). Infants were filmed during the experiment with a video camera.

EEG activity was recorded with a high-density Geodesic sensor net 200 GSN (Tucker, 1993) produced by Electrical Geodesic Inc. The EEG net, consisted of 128 electrodes, each made up of a 12 g aluminum sensor was worn on the head of the participant. The signals picked up by these electrodes were amplified and recorded by Net Station Software on a MacIntosh computer. Sampling rate was set at 500 Hz with a low pass filter of 100 Hz and high pass of 0.1 Hz.

To optimize signal-to-noise ratio, the impedance was kept at 50 kΩ. Triggers about the on- and offset of the looming stimulus were communicated to the Net Station by E-Prime, a psychological measurement software tool (Psychology Software tools, Inc). Data were stored on the hard disk of the Mac computer for offline processing.

A
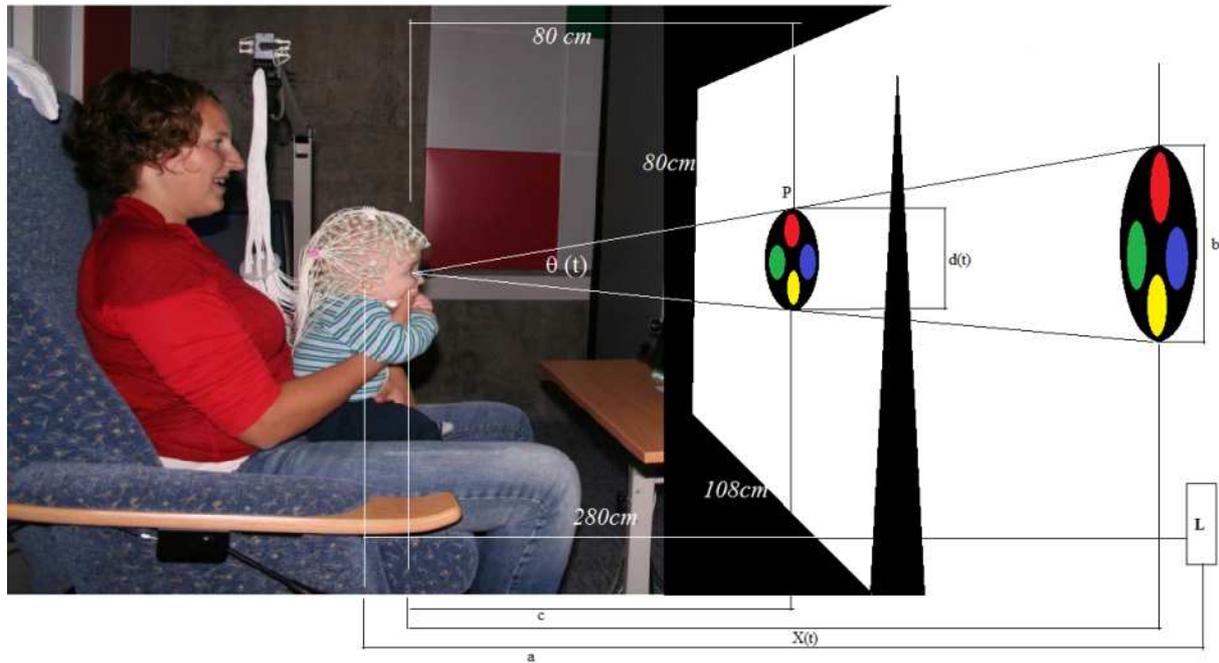
B

$$\frac{b}{x(t)} = \frac{d(t)}{c}$$

C
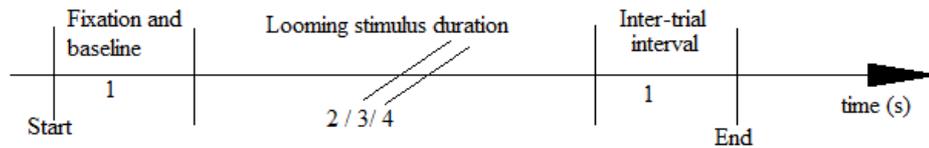
*Figure 1. Experimental setup with a diagram of the stimulus configuration. (A) An infant sitting on the lap of the mother. Each infant in this study was shown a flat two-dimensional circle filled with four smaller circles of red, blue, green and yellow colors. The auditory stimulus, which was synchronously looming with the visual stimulus, was presented through two Logitech loudspeakers (**L**) on either side behind the projection screen. The looming visual and auditory stimuli simulated an object approaching from far away on a direct collision course under constant accelerations of -21.1 ms², -9.4 ms², -5.3 ms² for 2, 3 and 4 seconds, respectively. The looming stimuli approached the infant as the image on the screen grew and the sound became louder, and stopped when the image filled the entire screen and the sound made a 'whoop effect'. (B) A mathematical equation describing the growth of the audiovisual loom. (C) Timeline showing the approach of the looming stimuli and the time duration during the phase of fixation, looming, and inter-trial interval from start to end of a single trial.*

2.3 Stimuli

The visual stimuli consisted of a round 2D flat circular disk with four colored circles (red, yellow, blue and green) all rotating inside (van der Meer et al., 2013). The entire circular disk was rotating at a constant angular velocity of 300 degrees per second on the screen (Fig 1). The inner circles were 1/3 of the diameter of the larger outer circle. The image was programmed on E-Prime to simulate an object approaching the infant on a direct collision course and finally virtually colliding with the infant.

The auditory loom consisted of a simple harmonic tone which was programmed to mimic a natural sound approaching the infant on a direct collision course. This stimulus was recorded and edited with the Audacity sound software (Audacity 2.0.3, The Audacity Team, 2012), and was made up of three sound files for the three looming conditions. These looming sounds were all sampled at a rate of 44.1 kHz, and at a constant intensity level of 60dB.

Both the auditory and the visual looms were programmed to appear simultaneously, and grow towards the observer with the same acceleration, eventually making a virtual collision with the infant. For the visual loom, the image appeared on the screen and stayed at its smallest size for 1 second at a virtual angle of 5º (diameter of 6.5 cm) at a virtual distance of 43.1 m, before it expanded during a looming phase and finally reached its largest size at a virtual angle of 131º (diameter of 350 cm) at a virtual distance of 0.8 m and then disappearing from the screen. The screen was then blank for an inter-stimulus break of 1 second. There were three conditions of looming, and in each of these conditions, the stimulus took a total of 2 seconds ($-21.1 m/s^2$), 3 seconds ($-9.4 m/s^2$) or 4 seconds ($-5.3 m/s^2$) respectively to complete the looming sequence – from appearing to making a virtual collision. In all these three looming conditions, the size of visual loom and the pitch of the auditory loom from the beginning of the looming phase to the virtual collision were kept the same. For the auditory looms, the sound increased in pitch, from 140 Hz which was barely audible, to 460 Hz which was loud enough to simulate a virtual collision of a looming sound. The sound stayed at its lowest pitch of 140 Hz for a second, and then became louder with increasing frequency through the looming phase. As the sound's growth approaches collision, a 'whoop' effect was clearly heard at its loudest level, exactly the same time as the colored circle would make a virtual collision with the infant.

Infants were not harmed in anyway by the audiovisual loom, as no indication of any fear-induced response was observed. The 'whoop' sound of the auditory loom and the growth of the colored circles simulates very well an approaching visual object with a sound component that became bigger and louder as it made a collision with the viewer.

2.4 Procedure

When the baby and parents arrived in the lab, one experimenter received them and informed the parents about the experiment while the other played with the infant. This was to form a bond between the baby and the experimenter which was vital in making the baby comfortable with the lab setting. After about 10 minutes of playing and interactions, the head circumference of the baby was measured and the right electrode net selected for the experiment. The net was then soaked in an electrolyte solution of potassium chloride and a few drops of shampoo. The net was then dried gently to prevent water dripping down the baby's face and body and carefully mounted on the infant's head. The entire process was carried out with the baby sitting on the parent's lap, while one experimenter was distracting the attention of the baby by blowing soap bubbles, and creating funny sounds with baby toys. The infant and the parent were then moved to the testing room where the baby sat comfortably on the parent's lap and the electrode net was plugged into the amplifier. The impedance of the electrodes was checked by the second experimenter in the recording room. One experimenter was present with the baby and the parent in the testing room during the entire experiment. Before the experiment began, the chair was adjusted properly, so the eyes of the baby were almost exactly fixated onto the middle of the screen in front of it. Infants were given short pauses to relax if they became inattentive.

Each infant participated in three different experiments-optic flow, looming, and occlusion, each lasting about 5 minutes. The looming experiment was conducted after the optic flow experiment. The testing for each infant lasted 20 minutes in total. Each infant contributed on average a total of 29 trials (SD = 3.87, range = 21 - 37), distributed almost evenly among the three experimental conditions.

2.5 Data analysis

Analysis of EEG data was carried out in the Brain Electrical Source Analysis (BESA) 5.3.1 software. EEG recordings were segmented by Net Station and exported to BESA for analysis. In the BESA software, a standard channel configuration and digitized head surface points were added to the raw data for each infant before processing began. Trials and bad channels contaminated with artifacts were removed by visual inspection. None of the participants had more than 10% channels defined as bad. Notch filter was set at 50 Hz to remove mainline noise interference in the EEG data, while low cut-off filter (high band pass) was set at 1.6 Hz to remove slow drift in the data, and high cut-off filter (low band pass) was set at 15 Hz. There was no averaging of EEG data and no artifact correction. All looming peaks were identified on a trial-by-trial basis.

In order to simplify the data for easy analysis, a reference-free montage of 27 channels was used. Virtual polygraphic channels H_EOG and V_EOG were added to the 27 channels for easy identification of the effects of the horizontal and vertical eye movements.

An event-related potential (ERP) represents a transient brain electrical activity generated by the summation of dendritic postsynaptic activity of neurons firing synchronously in response to a stimulus (Allison, Wood, & McCarthy, 1986; Li, McLennan, & Jasper, 1952; Luck, 2005; Nunez & Srinivasan, 2006). The different arrangements (perpendicular or parallel) of the pyramidal neurons of the cerebral cortex creates a dipolar field of positive and negative charges which enables the flow of current through it (Coles & Rugg, 1995).Visual evoked potentials (VEP) and auditory evoked potentials (AEP) represent the ERPs of the visual and auditory cortices. To localize the effects of the audiovisual looming stimuli on brain responses, a trial-by-trial examination was performed. Prominent VEPs and AEPs were marked at channels Oz and Cz, respectively (see Figures 2a and 2b). These marked VEP and AEP peaks provide information about visual and auditory activity in the brain regions as a direct measure of amplitude channel activity. These activities could also be visualized by a 3D mapping of a buildup (negative) and decline (positive) voltage activity in the visual and auditory cortices over time. The criteria for selecting VEP and AEP peaks was based on this 3D mapping procedure and the visual inspection of peaks on a trial-by-trial basis. The time-to-collision of the looming stimulus was taken as the time at which a looming-related VEP/AEP peak occurred.

a.
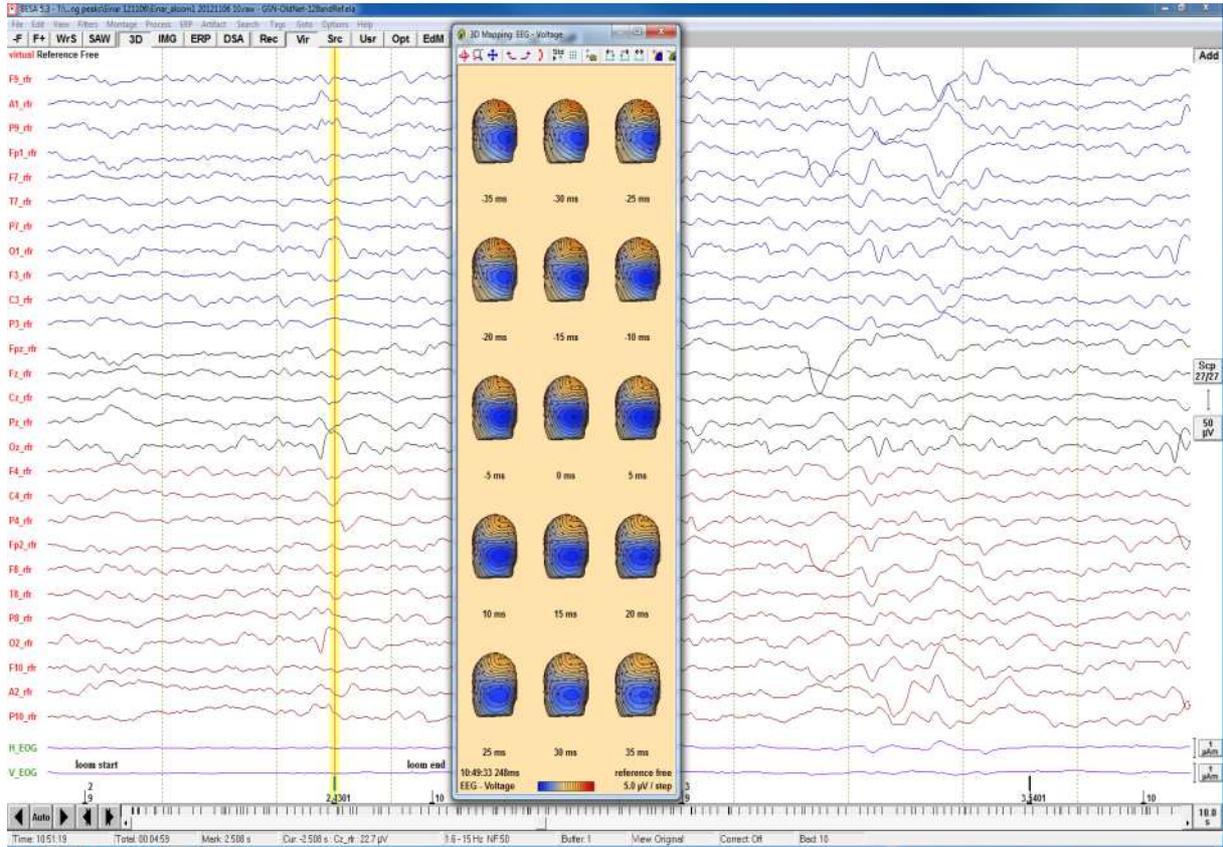
b.
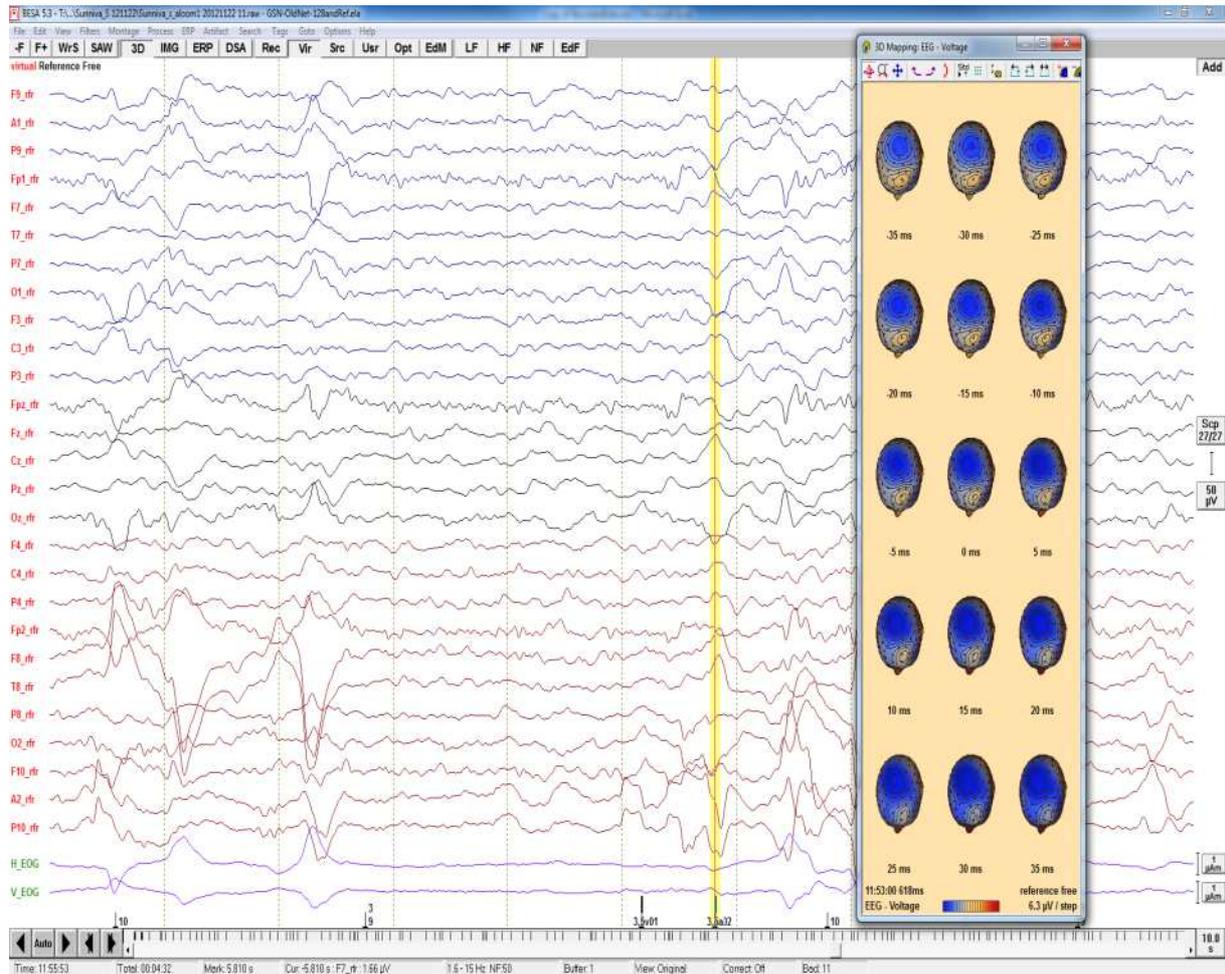
*Figure 2. EEG data showing prominent VEP peaks of a 2 s loom (**a**), and AEP peaks of a 4 s loom (**b**) and their 3D mappings over time. The VEP peaks, at channel Oz and the AEP peaks at channel Cz are marked by the yellow vertical line. The 3D mappings show a high cortical activity in the visual and auditory cortices building up over time.*

Occasionally, several VEP and AEP peaks were observed in the same trial making it difficult to determine which peak represented the looming-related response.

In case of multiple peaks, the peak occurring closest to the stimulus end was assumed to be more functionally related to the loom. When more than one peak occurs closer to contact, the peak showing the best cortical activity in the 3D mapping was taken as the most functionally relevant looming-related peak. Peaks too close to the end of stimulus were assumed to

represent other evoked potentials that are not related to the timing of the looming-related response.

In addition to recording the timing of the VEP and AEP peak with respect to the virtual collision, the duration of every looming-related VEP and AEP response was recorded (see Figure 3). The VEP or AEP duration was defined as the difference in time between the start and the end of the looming-related peak (van der Meer et al., 2013).
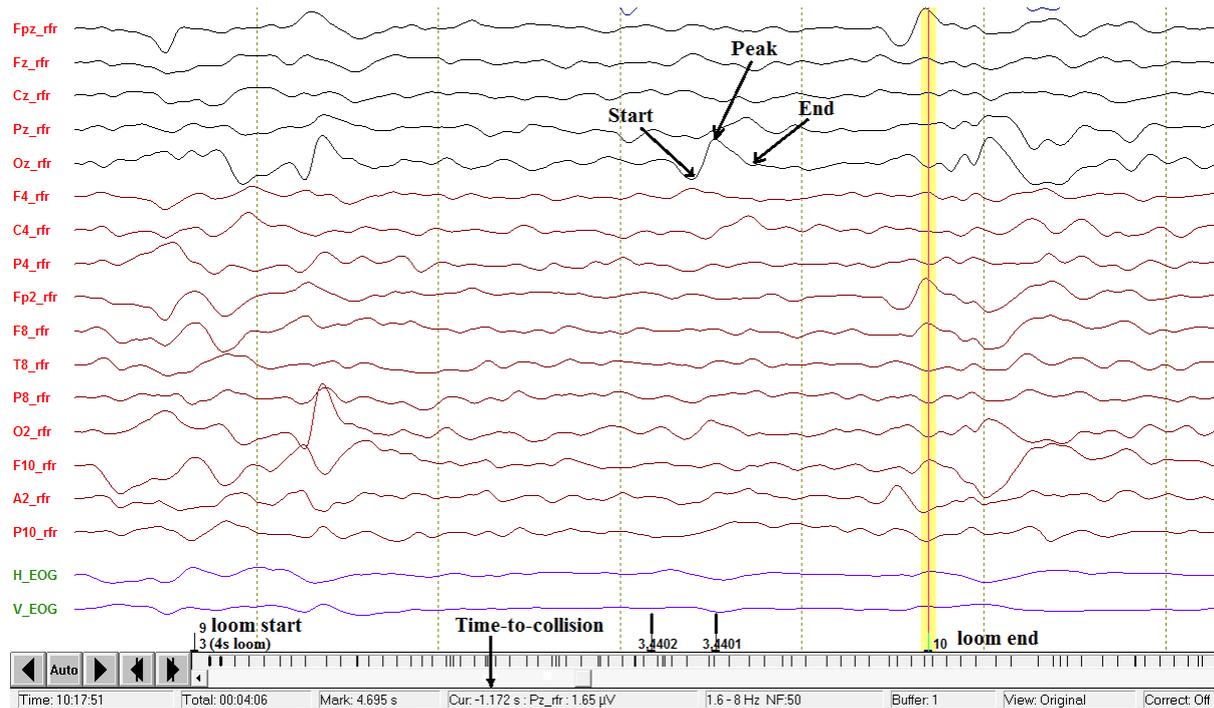
Figure 3. Marking and timing of individual VEP in raw EEG data, showing how the start, peak and end of the looming-related VEP were manually marked in the Oz electrode of single trials.

2.5.1 Timing strategies

Infants may depend on different optical and acoustic variables of the audiovisual looming stimulus to time their brain responses to its virtual collision. Any strategy used will depend on the variable the infant holds constant across trials.

This study investigated the strategies infants used in timing their brain responses. These strategies which are based on the variables of the audiovisual stimulus are the visual loom's

angle, its velocity, and time-to-collision and the auditory loom's pitch, its velocity and time-to-collision. These variables are a function of the looming stimulus' approach velocity and the duration of the looming sequence.

A strategy based on the visual angle/pitch of the audiovisual loom means infants use the changes occurring in the angle subtended by the edges of the visual loom and the pitch of the auditory loom to time their looming-related brain responses (Fig. 4i). If these variables are held constant (a) and the loom's acceleration decreases, the loom's velocity would decrease (b) while time-to-collision would increase (c).

Infants may also depend upon the velocity of the audiovisual loom to time their brain responses. A strategy based on the loom's velocity implies that infants would show a looming-related response when the loom reaches a certain velocity (Fig 4ii). By holding the velocity constant (d) and the loom's acceleration decreases, the time-to-collision would decrease (e) while visual angle/pitch would increase (f).

(i) Visual angle/Pitch strategy   **(ii)** Velocity strategy   **(iii)** Time strategy

Stimulus duration (s)

Acceleration (m/s^2)
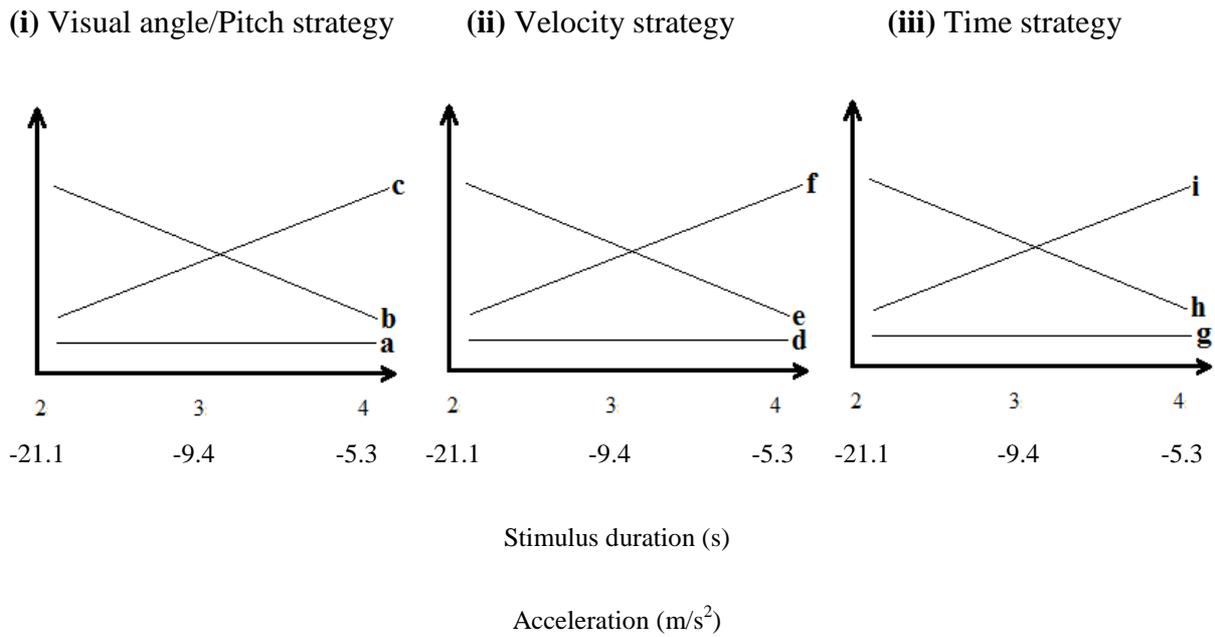
Figure 4. A graph showing the different timing strategies infants may have used. In each of the three graphs, a preferred timing strategy is used when that variable is held constant across the loom speeds. Whenever a variable is held constant, other variables vary either by increasing or decreasing.

Infants using visual angle/pitch and velocity strategies run the risk of under- or overestimating the loom's virtual collision as these variables do not accurately predict the loom's time-to-collision. When looming stimuli with different speeds approach the infant, brain responses based on the angle/pitch and velocity of the looms would be influenced by the size, frequency and speed of the looms. The approaching loom then would have reached a certain visual angle/pitch and velocity at a different time from virtual collision for each loom speed. This would create a problem for infants as they may not be able to time accurately the loom's time-to-collision with changing approach loom speed.

A more sophisticated strategy is based on showing brain responses at a specific time before the loom makes a virtual collision (Fig 4iii). By holding time-to-collision constant as the loom's acceleration decreases, (g) the visual loom's velocity decreases (h) and the angle/pitch increases (i).

Every time a looming related peak occurred, the peak's corresponding values – angle, velocity, and time-to-collision for VEP peaks; and pitch, velocity, and time-to-collision for AEP peaks were recorded. To determine which variable infants kept constant, the three

20

variables for each stimulus modality were compared using their index of dispersion values. An index of dispersion measures how much a set of variables varies from its central tendency. This index of dispersion is calculated by dividing the standard deviation by the mean for each variable across loom speeds. It is assumed that the variable with the lowest index of dispersion was the infant's preferred variable used in timing their looming-related brain response.

2.5.2 VEP and AEP analysis at the electrode level

An average of all looming-related peaks observed for each of the two stimulus modalities on all trials was obtained for each infant. This average represented AEPs and VEPs for all trials in which a looming-related peak was detected. These individual averages were then interpolated to the 81-standard channel electrode. The amplitudes of peaks at channels Oz and Cz for each of the three loom speeds were recorded from these average files for each infant. These amplitude values were then compared with one another using ANOVA statistics. Individual averages of each infant were combined to form a grand average. Amplitudes of peaks at channels Oz and Cz were recorded.

3. RESULTS

3.1. VEP and AEP Responses

The channels Oz and Cz were selected as the sites for maximum activation in response to looming visual and auditory stimuli, respectively. Infants in this experiment provided a total of 183 trials where both auditory (AEP) and visual looming-related evoked potentials (VEP) co-occurred on the same trial. In total, infants provided 413 trials in which any one of the two stimuli provided a looming-related peak. On average, each infant provided 29 trials where any one of the looming-related peaks was observed and 13 trials where both Oz and Cz looming-related peaks were observed. Infants contributed more looming-related VEP peaks compared to looming-related AEP peaks to the final analysis. Looming-related peaks were more or less evenly distributed among the three loom speeds.

The averaged VEP and AEP peak responses for the three loom speeds were calculated from all the trials on which a looming-related response peak was identified. For the 2s loom, averaged looming VEP peak occurred at 0.91s (SD = 0.13) to contact, while averaged AEP peak response was observed at 1.03s (SD = 0.19) to contact. For the 3s loom, averaged VEP was observed at 1.13s (SD = 0.17) before contact, while averaged AEP was observed at 1.27s (SD = 0.01) before contact. For the 4s loom, averaged VEP occurred at 1.18s (SD = 0.15) before contact, while averaged AEP was observed at 1.34s (SD = 0.20) before contact (see Fig 5).

A repeated measures ANOVA 2 (stimulus modality: visual, auditory) x 3 (loom: 2s, 3s, 4s) was performed on the averaged looming-related peaks obtained from trials where any one of the two stimulus modalities provided a response peak. This showed a main effect of stimulus modality, $F (1,13) = 20.05$, $p < 0.005$, indicating that averaged looming-related VEP peaks occurred closer to contact in the looming sequence than averaged looming-related AEP peaks (see Fig. 5).

A main effect of loom was also found, $F (2, 26) = 22.18$, $p < 0.0001$, indicating that infants showed looming-related responses significantly closer to contact for the fastest 2s loom (-0.968s, SD = 0.169) compared to the 3s (-1.200s, SD = 0.153) and 4s (-1.257s, SD = 0.194) looms (see Fig 5).
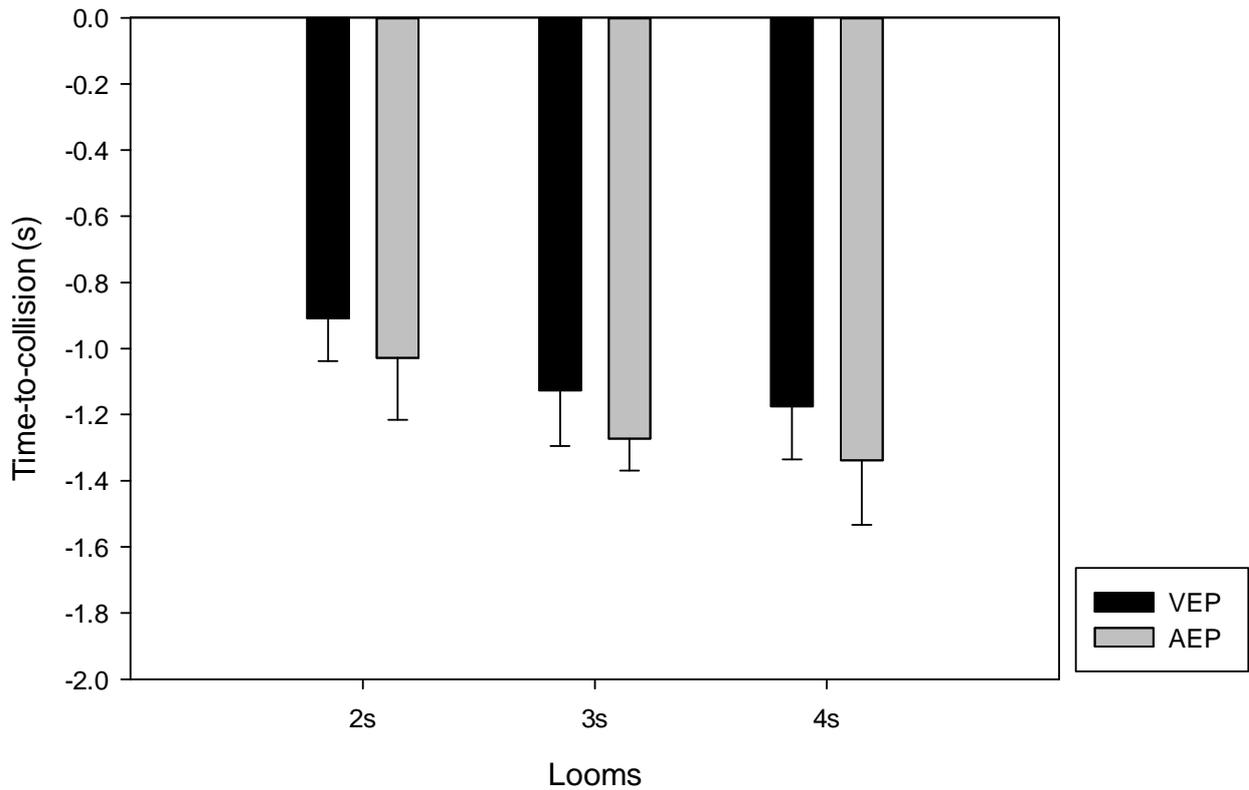
Figure 5. Averaged looming-related peak activation (with SD bars) of the three looms for both visual (VEP) and auditory (AEP) stimulus modalities. For all three looms, averaged VEP peak activation was observed closer to contact than averaged AEP peak activation. In addition, looming-related peaks for the fast 2s looms occurred closer to contact than for the slower looms.

3.2. Duration of VEP and AEP activation

The duration of VEP and AEP peak activations was investigated. The duration of activation was defined as the difference in time between the start and end of a looming-related peak, i.e, VEP duration = $VEP_{start} - VEP_{end}$, (see Figure 3). Averaged VEP duration was 0.279s (SD = 0.05), while averaged duration for AEP peak activation was 0.283s (SD = 0.06). A repeated measures ANOVA, 2 (stimulus modality: visual, auditory) x 3 (loom: 2s, 3s, 4s) was performed on the averaged looming-related peak durations. No significant main effect of stimulus modality on peak duration was found $F_{(1, 13)} = 0.223$, *ns*, indicating that VEP and AEP peak durations were about the same. No significant main effect of loom on peak duration was found, nor an interaction effect.

Taken together, these findings show that averaged peak AEP activation appeared earlier than averaged peak VEP activation in the looming sequence. This activation occurred closer to virtual contact in the faster 2s loom than in the 3s and 4s looms. There were, however, no differences in peak duration for AEP and VEP activations.

3.3 Timing strategies.

The timing strategies used by infants to time their brain responses to the audiovisual looming stimulus were investigated. When paying attention to a looming audiovisual stimulus on a direct collision course, infants use different information variables to time their responses. For the visual looming stimulus, infants may depend upon the loom's visual angle, its velocity, or the time-to-collision, while for the auditory looming stimulus, the loom's pitch, its velocity, or time-to-collision may be used. These variables were then compared with one another, using an index of dispersion analysis (ID), where the variable with the least variability in each information domain was assumed to be the infants' preferred timing strategy (Kayed, Farstad, & van der Meer, 2008; Kayed & van der Meer, 2000; 2007; van der Meer et al., 2013).

Infants	VEP			AEP		
	Angle	Velocity	Time	Pitch	Velocity	Time
BG	*0.266*	0.278	-0.273	*0.186*	0.264	-0.293
MG	0.294	0.236	*-0.215*	*0.191*	0.281	-0.293
MJ	*0.224*	0.281	-0.324	*0.168*	0.235	-0.221
ER	*0.205*	0.249	-0.235	*0.203*	0.279	-0.277
MR	0.355	*0.253*	-0.283	*0.211*	0.377	-0.314
SV	*0.208*	0.289	-0.335	*0.172*	0.239	-0.242
VG	*0.169*	0.307	-0.337	*0.139*	0.316	-0.306
OL	*0.212*	0.237	-0.299	*0.232*	0.322	-0.330
SN	0.332	*0.286*	-0.304	*0.221*	0.293	-0.311
AJ	*0.258*	0.292	-0.344	*0.152*	0.357	-0.340
AL	*0.260*	0.329	-0.383	*0.167*	0.285	-0.219
BR	0.259	0.229	*-0.225*	*0.178*	0.276	-0.326
TA	0.273	0.243	*-0.218*	0.216	*0.144*	-0.180
LV	0.257	*0.247*	-0.276	*0.153*	0.249	-0.288

Table 1. Index of dispersion (ID) values showing the information variables infants used to time their brain responses to the audiovisual looms. The timing strategy infants used is highlighted in bold (the variable with the lowest ID in each information domain). Most infants used the visual loom's angle, and the corresponding pitch of the auditory loom to time their looming-related brain responses.

In each stimulus modality, the lowest ID value of the three timing strategies was assumed to be the variable being kept constant.

From Table 1, it can be seen that eight infants used the visual loom's angle, three used the loom's velocity, and three used time-to-collision to time their looming-related VEPs. Thirteen infants used the auditory loom's pitch, while only one infant used the auditory loom's velocity to time their looming-related AEPs. This one infant, TA, used time-to-collision (time strategy) to time his looming-related VEPs in the visual domain. No infant in this study used a strategy based on time in timing their brain responses to the auditory looms. Using a strategy based on time would mean infants would show responses to the loom at a relatively fixed time before it would make a virtual contact. This strategy would not be influenced by the velocity of the approaching loom, meaning infants' responses would be less prone to errors.

All eight infants who used an angle strategy in timing their looming-related VEPs also used

the pitch strategy in timing their looming-related AEPs. Infants used time strategy in the visual but not auditory domain. Three infants used the visual loom's time-to-collision to time their looming-related VEPs while using the pitch and velocity of the auditory loom to time looming-related AEPs.

3.4 VEP and AEP amplitudes

An average of looming-related VEP and AEP peaks of all three looms for each infant was obtained by averaging only marked peaks which were identified as looming-related on single trials. These averages were then interpolated to standard 81 channel electrodes for each infant. The amplitudes of peaks at channels Oz and Cz for each of the three looms were recorded from each of these averages. The averages of all the 14 infants were then combined to form a grand average.

A repeated measures ANOVA, 2 (stimulus modality: visual, auditory) x 3 (looms: 2s, 3s, 4s) was performed on the recorded amplitudes at channels Oz and Cz for all infants. This ANOVA showed a main effect of stimulus, $F (1, 13) = 8.459$, $p < 0.01$, indicating that amplitudes for looming-related VEP peaks obtained at channel Oz were significantly higher than those of AEP peaks at channel Cz (see Figure 6). No main effect of loom speed on amplitude of looming-related VEP and AEP peaks was observed, neither was there any interaction effect.
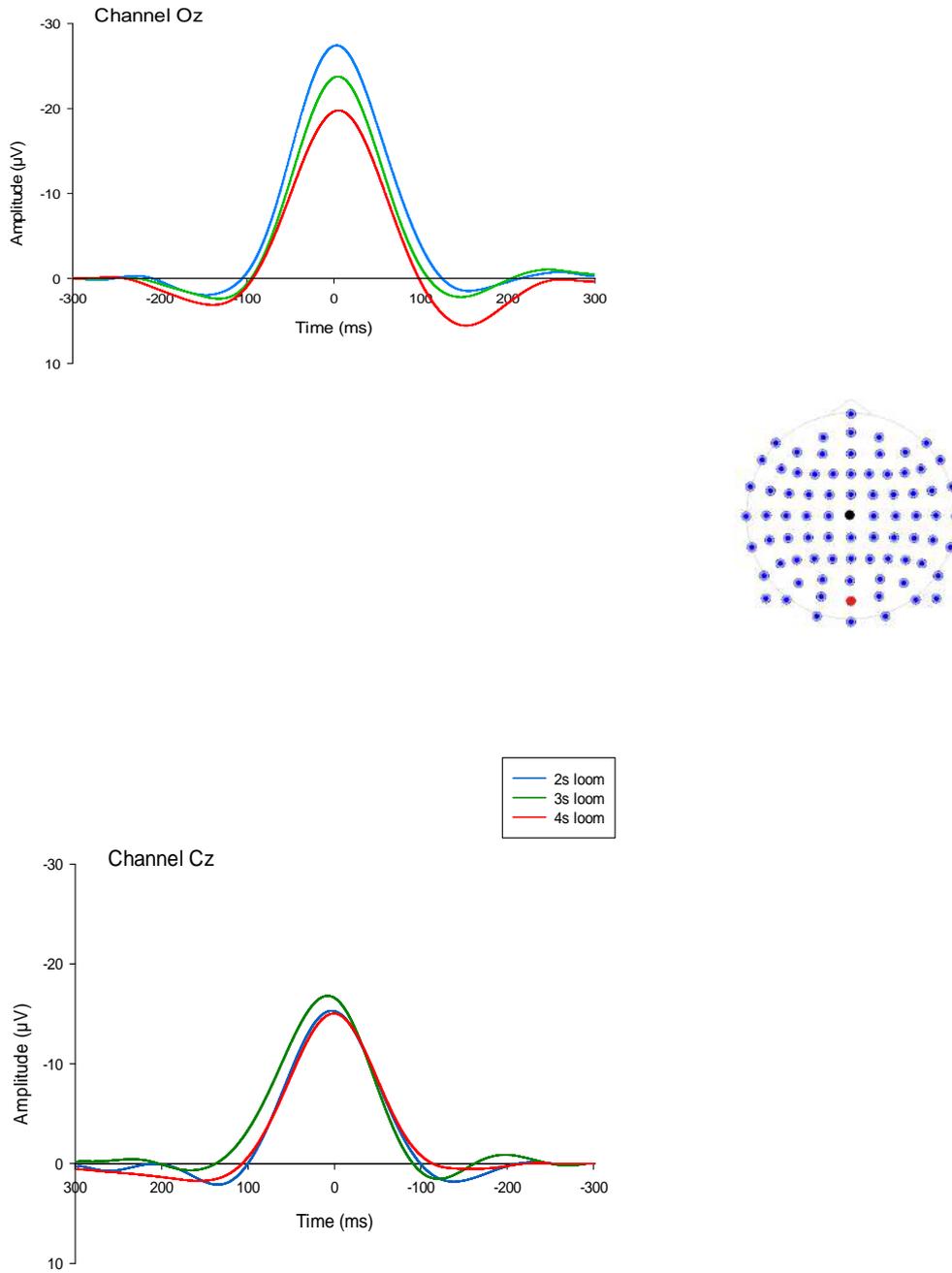
*Figure 6. Grand average of looming-related VEP and AEP peaks observed at Channels Oz and Cz, respectively. The head drawing, (nose up) shows the scalp localization of the 81 standard electrodes. The two channels of interest: Oz (**red**) and Cz (**black**) are indicated with filled colored circles. The VEP peak observed at Oz had higher amplitude compared to the AEP peak observed at Cz for all three loom conditions.*

4. DISCUSSION

This study investigated infants' cortical responses to an audiovisual looming stimulus using high-density EEG. Looming-related AEP and VEPs were recorded as a measure of cortical responses to audiovisual looms approaching the infant under three different accelerations. The timing strategies infants used to time their looming-related brain responses were investigated. The duration of loom processing, as well as the amplitudes of VEP and AEP peaks for all trials with a looming-related peak were also investigated.

4.1 VEP and AEP responses

Infants on average showed looming-related AEP peaks earlier in the looming sequence compared to looming-related VEP peaks. These looming-related AEP peaks, on average occurred 140 ms earlier in the looming sequence compared to the averaged VEP peaks across all the three loom speeds. The relatively late looming-related VEPs shown by infants could represent their active attention shown to the visual loom over that of the auditory loom (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990). The sudden appearance of a rotating colorful ball on a white projector screen in a dark experimental room was enough to dominate the attention given to the auditory loom. This spatially huge influence of the visual loom on infants' attention was seen in their late looming-related VEP responses, as they tried to concentrate on timing the collision of the visual loom over that of the auditory loom. Attention has a bidirectional effect on the perception of multisensory information, and depending on the particular sensory modality and task, one component of the multisensory stimuli will always produce a faster response over the other (Talsma, Senkowski, Soto-Faraco, & Woldorff, 2010). This result confirms studies in ventriloquism effect (Recanzone, 2009) and audiovisual integration of speech perception (Navarra, Alsius, Soto-Faraco, & Spence, 2010), that have all reported an enhancement of the responses in the sensory system with the highest acuity with respect to the task being performed. Infants' only task in this experiment was to keep their fixation on the white screen placed a few centimeters away from them, which in itself could benefit the attentive processes given to the visual loom over that of the auditory. Visual information in general has long been known to possess a higher spatial resolution than auditory information, and recruits attention exogenously in multisensory tasks that requires spatial fixation (Spence & Driver, 1997).

Furthermore, infants' attention was also locked onto the visual loom at the start of the experiment partly due to the enhancing capacity of the auditory loom (Leo et al., 2011; Lewis & Noppeney, 2010; Posner, Nissen, & Klein, 1976; Vroomen & de Gelder, 2000). When in synchrony with visual loom, the auditory loom enhances the perception of visual motion in the primary and secondary visual and auditory cortices (Lewis & Noppeney, 2010). In the visual cortical areas processing motion, these attentional processes of the auditory loom can enhance the firing patterns of area MT neurons, which could lead to a more accurate timing of the loom's collision (Treue & Maunsell, 1996). Zhou et al. (2007) found adult subjects to rely mostly on the visual as opposed to the auditory stimuli in judging the time-to-collision of an audiovisual loom. The auditory loom, according to the authors, was only important in specifying the distance of the approaching visual loom, thereby serving an enhancing role. As the experiment progressed, this active attention given to the visual loom might have become a little difficult to disengage from (Posner & Petersen, 1990; Turatto, Benso, Galfano, & Umilta, 2002) causing infants to show delayed responses to the visual loom compared to the auditory loom. Showing delayed as opposed to early responses to a looming stimulus has been known to improve the estimation of the time-to-collision, as the loom's variables that could be used to compute the time-to-collision would have reached their highest levels before the loom makes a virtual collision (Kayed & van der Meer, 2000; 2007; Lee, 1976).

Infants' early brain responses for the auditory loom could mean that they were perceiving the rising pitch of the sound as its loudness (Ghazanfar & Maier, 2009; Neuhoff et al., 1999) while trying to take precaution in avoiding a virtual collision with the looming sound by underestimating the loom's time-to-collision (Neuhoff, 1998, 2001; Rosenblum, Wuestefeld, & Saldana, 1993). This underestimation of time-to-collision of the auditory loom could be an evolutionary adaptive bias for survival (Ghazanfar & Maier, 2009; Ghazanfar et al., 2002; Neuhoff, 2001; Popper & Fay, 1997). The higher underestimation of the auditory loom's time-to-collision compared to that of the visual loom confirms a recent behavioral study of motion perception, where it was found that adult subjects underestimated the time to contact of the auditory loom in a 3D film on about 93% of the trials, compared to 78% underestimation for the visual loom (Wilkie & Stockman, 2012). The response underestimation time (time-to-collision) in their study was the time difference between the subject's response time and a defined 'peak' time. These adult subjects' responses, contrasted with infants in this study, shows that the evolutionary adaption of underestimating the loom's time-to-collision does remain fairly constant through the lifespan. In fact, our auditory

perceptual systems function not to provide an accurate detection of sound localization but rather to provide an input into our perceptual models of the environment, an advantage that increases our chances of survival (Popper & Fay, 1997).

Showing an earlier time-to-collision brain responses for the auditory loom could also be infants' perception of urgency, as the pitch of the loom increased through the looming sequence (Gordon et al., 2013). Higher pitch sounds possess a behaviorally relevant alerting property that recruits our visual perceptual system by directing our gaze towards the direction of the sound (Ghazanfar & Maier, 2009; Guski, 1992). According Guski (1992) the role of the auditory system in a multimodal looming perception is to direct the visual system to the looming danger, acting as a warning system.

4.2 Timing strategies

Infants in this study were mostly using the less sophisticated timing strategies to time their responses to the looming audiovisual stimulus. In timing the visual loom's collision, infants mostly used the visual angle and velocity - less sophisticated variables. Not all infants in this experiment were using these less sophisticated strategies to time their VEPs though. Three infants used the visual loom's time-to-collision to time their looming-related VEP responses. In timing their looming-related AEP responses, all but one infant used the auditory loom's pitch. All infants using an angle strategy in the visual domain used the auditory loom's pitch, the analogous timing strategy in the auditory domain to time their AEP responses.

The visual angle and pitch strategies pose a challenge to infants as they are the least accurate of the timing strategies investigated. As the audiovisual loom approaches on a collision course, the angle subtended by the edges of the visual loom, and the pitch of the auditory loom increase nearly exponentially. When responses are based on the angle, and pitch of the audiovisual loom, infants would overestimate the audiovisual loom's time-to-collision (Kayed & van der Meer, 2000) as approach speed increases, or underestimate as the speed decreases (Gordon et al., 2013). This dependence of the visual angle and pitch strategies on the approach velocity and acceleration means infants' responses would vary with varying loom speeds. As was expected, the fastest approach speed (2s loom) produced VEP and AEP peak responses closer to contact compared to the 3s and 4s looms.

This results are in line with previous behavioral (Kayed & van der Meer, 2000; 2007) and ERP studies (van der Meer et al., 2013) that found infants within 5 and 6 months using the visual angle or just about transiting to the more sophisticated time strategy, based on the visual loom's time-to-collision. In their longitudinal study, Kayed and van der Meer (2007) showed that infants adopt a more accurate timing strategy as a function of their age and locomotion experience. If locomotion and maturity improves the accuracy of timing, then infants younger than the ones used in their study should mostly be using the less sophisticated visual angle, pitch and velocity strategies. This was confirmed in this study. Eleven of the fourteen infants used the less sophisticated visual angle and velocity strategies, while only three used the more sophisticated time strategy in timing their VEP responses. In timing their AEP responses, all fourteen infants used the less sophisticated timing strategies – pitch (13 infants) and velocity (1 infant) of the auditory loom.

Infants' functional brain development occurs rapidly within the first year of birth and all throughout childhood. However, within the first 4 months of life most of the synaptic activity is at its rudimentary form with neural pathways still in the process of further differentiation and specialization (Johnson, 2000). Synapses in these pathways are not yet specialized, as the pruning process has just begun (Jacobs, 1999) and total efficiency of the synaptic process is relatively low, compared to older infants and adults (Johnson & Shrager, 1996). This means that neural pathways, particularly those processing the perception of motion, will be greatly disadvantaged in their accuracy to estimate the time-to-collision of the audiovisual loom. Apart from the synaptic activities, the amount of cortical white matter due to myelination of the axons of neurons could also account for the results observed. The myelination of the axons of neurons speeds up the conductivity velocity of signal transmission along the axon which is necessary for communication between neurons in the neural pathways (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; Webb, Long, & Nelson, 2005). Between 3 and 4 months, neuronal maturation due to myelination is rapidly on-going but not yet ready for more complex computations (Grieve, Emerson, Fifer, Isler, & Stark, 2003; Johnson, 2000).

The inexperience of these young infants in locomotive activities (van der Meer, Fallet, & van der Weel, 2008; van der Weel & van der Meer, 2009) could also account for their use of less sophisticated timing strategies. With an average age of 13 weeks, all infants in this study had less than three episodes of rolling over their stomachs, and in general very little locomotion experience compared to infants in the Kayed and van der Meer (2000;2007) experiments, who

were all well above 20 weeks of age. Locomotion improves the perceptual abilities of infants (Adolph, 1997; Anderson et al., 2001; Campos et al., 2000), and it is perhaps the single most important physical activity that shapes the perception of looming in infants within the first year of life (van der Weel & van der Meer, 2009). The exploration of the environment as infants crawl about, improves rapidly their processing of optic flow patterns (Gilmore, Baker, & Grobman, 2004) which they generate by their self-locomotion (Higgins, Campos, & Kermoian, 1996). These optic flow patterns are vital for the computation of time-to-collision perceptions in the visual cortex (Regan & Vincent, 1995).

Although most infants were using the less sophisticated visual angle and velocity strategies to time their looming-related VEPs, three out of the fourteen infants had already developed a strategy based on the loom's time-to-collision. These infants appeared to be keeping the time-to-collision constant relative to the visual loom's angle and velocity. These 'time infants' may have developed this sophisticated timing strategy earlier than their peers due to their extensive use of the visual system (Johnson, 2000; Lee & Aronson, 1974). The over-reliance on the visual system may have biased this pathway over that of the auditory, making these infants show a sophisticated timing strategy with respect to the visual loom, while still using the less sophisticated strategies in timing their looming-related AEPs. This asymmetry in the perception of audiovisual loom's time-to-collision has also been reported in adult subjects, where accuracy in judging the visual loom's time-to-collision was higher than that of the auditory loom (Zhou et al., 2007).

4.3 Loom speed and duration

Infants on average were showing responses significantly closer to contact for the faster looms. This could mean these infants were using the visual angle/pitch and velocity of the loom to time their brain responses. These timing strategies are dependent on the speed of the loom. As the loom speed increases, the time it takes for the visual angle and pitch of the audiovisual loom to reach their highest levels decrease, causing infants to show looming-related brain responses closer to contact. With slower loom speeds, the time it takes the visual angle and pitch to reach their highest levels would increase, thus infants would be making looming-related brain responses earlier in the looming sequence compared to when the loom was fast. Intuitively, delaying responses for the faster looms would seem rather odd, as an early

underestimation of the time-to-collision of a fast moving object should be the perfect precaution. As the loom speed became slower, response underestimation also increased (Schiff & Oldak, 1990). This higher underestimation as loom speed became slower has been reported to affect accuracy of collision judgments (McLeod & Ross, 1983; Rosenblum et al., 1993; Schiff & Detwiler, 1979). According to McLeod and Ross (1983) responses made when time-to-collision is more than a few seconds is less informative in judging the collision of the object. Schiff and Oldak (1990) found a higher underestimation for the auditory loom compared to the visual loom when the approach duration of the loom exceeded four seconds.

The duration of loom processing, taken as the difference in time of the start and end of the looming-related peak (van der Meer et al., 2013) is indicative of the speed and efficiency of the cortical regions processing the looming stimuli (Johnson, 2000). This study did not find any significant differences between the duration of AEP and VEP looming-related peaks, nor were there any differences in peak duration of the three loom speeds. Though the looming-related AEPs occurred on average earlier than the VEPs in the looming sequence, their speed of processing was not significantly different. However, compared with the 5/6 month old infants in the van der Meer et al. (2013) study who recorded an average VEP peak duration of 0.18s, infants in this experiment had an average VEP peak duration of 0.28s. This higher averaged VEP peak duration by a younger age group (3/4 months) indicates the relatively lower processing speed and inefficiency at this age. According to Johnson (2000), cortical areas processing looming stimuli become specialized as infants continue to interact with specific stimuli which activate these particular brain regions.

4.4 Amplitudes at Channels Oz and Cz

Infants on average showed significantly higher amplitudes for VEP activation compared to AEP peak activation for all three loom speeds. ERP amplitudes represent the amount of active neurons firing in synchrony (Pfurtscheller & da Silva, 1999). The higher VEP peak amplitudes observed at the visual channels could mean more cortical neurons were firing in synchrony in the visual cortex compared to the cortical auditory areas. These larger number of active neurons firing in synchrony in the visual cortex also suggest larger unspecialized cortical pathways (Huttenlocher, 1990) that are involved in the processing of visual motion, while the lower amplitudes observed in the auditory cortex could mean the relatively fewer

population of active neurons that are responding to auditory motion became briefly desynchronized (Elul, 1971) in the course of processing the loom. Large cortical synchronization has been previously shown to underline the integration of bimodal perception of audiovisual stimuli (Hipp, Engel, & Siegel, 2011; Maier, Chandrasekaran, & Ghazanfar, 2008), which means the larger scale cortical synchronization in the visual cortex improves the perception of the audiovisual loom in the visual areas compared to that of the auditory cortex. Higher amplitudes observed in the visual cortex could be also be due to infant's active attention to the visual loom which resulted in the recruitment of more visual cortical pathways (Johnson, 1990).

4.5 Conclusion

The present findings have shown infants to respond significantly earlier in the looming sequence to the auditory loom than the visual loom. Infants' early looming-related AEPs were attributed to an evolutionary bias which prioritizes an earlier auditory loom response over a visual loom response in an audiovisual looming perception. The relatively late looming-related VEPs observed in the looming sequence were attributed to the visual loom's huge spatial resolution over that of the auditory loom, which recruited infants' spatial attention. Infants in this study were found to mostly use the visual angle/pitch and velocity strategies in timing their looming-related brain responses. When the amplitudes of looming-related peaks at occipital channel Oz and auditory channel Cz were compared, Oz channels were found to be significantly higher in magnitude for all three loom speeds. This was attributed to larger amounts of neurons in less differentiated visual cortical pathways being activated compared to that of the auditory cortical pathways. Future research could investigate how infant brain response asymmetry and timing strategies change as a function of their age.

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