

# **Multisensory integration by audiovisual looming in infants: A longitudinal study with high density EEG**

by

**Farzana Islam**

Developmental Neuroscience Laboratory

Department of Psychology

Norwegian University of Science and Technology (NTNU)

Trondheim, Norway

## **Table of content**

Acknowledgement	3
Abstract	4
1. Introduction	5
2. Method	10
2.1 Participants	10
2.2 Apparatus	10
2.3 Stimuli	13
2.4 Procedure	14
2.5 Data analysis	14
2.5.1 VEP and AEP analysis at the electrode level	18
3. Result	19
3.1 VEP and AEP responses	19
3.2 VEP and AEP amplitudes	22
4. Discussion	24
4.1 VEP and AEP responses	24
4.2 Amplitudes at different channels	26
4.3 Conclusion	29
5. References	31

## **Acknowledgments**

The research presented in this Master's thesis was carried out at the Developmental Neuroscience Laboratory at the Norwegian University of Science and Technology (NTNU).

I would like to thank my supervisor and co-supervisor, Audrey van der Meer and Ruud van der Weel for their valuable assistance, constructive discussion, and intellectual support during the work. I would also like to thank Magnus Holth, Seth Agyei and Desmond Agboada for technical support and fruitful discussions during this work. I am thankful to my family, especially my parents for their love and prayers, my husband Mohammad Sohrab Hossain for moral support in tough and stressful conditions and my kid Shayaan for his love and support.

Last but not least, I would like to thank all infants and their parents, without whom this study would not have been possible.

Farzana Islam

Trondheim, January 2015.

## **Abstract**

Infants' cortical electrical activity as a function of audiovisual looming perception was investigated using high-density electroencephalogram (EEG). Prospective control when responding to a looming object approaching on a direct collision course was studied longitudinally in infants aged 3/4 and 9/10 months. Different characteristics of peak VEP and AEP activity from infants' brain electrical recordings were explored and compared between the infants at these different ages. The aim of this study was to find evidence for infant brain electrical responses to an audiovisual looming stimulus approaching the infant under three different accelerations. The results showed that there were differences in peak VEP and AEP activations with age. At the age of 3/4 months, infants showed peak VEP and AEP activation earlier in the looming sequence compared to when they were 9/10 months of age. AEP peaks occurred before VEP peaks in the looming sequence at both ages. Further, it was found that peak VEP activation in the investigated Oz and Pz areas propagated from the O area to the P area, indicating that the highest activation was observed in the O area at the age of 3/4 months, whereas the P area showed the highest activation when the infants were 9/10 months old. Furthermore, amplitude activity occurring in the channels Cz and C3 showed differences in amplitude activity referring to an increased auditory area when infants were 9/10 months of age. The results suggest an evolved capacity to integrate multisensory looming objects. The decrease in processing time together with a peak VEP and AEP activation closer to the loom's time-to-collision indicate a developmental trend in infants' prediction of an object's time-to-collision. Moreover, AEP occurring before VEP in the looming sequence suggested an enhancement in audiovisual looming perception. Amplitude activity at different channel shed light on audiovisual cortical pathways and indicated cortical pathways involved in multisensory looming perception.

# 1. Introduction

Animals have to avoid danger from the surrounding world in order to survive. Humans potentially face daily threats such as suddenly approaching objects that they must adequately respond to in order to avoid accidents. A successful and quick detection of such potential threats is vital when preparing a proper defensive motor response (Bach et al., 2009). Such a defensive motor response largely involves perception of both auditory and visual information from the surroundings. This is referred to as multimodal perception (Alais, Newell, & Mamassian, 2010). Humans pick up different information using different senses. Information from each sense creates a qualitatively different impression of objects and events in the environment that may further evoke impressions from other sensory modalities. For example, walking towards an observer can be perceived using sight combined with the sound impression of approaching footsteps. In such instances, an observer combines both visual and auditory signals into a unified multisensory percept (Alink et al., 2012).

It is evident from several studies that human infants (Bahrick, Lickliter, & Flom, 2004; Bahrick & Lickliter, 2000; Bahrick et al., 2004; Lewkowicz & Kraebel, 2004), human adults (Hershenson, 1962; Stein & Meredith, 1993) and animals (Partan & Marler, 1999; Rowe, 1999) can encode multimodal perception which facilitates attention, learning and discriminations about an object. It is also found that a multisensory sequence specified by audio and visual attributes enhances a young infant's response due to multisensory redundancy. Therefore, in order to gain better understanding of development sequences of perception and learning, more studies on infant responses to multisensory event sequences are needed (Lewkowicz, 2008).

Looming is referred to as a motion which can provide information by rapid symmetrical growth on the human or animal retina about an object accelerating towards the eye (Kayed & van der Meer, 2007; Maier, Neuhoff, Logothetis, & Ghazanfar, 2004a; Schiff, Caviness, & Gibson, 1962). Though the retinal image of an object contains a lot of information about motion perception, it may not contain all the information about an object's actual size. Moreover, it has been suggested that multisensory processing could facilitate information about the actual size or distance of an object by increasing the brightness, duration, and visibility of an image while the sound has an enhancing capacity on visual perception (Jaekl, Soto-Faraco, & Harris, 2012; Shams & Kim, 2010).

In an magnetoencephalography (MEG) study, Holliday & Meese(2005)found that different brain regions are responsible for responding to a visual looming stimulus which evokes larger responses compared to other motion sequences in human adults. Moreover, retinotopic mapping in functional magnetic resonance imaging (fMRI) study of the human brain suggested that primary as well as secondary visual cortex was responsible for responding to looming stimuli and involved in the critical processing of looming stimuli in humans (Dougherty et al., 2003). When visual information travels from lateral geniculate nucleus (LGN) to primary visual cortex (V1),the information is divided into two interconnected pathways named the dorsal and ventral stream.

The dorsal stream comprises of V1,V2 and V5 or middle temporal area (MT+) which is involved in the processing of motion, while the ventral stream is responsible for object recognition (Braddick, Birtles, Wattam-Bell, & Atkinson, 2005; Dougherty et al., 2003; Holliday & Meese, 2005). However, it has been recently found that different brain areas in addition to cortical regions are also involved in motion perception and can respond to looming stimuli. Those areas are suggested to form a network consisting of a warning system (tectopulvinar), a preparatory system (motor cortex), and an advanced computation system (insula) in response to looming (Billington, Wilkie, Field, & Wann, 2011).

Research has already established that most of the neurons of auditory cortex are found in the superior portion of temporal lobe, specifically on the superior surface of the superior temporal gyrus (STG) which is most prominent in humans but not in other animals (Hackett, Preuss, & Kaas, 2001; Tramo, Cariani, Koh, Makris, & Braida, 2005). Auditory afferent information is transmitted by the neurons of medial geniculate nucleus (MGN) of the thalamus to STG. Moreover, these densely packed neurons are known as koniocortex found in STG area. One or more areas surrounding these koniocortical fields are called primary auditory area (A1) or core area which contains frequency selective neurons, receiving sensory information from ventral division of MGN. In addition to A1 area, there are some areas surrounding the A1 known as belt areas which also have frequency selective neurons and receive information from the ventral MGN, dorsal MGN, and other thalamic nuclei (Tramo et al., 2005). Neurons in STG make synapses with other STG neurons and send information to other cortical areas like temporal, frontal, and parietal cortical areas. Therefore, STG is referred to as multimodal cortex where neurons are able to respond to two or more sensory modalities (Hackett et al., 2001) and maintain while reciprocal connections (Tramo et al., 2005).

In the field of auditory research, over 40 years of studies on adults and children showed that pitch is an important factor which relates a number of cross-modal correspondences (Evans & Treisman, 2010). Pitch refers to subjective properties of a sound's fundamental frequency where the audible frequency range is around 20 Hz to 20 kHz (Bendor & Wang, 2005; Tramo et al., 2005). Pitch depends on both the temporal regularity and average repetition rate of the acoustic waveform. This means different sounds sharing the same frequency will show the same pitch (Bendor & Wang, 2005). So, different frequency can also be used as a cue to detect approaching sound sources (Rosenblum et al., 1987). There is a close relationship between rising or falling frequency and perception of an increase or decrease in loudness of sound when sound intensity is constant (Neuhoff, McBeath, & Wanzie, 1999). Humans show a perceptual bias toward rising frequency as opposed to falling frequency when rising frequency affects loudness and thereby, a looming sound. However, a pitch of a moving sound can be perceived as rising of pitches while approaching, and where velocity is constant (Neuhoff & McBeath, 1996; Ghazanfar & Maier, 2009).

The brain can combine information from different sense modalities which can modulate the speed and accuracy and thus enhance the detection of objects and events (Evans & Treisman, 2010). It was found that visual perception became more precise when it was present with high pitch of sound. Moreover, a bright surface congruent with higher pitch showed faster response. However, the dark surface with a low pitch also showed faster response (Evans & Treisman, 2010).

Behavioral studies have reported that young infants (Lewkowicz, 2008) and monkeys (Maier, Neuhoff, Logothetis, & Ghazanfar, 2004b) are selective to integrate multisensory looming signals, and can discriminate between looming and receding signals. Multisensory looming signals have also been found to gain behavioral benefit by using short time in target detection compared to a receding or static signal. Moreover, in multisensory looming signals, auditory looming signals induced enhancement on visual looming perception and showed behavioral benefit on looming perception while a receding or static signal did not give any enhancement (Cappe et al., 2009; Tyll et al., 2013). Research on infant looming perception has been investigated and discussed widely in the 1960's and 1970's where infants' defensive responses to looming stimuli was the main issue to understand. It was found that they could produce adaptive avoidance responses to both real and simulated looming cues (Bower, Broughton, & Moore, 1971; Schiff et al., 1962; Yonas, Pettersen, & Lockman, 1979). In 1962,

Schiff and his colleagues found that rhesus monkey responses to a rapidly expanding circular shadow where infant and adult rhesus monkeys produced persistent avoidance responses to looming compared to rapidly contracting shadows where they did not show any fear response to those looming stimuli (Schiff et al., 1962). The same experiment was also done with human infants and the same result was found (Ball & Tronick, 1971). Previous studies suggest that human listeners showed a perceptual bias for auditory looming and can underestimate the arrival time of a moving sound before the sound actually reach to the listeners (Rowe, 1999; Schiff & Oldak, 1990). Walker-Andrews & Lennon (1985) examined 5-month-old infants and found that infants preferred to respond to those stimuli where the visual and auditory looming were both present. These infants responded to looming sounds as well as receding sounds but the effect was selective when structured sound was present compared to noise. Maier and his colleagues (2004) have demonstrated that rhesus monkeys show a strong attentional bias to a visual looming stimulus when auditory stimulus was also present and were able to match the auditory looming with visual looming but not with the receding sound. They also found that monkeys have evolved the capacity to integrate bimodal looming signals. Moreover, superior temporal sulcus (STS) works as an area in the brain where multimodal perception takes place (Maier et al., 2004b). It was also found that in humans, STS is responsible for auditory looming signals compared to receding signals (Seifritz et al., 2002).

Infants' defensive responses to looming stimuli has been based on Gibson's (1966, 1979) insights, who argued that movement transforms the ambient optic array into a flow field that indicates the direction of motion and/or the imminence of collision. It has been well established that adults as well as infants will respond to collision with defensive blinking. In early infancy, blinking acts as one of the most reliable indicators of awareness to stimuli on a collision course to protect the eyes from any danger which is about to hit. Blinking occurring too early or too late does the infant no good. An earlier response would lead to underestimation of the loom's time to collision while a late response could result in injury. Therefore, to avoid the danger of a collision, an accurate estimate of the time to collision (TTC) of an approaching object has to be made (Lee, 1998a; Von Hofsten, 2004; Von Hofsten, 2007; Van Der Meer, Svantesson, & Van Der Weel, 2013). Using infants aged from 1 to 9 months old, Yonas and his colleagues (1977) conducted three experiments involving presentation of three types of shadow projection displays to investigate the developmental course to information for impending collision and how very young infants respond to an



approaching object by performing defensive blinks. They found that 1-2 months old infant did not show any evidence of avoidance behavior to impending collision while avoidance behavior to impending collision appeared from 4 months of age and was still present when infants became 9 months old. Van der Weel & Van der Meer(2009) conducted a high density electroencephalography (EEG) study testing 5-11 months old infants to investigate how infants process information about impending collision. Using tau coupling analysis, they established that older infants (10-11 months) could differentiate between three loom speeds whereas younger infants (5-7 months) could not. It was suggested that infants showed improved processing of looming information in the brain with increasing age.

The use of high-density EEG allows the investigation of how the human brain processes information available in our surroundings. The advances in the technology of recording event-related electrical potentials at the scalp make it possible to use this method with young infants (Tucker, 1993).

In our present study, high-density EEG measurements of infants' brain electrical activity are used to study infants' perception and processing of audiovisual looming that approaches them on a direct collision course. This method is used to detect electrical changes as groups of neurons fire within the cerebral cortex. The cerebral cortex is associated with higher cognitive functioning and is also thought to play a central role in the development of cognitive and perceptual development (Tucker, 1993). The aim of this study is to identify the neural underpinnings of audiovisual looming processing in infants with event-related EEG and the exact network of brain regions related to multisensory looming processing. Thus, the development of prospective control of the timing of looming-related brain responses under three different accelerations will be investigated through a longitudinal study by testing infants at the age of 3/4months and again at the age of 9/10 months.

## **2. Method**

### **2.1 Participants**

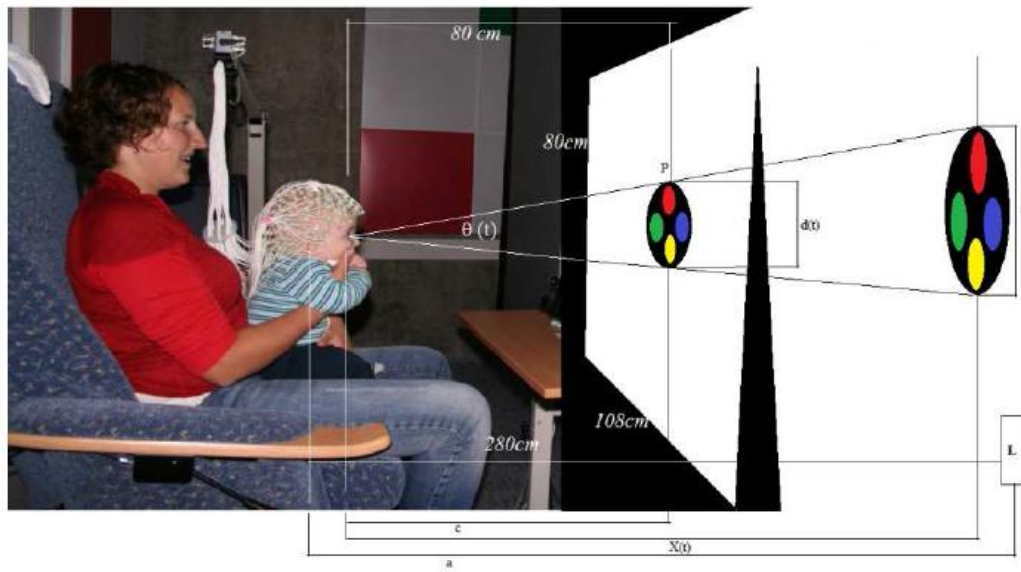
In this longitudinal study, a total of 14 babies were recruited from newspaper birth announcements to take part in the experiment. Students and other workers in the Department of Psychology at NTNU who recently had a baby were also invited to participate in the study. Those who were willing to participate were then enrolled in the study. We ensured that there was no severe injury during birth process or any brain damage, retinopathy of prematurity (ROP) and other perinatal issues requiring serious medical interventions which could lead to abnormal development. However, experimenters were unaware of the infants' neurological status, birth history and any events during the stay at the hospital.

Four of the babies out of 14 were excluded later. Three of the excluded babies were fussy during the experiment and lost interest in the stimulus early in the test session. All four excluded infants provided very few trials at the test session at 9/10 months, resulting in inadequate data for our analysis. Ten infants (6 boys) provided data for the final sample and were first tested at an age of 3/4 months, with a mean age of 14.39 weeks (SD = 1.76). The second test session was performed when the infants were about 9/10 months, with a mean age of 41.73 weeks (SD = 1.69). At the first session none of the infants had any crawling experience, but all of them had several weeks of crawling experience the second time they were tested. All infants showed typical development and none had any birth complications as determined by parental report.

### **2.2 Apparatus**

To record EEG activity, a high density 126 channel Geodesic Sensor Net (GSN) 200 (Tucker, 1993) was used. Across the head surface, arrays of 12g Ag/AgCl sponge sensors were evenly distributed. Net Station software on a Macintosh computer was used to record the amplified EEG signals, using a sampling rate of 500 Hz with a low pass filter of 100 Hz and 0.1 Hz high pass filter. To ensure an optimal signal-to-noise ratio, all electrode impedance was kept under 50 k $\Omega$  as recommended for the high-input-impedance EGI amplifiers (Ferree, Luu, Russell, & Tucker, 2001) and (Picton et al., 2000). Triggers about the onset and offset of the looming stimuli were communicated from E-Prime (Psychology Software Tools, Inc) onto the EEG recordings of infant brain electrical activity. For off-line analyses, data were stored on a hard disk.

The infant was placed with her face 80 cm away from the screen in a baby car seat. The visual looming stimulus was projected on a white screen (108 cm wide, 70.5 cm high) (see Figure 1A). During the experiment, the infant's attention and behavior was monitored with two digital cameras. Tobii x50 was used to record the gaze of both eyes of the infants by picking up corneal reflection.

**A****B**

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

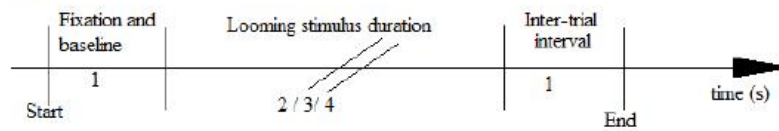
**C**

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  $-21.1 \text{ ms}^{-2}$ ,  $-9.4 \text{ ms}^{-2}$ ,  $-5.3 \text{ ms}^{-2}$  for 2, 3 and 4 seconds, respectively. The looming stimuli approached the infant as the image on the screen grew and the sound became high pitched, 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 visual 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 in 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 5° (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 131° (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 ( $-21.1\text{m/s}^2$ ), 3 seconds ( $-9.4\text{ m/s}^2$ ) or 4 seconds ( $-5.3\text{ m/s}^2$ ) respectively to complete the looming sequence – from appearing to making a virtual collision. In all these three looming conditions, the size of the 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 approached collision, a 'whoop' effect was clearly heard at its loudest level, at exactly the same time as the colored circle would make a virtual visual 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 simulated very well an approaching visual object with a sound component that became bigger and high pitched as it made a collision with the viewer.

## **2.4 Procedure**

Parent(s) arrived with their infant some time prior to the experiment. Parents of the babies participating in the experiment were given a brief introduction on electroencephalography and all their concerns satisfied before the testing session began. All parents also signed an informed consent before the commencement of the experiment and were free to withdraw at any point of the study. At the same time, one experimenter played with the baby so that the baby became familiar, relaxed, and settled down before the experiment. In the process, an assistant measured the infant's head circumference for the correct size selection of the GSN 200. To optimize electrical conductivity, the appropriate electrode net was soaked in a saline electrolyte. After that, the net was mounted on the infant's head while he/she was sitting on the parent's lap. The infant's attention was distracted from the net with the help of small sounding toys and soap bubbles. After mounting the net, the infant was positioned in front of the screen while sitting on the parent's lap (3/4-month-olds) or placed in a baby car seat (9/10-month-olds) with one parent present in the experimental room, to avoid any stress an absent parent may have on the infant. An assistant was also present in the experimental room to help the infant focus on the screen. The net was connected to the amplifier and the impedance of the electrodes was checked. The experimental room was separated by a transparent glass partition from a control room where two assistants controlled the computers necessary for the data acquisition. An experimental session started immediately after calibrating the infant's eye movement in virtual space to the Tobii x50. In both groups of infants, each infant completed between 40-80 trials. If an infant lost interest in the stimuli or started fussing, the experiment was ended. Each infant was tested individually and testing sessions lasted for about 20-30 minutes. Each session consisted of an optic flow, looming, and occlusion experiment. The looming experiment was usually conducted after the optic flow experiment, about 5 minutes into an experimental session.

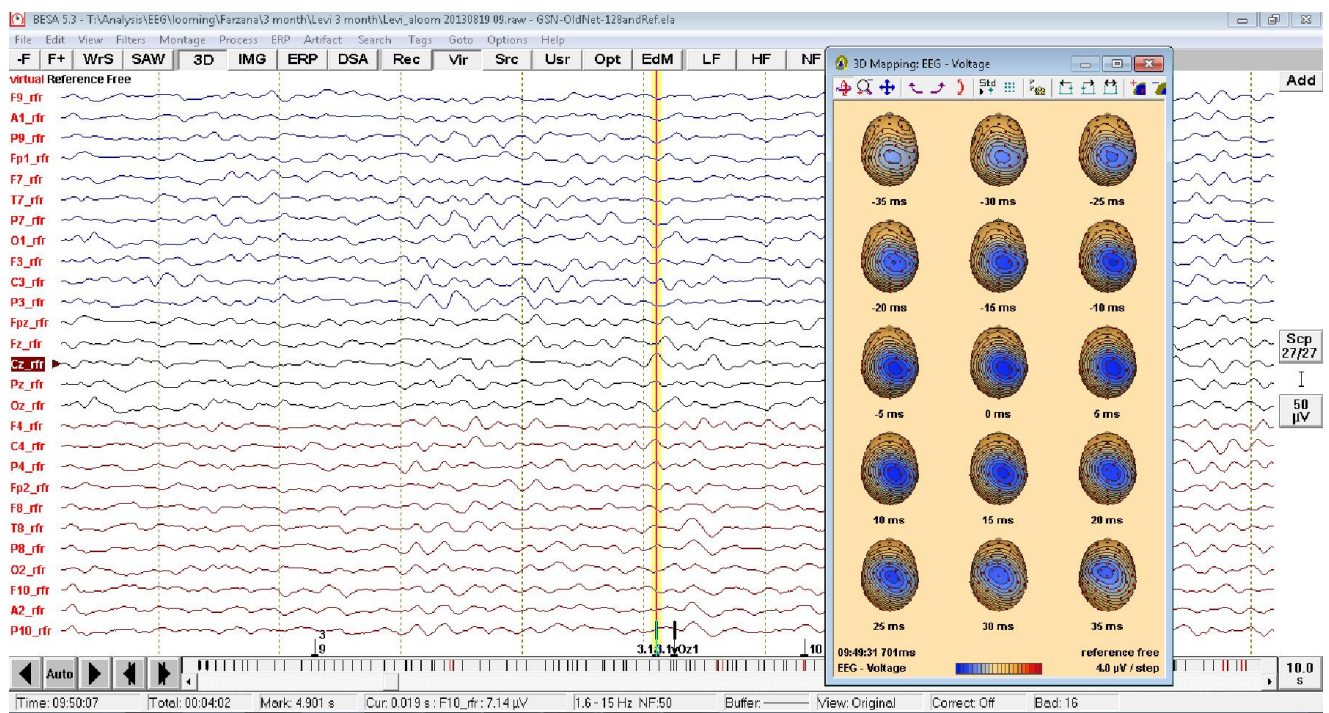
## **2.5 Data analysis**

Brain Electrical Source Analysis (BESA) research software version 5.3 was used to analyze the raw EEG data. Same methods were used to analyze the data for both testing sessions. Recordings were segmented with the Net Station software as an initial pre-processing step and then exported as raw files to BESA for further analyses. By visual inspection, bad channels and trials contaminated with artifacts from body/head movement were discarded. None of the participants had more than 10% of the channels defined as bad. Notch filter was set at 50 Hz

to remove 50 Hz lines interference from the recorded data. Low cut-off filter (high band pass) was set at 1.6 Hz to remove slow drift in the data while a high cut-off filter (low band pass) was set at 15Hz. A reference free montage showing EEG at 27 standard electrodes was used. 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 create 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. A VEP is the post synaptic firing pattern of neurons at a particular time in relation to a particular visual stimulus (Webb et al., 2005). It represents the changes in the brain's electrical activity at a high temporal resolution by using high density EEG. For typical looming related VEP responses, the main occipital and parietal electrodes were specifically observed for the three different looming conditions. Highly prominent VEP peaks were marked at electrode site Oz based on earlier studies investigating visual evoked potentials (Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002; van der Meer et al., 2012). These VEP peaks provided information about the looming-related brain activity at the selected brain region. To localize the effects of the audiovisual looming stimuli on brain responses, a trial-by-trial examination was performed. Prominent VEPs were marked at electrode Oz and Pz while AEPs were marked at electrode Cz and C3 (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. When a number of consecutive looming picks were seen in the same trial, it became difficult to select the right one. 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 occurred closer to contact, the peak showing the dense and well centered cortical activity in the 3D mapping was taken as the most functionally relevant looming-related peak. Trials where looming responses were not prominent or occurring too early or too late in the looming sequences were excluded from further analysis. Some trials which displayed a little

shifted area of activity (slightly downwards at occipital region) on the 3D map but showed a typical wave pattern were also selected as looming responses. These trials were confirmed from video and eye data showing that different area of activity was either due to pushing the neck backwards or eye movements (blinking) as a defensive response to the looming stimulus. These waves were included when they appeared in a similar time span and displayed 3D brain activity as in a typical looming VEP or AEP. All these successful trials were marked and then further analyzed.

a)





b)

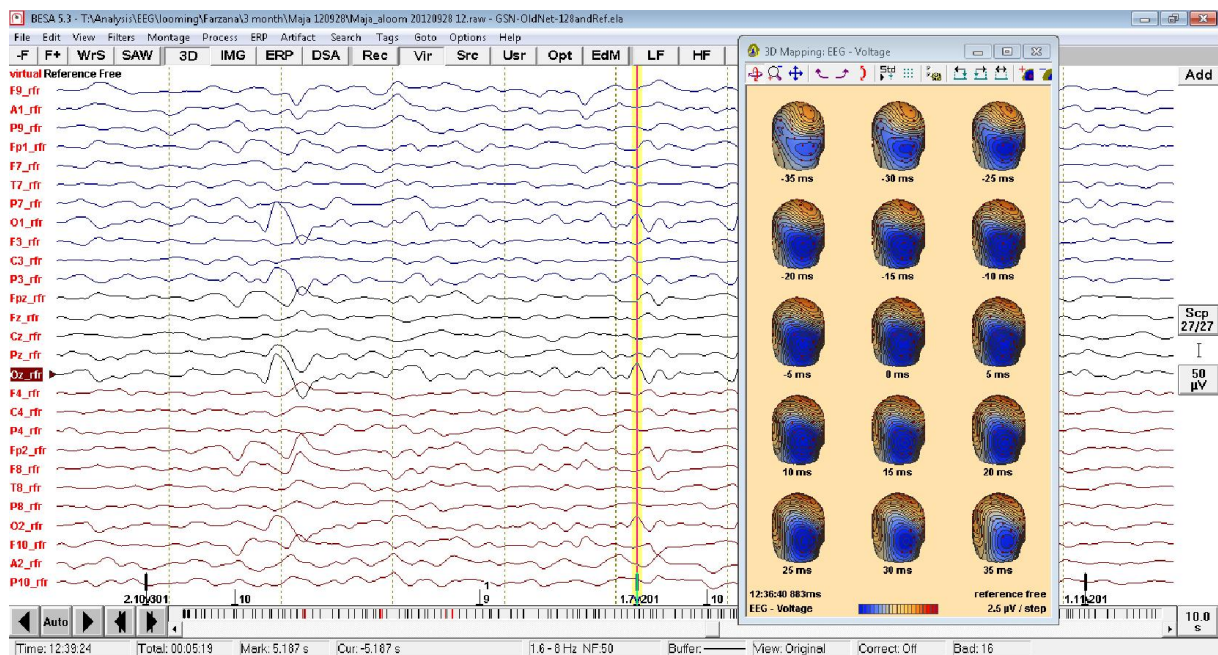


Figure 2. EEG data showing prominent AEP peaks of a 4 s loom of a typical baby boy (3-4 months old)(a), and VEP peaks of a 4 s loom of a typical baby girl(3-4 months old)(b) and their 3D mappings over time. The AEP peak at channel Cz and the VEP peak at channel Oz are marked by the yellow vertical line.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

In addition to recording the timing of the VEP and AEP peaks 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).

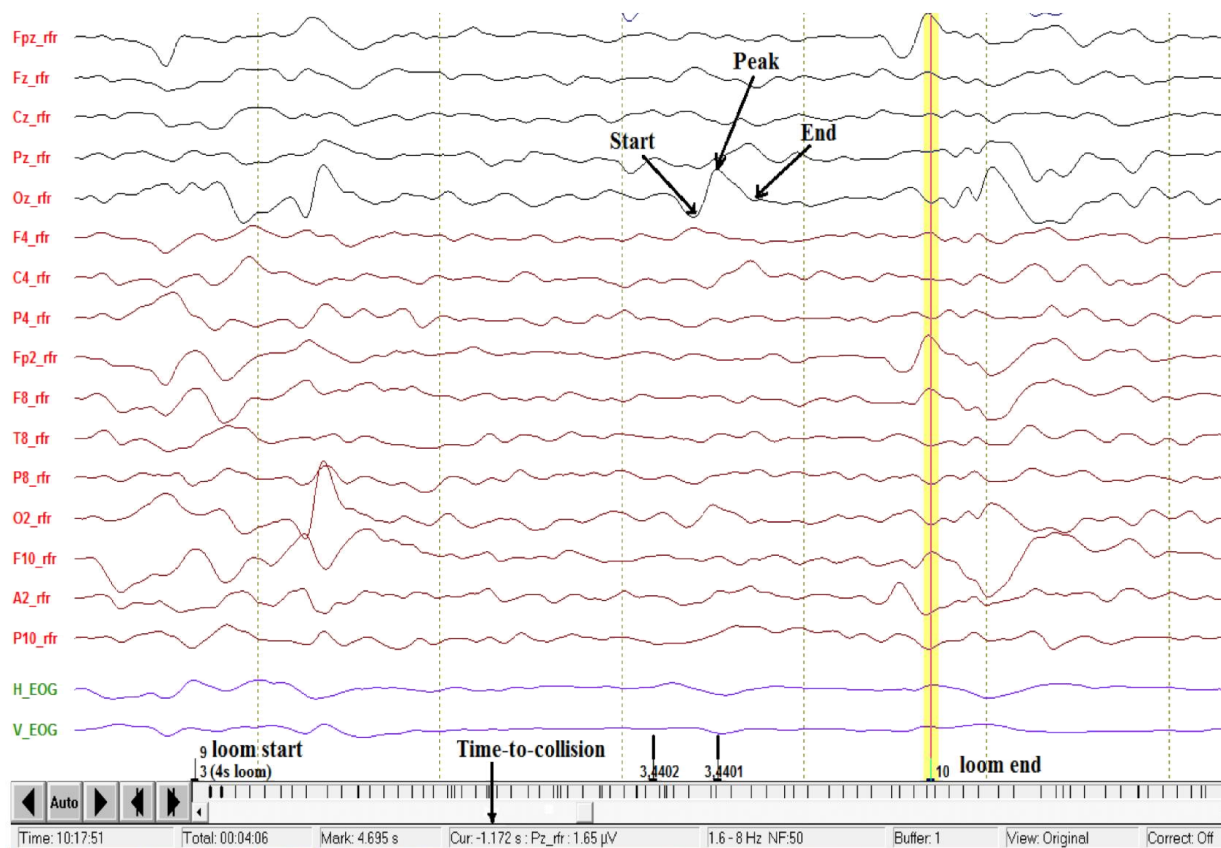


Figure 3. Marking and timing of individual VEP in raw EEG data, showing how the start, peak and end of the looming-related VEP were manually marked in the Oz electrode of a single trial. Positioning of the yellow vertical line aligned with loom end, was considered as reference to take the time of the looming peak.

### 2.5.1 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, Pz, Cz and C3 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.

### 3. Results

#### 3.1 VEP and AEP responses

The channels Oz and Pz were selected for visual looming stimuli and Cz and C3 were selected for auditory looming stimuli as these sites showed maximum activation in response to looming visual and auditory stimuli, respectively. The analyses were performed on a total of 554 trials in which 273 trials were performed at the age of 3/4 months and 281 trials were performed at the age of 9/10 months. Infants in this experiment provided 207 trials out of 554 trails where both auditory evoked potentials (AEP) and visual evoked potentials (VEP) co-occurred on the same trial, more or less equally divided over the two test sessions. Looming related VEP responses were observed in the occipital area and parietal areas, especially in Oz and Pz and AEP responses were mostly observed in Cz and C3 areas some time before the loom would have made contact with the infant.

3/4 months old infants showed their looming-related VEP responses on average 0.882 s (SD = 0.11) and their looming-related AEP responses occurred 0.996 s (SD=0.172) before contact. 9-10 months old infants showed their looming-related VEP responses on average 0.737 s (SD = 0.09) and AEP responses occurred 0.827 s (SD=0.13) before contact. For the 2s loom, 3s loom and 4s loom, average VEP response occurred at 0.853 s (SD=0.11), 0.876 s (SD=0.15) and 0.918 s (SD=0.06) respectively before contact while average AEP responses occurred at 0.876 s (SD=0.15), 0.951 s (SD=0.19) and 1.148 s (SD=0.19) respectively before contact at the age of 3/4 months. 9/10 months old infant showed their looming related VEP responses for the 2s loom, 3s loom and 4s loom on average 0.672 s (SD=0.07), 0.759 s (SD=0.11) and 0.774 s (SD=0.11) respectively before contact while average AEP responses occurred at 0.754 s (SD=0.08), 0.875 s (SD=0.21) and 0.827 s (SD=0.13) respectively before contact.

A 2 (modality: VEP and AEP) x 2 (age: 3/4 month and 9/10 months) x 3 (loom condition: 2, 3, and 4 s) repeated measures ANOVA was performed on averaged looming-related peak activation. Adjustment for multiple comparisons was made by Bonferroni correction. The results showed a main effect of age,  $F(1, 9) = 46.61$ ,  $P < 0.005$ , indicating that with age, both VEP and AEP responses occurred at smaller values of time-to-collision across the three loom speeds (see Figure 4).

The result showed a main effect of modality,  $F(1,9) = 6.86$ ,  $P < 0.05$ , indicating that irrespective of age, looming-related AEP peak occurred before looming related VEP peak in the looming sequence.

The results also showed a three-way interaction effect of age, modality and looming condition,  $F(2, 18) = 7.48$ ,  $P < 0.005$ , indicating that VEP and AEP responses occurred closer to contact at the age of 9/10 months compared to at the age of 3/4 months and both age groups showed AEP responses before VEP responses in the looming sequences. The results also showed that looming-related responses occurred at a fixed time to contact, with the exception of AEP responses at the age of 3/4 months where infants showed looming related responses significantly closer to contact for the faster 2s loom than for the 3s and 4s looms (see Figure 4).

The results also showed a main effect of looming conditions (2s, 3s and 4s) which was not real effect, but was caused by the three way interaction.

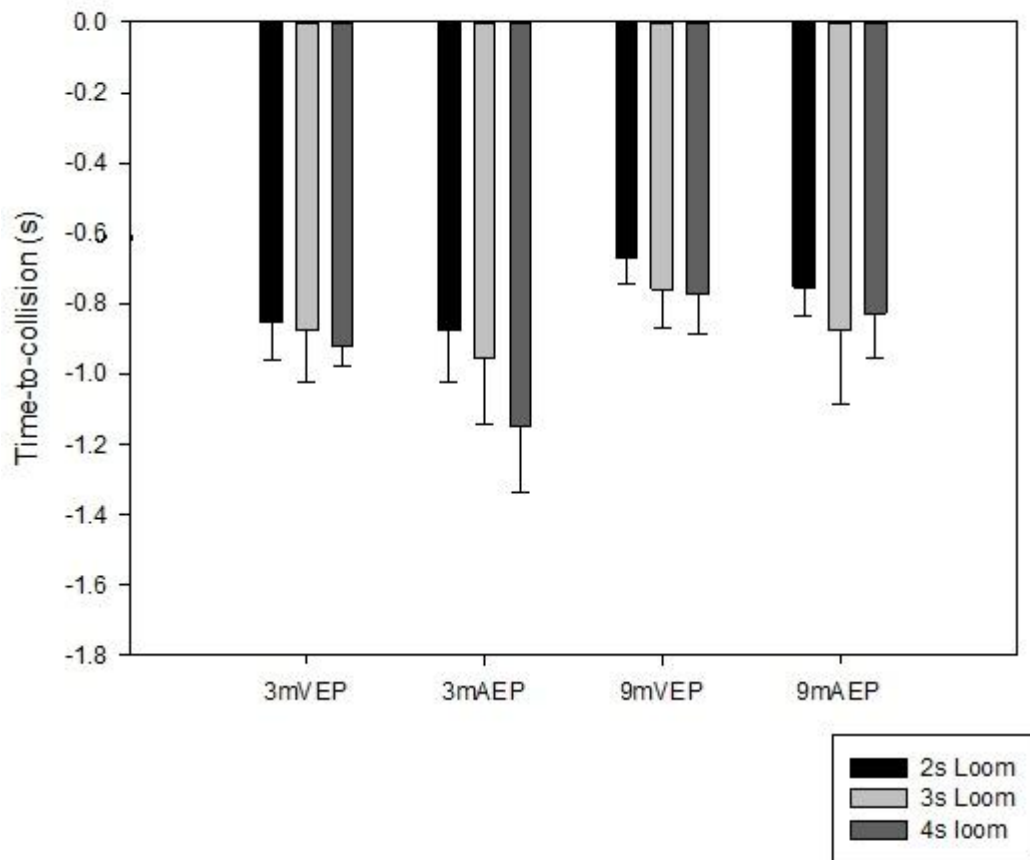


Figure 4: Averaged looming-related VEP and AEP peak activation (including SD bars) for the three looms at the age of 3/4 months and at the age of 9/10 months. With increasing age both VEP and AEP responses occurred at smaller values of time-to-contact across the three loom speeds. In addition, irrespective of age infants responded at a fixed time-to-collision for both VEP and AEP, except for AEP responses at the age of 3/4 months, where infants showed their looming-related responses at significantly smaller values of time-to-collision for higher loom speeds.

### 3.2 VEP and AEP amplitudes

An average of looming-related VEP and AEP peaks of all three looms for each infant at the age of 3/4 months and at the age of 9/10 months 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 at both ages. The amplitudes of peaks at channels Oz and Pz for VEP and Cz and C3 for AEP for each of the three looms were recorded from each of these averages. The averages of all the 10 infants at both ages were then combined to form a grand average.

A 2 (age: 3/4 months and 9/10 months) x 4 (Channel: Oz, Pz, Cz and C3) repeated measures ANOVA was performed on averaged peak VEP and AEP activations. The investigated 4 different channel areas were selected based on anatomical positioning of the brain areas involved in visual (Braddick et al., 2005; Cheng et al., 1995; Dougherty et al., 2003; Holliday & Meese, 2005; Morrone et al., 2000; Rosander et al., 2007; Shirai & Yamaguchi, 2004) and auditory processing (Alkak, Kedzior & keskindemirci, 2007). The results showed a main effect of age,  $F(1,9) = 7.03$ ,  $P < 0.05$ , indicating that amplitude activity for both VEP and AEP increased with age.

The results also showed a main effect of channel,  $F(3,27) = 39.81$ ,  $P < 0.005$ , indicating that irrespective of age, amplitude activity among at four different channels were significantly different.

A significant two-way interaction effect between age and cortical area was found,  $F(3,27) = 5.33$ ,  $P < 0.005$ , indicating that the activity in our investigated occipital and parietal areas differed between the measurements performed at 3/4 months and 9/10 months. The amplitude activity in cortical area channel Oz did not change significantly with growing age, while amplitude activity in cortical area channel Pz increased significantly with increasing age referring to a shift of area for VEP from occipital to parietal with increasing age. It also showed amplitude activity at channel Cz which did not show significant change with age, while the activity at channel C3 increased with age referring to an increase of cortical area for AEP (see Figure 5).

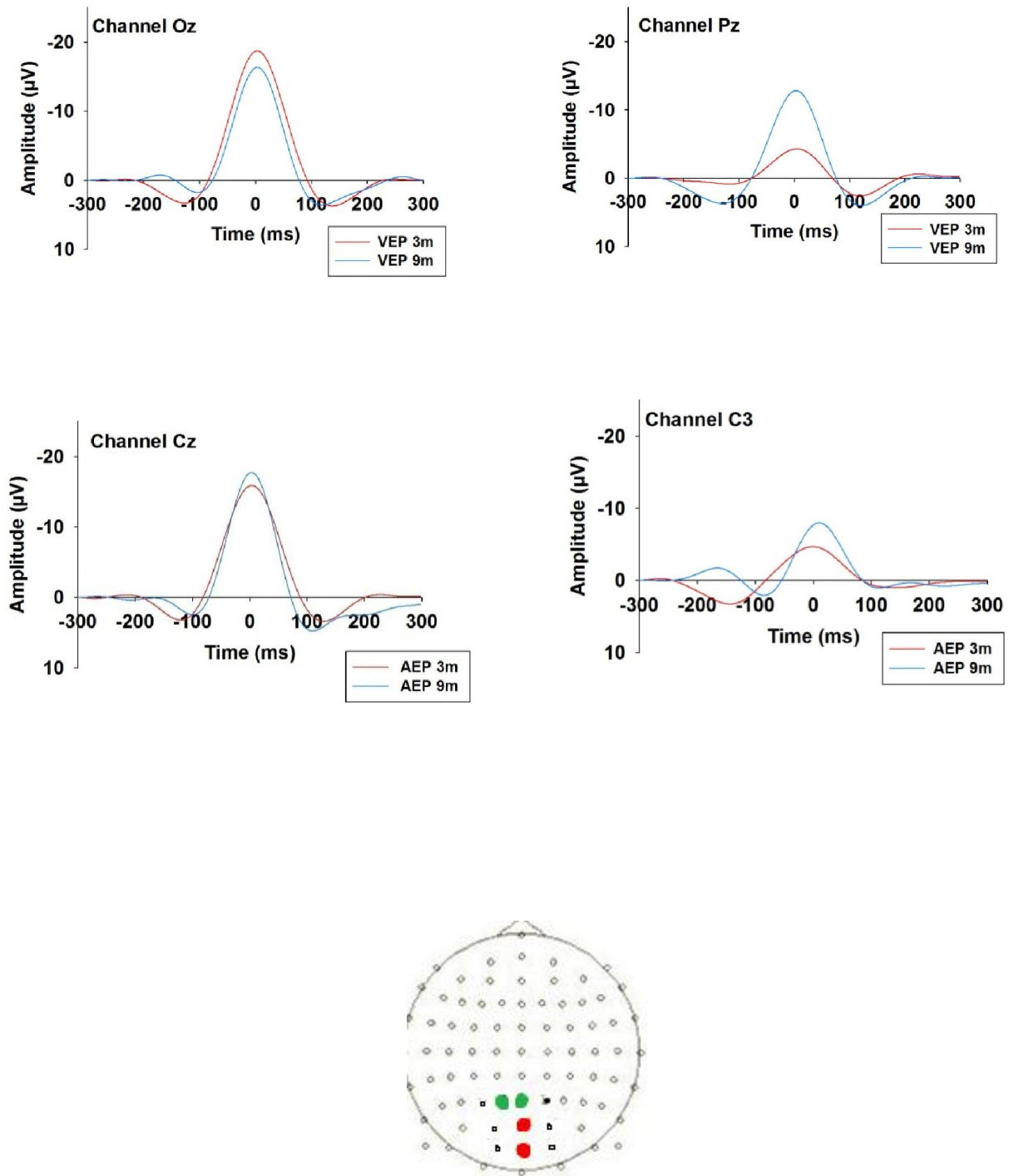


Figure 5. Grand average of looming-related VEP and AEP peaks observed at Channels Oz, Pz and Cz, C3, respectively. The head drawing (nose up) shows the scalp localization of the 81 standard electrodes. The four channels of interest: Oz, Pz (red) and Cz, C3 (green) are indicated with filled colored circles. With increasing age the amplitude activity at channel Oz did not change significantly, while amplitude activity at channel Pz increased significantly with increasing age. The amplitude activity at channel Cz and C3 also showed changes in activation with increasing age.

## **4. Discussion**

In order to respond adequately to a looming object approaching on a direct collision course, infants would have to perceive the collision before it happens and this requires the use of prospective information about the impending collision. This kind of processing is triggered by highly efficient visual systems (Lee, 1998b; Von Hofsten, 2007; Von Hofsten, 2004; Wilkie & Wann, 2003) and auditory systems (Maier & Ghazanfar, 2007) which integrate the information and produce appropriate responses (Alink et al., 2012; Cappe et al., 2012). Young infants are sensitive to process information specifying the serial organization of dynamic audiovisual sequences and have the ability to perceive audiovisual responses of different lengths which emerges early in human development (Lewkowicz, 2008). In this perspective, timing is an important factor. In the present longitudinal study, the development of visual and auditory motion processing of a looming object in infants at the ages of 3/4 and 9/10 months was investigated with high density EEG. VEP and AEP analyses were used to investigate whether there were any significant differences between young infants (3/4 months old) and old infants (9/10 months old) responses to audiovisual looming.

### **4.1. VEP and AEP responses**

In this study, 3/4 months old infants showed their looming-related VEP responses on average 0.882 s and their looming-related AEP responses on average 0.996 s before contact while 9/10 months old infants showed their looming-related VEP responses on average 0.737 s and AEP responses on average 0.827 s before contact. Irrespective of the loom's three different approach conditions, at 3/4 months the average brain response for both VEP and AEP appear relatively early in the looming phase, when the looming object is still far from the infant's face. At the age of 9/10 months, however, infants' average peak VEP and AEP activation appears much closer to the virtual collision. At the age of 3/4 months, infants responded to audiovisual looming stimuli at larger values of TTC compared to infants at the age of 9/10 months could be due to less developed neural pathways. The first four months of infants life most of the synaptic activations are in rudimentary form (Johnson, 2000) and synapses in these neural pathways are not yet fully specialized (Jacob, 1999). These neural pathways would lead to less accurate audiovisual responses. Though development of these neural pathways infant can estimate responses accurately (Johnson, 2000; Jacob, 1999).



Infants at 9/10 months of age responded at shorter values of TTC could also be due to increase of white matter in infants (Kushnerenko et al., 2013). Using MRI study in infant, it was observed that myelination of white matter began to appear in different cortical areas of the brain from 8-12 months of age (Paus et al., 2001). The 9-10 month-old infants displayed an in-between developmental stage. This could also be interpreted as an important sign of appropriate neural networks processing which has been established and the age of 9-10 months would be an important age for doing so. Moreover, crawling, an important step of infant development also starts at this age. These make sense from a perspective where brain and behavioral development run simultaneously (Johnson, 2000). In addition to these, there is also benefit of increasing age which showed that infants can obtain better control of self-produced locomotion and gain their perceptual abilities for perceiving looming danger which improves with age. Results also suggest that during the development of first year of infancy, their ability to pick up the looming information improves. At the same time, looming related post-synaptic current is flowing inside the neurons in a particular brain region where the brain signals are processing from visual cortical areas V1 to V3, V5/MT+ (Teder-Sälejärvi, Di Russo, McDonald, & Hillyard, 2005; van der Weel & van der Meer, 2009).

In the present study, infants at both ages (3/4 months and 9/10 months) showed AEP responses earlier than VEP responses in the looming sequence. AEP responses occurred on average 114 ms earlier than VEP responses at young age while in old infants AEP responses occurred on average 90 ms before VEP responses.

The results demonstrated that the visual loom was perceived more accurately when auditory responses occurred earlier in the looming sequence with a time difference of about 70-120ms between VEP and AEP. Jack et al. (2012) demonstrated that perceived size of visual image increases when the sound appeared about 0-120 ms before the visual component. However, accuracy of visual and auditory perception increases when time difference between the two responses (VEP and AEP) decreases. The sound and light need to be close enough to understand that both stimuli are coming from the same source. For example, when infants are given a choice between two moving visual stimuli and a sound that corresponds to the impact that one of these visual stimuli makes, they detect the temporal relationship between the visible and the audible impacts (Lewkowicz, 1992). In recent years, a number of studies have explored this kind of audiovisual temporal interaction which shed light on timing between auditory and visual components and confirmed its generality by showing that sounds can attract the timing of visual events and influence the strength of visual apparent motion

(Getzmann, 2007). Conversely, auditory motion can cause visual stimuli to be more perceived along its direction (Alink et al., 2012). Moreover, moving sounds enhance visual motion perception in the visual motion complex MT/V5+ area when its direction is congruent with that of visual motion stimuli (Alais et al., 2010). It was also shown in previous research that observed temporal interactions between auditory and visual motion perception and it was also showed that a striking influence of auditory responses was present on visual responses. (Shipley, 1964; Gebhard & Mowbray, 1959). Apart from this view, findings are supported by the emerging view that auditory motion stimuli can affect visual motion perception (Meyer & Wuerger, 2001; Meyer, Wuerger, Röhrbein, & Zetsche, 2005; Brooks et al., 2007; Freeman & Driver, 2008; Hidaka et al., 2009; Hidaka et al., 2011; Conrad, Bartels, Kleiner, & Noppeney, 2010; Teramoto et al., 2010; Alink et al., 2012). On average an earlier response to the auditory modality in a multisensory stimulus could enhance the perception of the visual modality. Romei and his colleagues found that looming structured sounds enhance visual perception by increasing cortical excitability in primary visual area (V1/V2) which can act as a potential threat and can be useful for obtaining further visual information (Romei, Murray, Cappe, & Thut, 2009; Leo, Romei, Freeman, Ladavas, & Driver, 2011). Furthermore, by using fMRI, it has already been found that primary visual cortex area V1, i.e., banks of calcarine sulcus, and several higher visual areas in lingual, fusiform, cuneus, lateral occipital, inferior temporal, and middle temporal gyri work as an area where multisensory processing occurs as a consequence of auditory stimulation (Burton, Snyder, Diamond, & Raichle, 2002; Röder, Stock, Bien, Neville, & Rösler, 2002). The looming bias in visual perception is influenced by looming sounds which amplifies the visual looming perception (Conrad et al., 2013).

## **4.2. Amplitude activity at different channels**

Amplitude of ERP components is referred to as the summation of neural activity resulting from greater neural activation, which is determined by a number of factors like thickness of the skull, the size of the population of active neurons, the position of the active and reference electrode and the distance between the electrode and the active neurons and the latency variability of the signal (Meyer, Baumann, Marchina, & Jancke, 2007; Webb et al., 2005).

The results from our study concerning averaged peak VEP and AEP activity at channels Oz, Pz, Cz and C3 showed that the activity at these sites varied according to the infant's age.

Results showed that amplitude activity increased with increasing age for both VEP and AEP modalities.

Amplitude activity refers to the amount of neurons firing in synchrony (Pfurtscheller & Lopes Da Silva, 1999), higher amplitudes could refer to the large cortical synchronization and these large synchronization could account for the integration of bimodal perception of audiovisual looming (Maier, Chandrasekaran, & Ghazanfar, 2008). Kushnerenko and his colleagues found amplitude activity to increase mostly between 3 and 9 months of age. This the authors explained as the growth and the sharpening of the morphology of neural generators of the cortex, advancing myelination, increased synaptic density, efficacy, and neuronal synchronization (Kushnerenko et al., 2002).

Results also showed that infants irrespective of age, showed different amplitude activity at different channel. There are several studies on the maturation of auditory and visual system in the brain which showed that neuroanatomical development of these systems is not parallel (Anderson et al., 2001; Anderson & Thomason, 2013).

Infants aged 9/10 months showed higher amplitude activity at channel Cz compared to amplitude activity at all other channels. This could mean more development occurred at auditory area as infants grow. Ruff and Rothbart (1996) found that a reduction in the response to visual stimuli occurred around 9 months of age. This finding was supported by Kushnerenko and his colleagues when they found infants to respond towards auditory stimuli which gradually increased between 3- 9 months of age (Kushnerenko et al., 2002). Behavioral studies have also shown that the orientation to high-energy stimuli gradually changes to attending to genuine novelty as well as other significant events by approximately 9 months of age (Kushnerenko, Van den Bergh, & Winkler, 2013). In addition to development, infants showed characteristic changes and different responses to visual and auditory stimuli. Thus, infants could reduce attention to irrelevant stimuli with increasing age (Gomes, Molholm, Christodoulou, Ritter, & Cowan, 2000b). Moreover, audiovisual interactions have been found in auditory cortex, and have been confirmed at the single-unit level (Fu et al., 2003; Ghazanfar et al., 2005) as well as by intracranial multicontact depth electrodes examining the time course of activation across cortical laminae (Schroeder et al., 2001). Evoked potential studies have also shown that audio-somatosensory interactions are mainly present in auditory cortex (Fuxe et al., 2000).

For infants aged 3/4 months showed more VEP responses at channel Oz than at channel Pz. This could mean that visual cortical areas processing looming were more active and more developed than other channel activity areas Moreover, at the age of 3/4 months higher

amplitude activity at channel Oz could also be due to infants' active attention to the visual loom which resulted in the recruitment of more visual cortical pathways (Johnson, 1990). At the age of 3/4 months the activation in the O area showed larger negative amplitudes than at the age of 9/10 months. An opposite pattern was observed in the peak amplitudes at the P area at 9/10 months. The decrease in activity in the O area and increase in the P area with age shows that activation in occipital areas propagates forward and starts to influence more advanced areas in parietal and temporal leads (Webb et al., 2005) where the dorsal stream appears as a complex and special area for advanced visual processing (Van Der Meer et al., 2013). Moreover, the shifting of amplitude activation between the different areas of the brain as well as findings of an increased processing speed could indicate that the visual pathway has become more specialized as infants aged from 3/4 to 9/10 months. This could also be due to myelination of the visual cortical pathway which may lead to an increase in processing speed (Dubois et al., 2008; Van Der Meer et al., 2013). This explanation also supports the finding that showed increased VEP amplitude at Oz electrode site at 3/4months compared to AEP amplitude at Cz electrode site. The lower amplitude at Cz electrode could mean that auditory cortical areas processing looming have not fully developed as this is the most crucial period for development of the neurosensory part of auditory system (Graven & Browne, 2008). It could also mean that more cortical neurons were firing in synchrony in the visual cortex than in the auditory cortex in young infants (Huttenlocher, 1990). AEP responses in the auditory cortex could refer to the relative fewer population of active neurons causing desynchronization on that area responding to auditory motion (Elul, 1972).

EEG measures the summation of neural activity that has propagated to the scalp, it may not adequately separate sources that temporally overlap. Findings of the propagated activity could therefore be a result of the temporal summation of changes in other components (Webb, 2005). It could also occur because of additional processes emerging, that are not yet identified or taken into consideration. Another factor that could have influenced our findings of differences in amplitude activation between the two age groups could be the result of an increase in skull thickness. Infant skull thickness increases most rapidly within the first year of life (Grieve, Emerson, Fifer, Isler, & Stark, 2003) resulting in a thicker skull at 9/10 months than at 3/4 months. However, increase skull thickness refer skull's poor conductivity. Despite the fact that the infants' skulls became significantly thicker as they aged from 3/4 months to 9/10 months, we still found an increase in averaged VEP activity in the P area as they became older. This supports the argument that infants' processing of the looming stimuli

propagates from occipital towards more specialized and advanced parietal neural pathways (Van Der Meer et al., 2013).

Results further showed that amplitude activity at channel Cz did not show significant increased amplitude activity as compared to amplitude activity at C3 when the infants became older. This could mean the development of the auditory cortex is occupying larger brain area than the infants have during early infancy. The auditory cortex is situated on the outer surface of the temporal lobe where neurons representing specific frequencies develop. The neural connections to the temporal lobe become functional from 28 to 30 weeks of gestational period. This supports the present findings as auditory cortical areas are developing and increasing with age (Graven & Browne, 2008; Hall, 2000). Furthermore, C3 electrode site in the 10-20 EEG montage is on the left cortical side. Findings from adult studies of collision judgments have shown a left centered cortical activation which supports the current finding that neural collision judgments may be localized in left cortical areas (Assmus et al., 2003; Coull, Vidal, Goulon, Nazarian, & Craig, 2008; Field & Wann, 2005; van der Weel & van der Meer, 2009; Van Der Meer et al., 2013). According to Tyll et al (2013), an increased audiovisual signal enhances multisensory processing within low level visual cortices, auditory areas and the left-hemispheric parietal cortex. In addition to this, lateral portions of the superior temporal cortex, the superior temporal sulcus, and intraparietal sulcus as well as the amygdala have been found to be sensitive to looming cues (Graziano & Cooke, 2006; Ghazanfar, Neuhoff, & Logothetis, 2002b; Seifritz et al., 2002). Regarding multisensory interconnectivity, several accounts have been advocated to explain multisensory interplay within low-level visual cortices. It was found by using retrograde tracing that there is a direct cortico-cortical connectivity between auditory cortices and sending information through monosynaptic projections from auditory cortices as well as areas of the superior temporal sulcus to V1 (Falchier, Clavagnier, Barone, & Kennedy, 2002).

### **4.3 Conclusion**

The present study identified looming-related brain electrical responses from the EEG recordings in infants with 3/4 months and 9/10 months. The study showed clear differences in VEP and AEP activities between infants with increasing age, shown by a decrease in processing time and peak VEP and AEP activation which was closer to the loom's time-to-collision. The measured peak VEP activation also propagated towards higher information processing areas in the visual pathway. The findings indicate a developmental trend in

infants' prediction of an object's time-to-collision. The amplitudes of looming-related peaks at occipital channel Oz and parietal channel Pz, and auditory channel Cz and C3 were compared. At the age of 9/10 months, infants showed more visual activity at Pz channel which could mean the shifting of visual area from 3/10 months of age. Furthermore, auditory activity at channel Cz and C3 at the age of 9/10 months increased with age and this area could act as a cortical area for multisensory integration. The observed differences could be reflected as neuroanatomical development occurring during first year of infants' life as well as a cortical area for processing multisensory looming perception.

## References

- Alais, D., & Burr, D. (2004). Ventriloquist Effect Results from Near-Optimal Bimodal Integration. *Current Biology*, *14*, 257–262. doi:10.1016/S0960-9822(04)00043-0
- Alais, D., Newell, F. N., & Mamassian, P. (2010). Multisensory processing in review: from physiology to behaviour. *Seeing and Perceiving*, *23*, 3–38. doi:10.1163/187847510X488603
- Alink, A., Euler, F., Galeano, E., Krugliak, A., Singer, W., & Kohler, A. (2012). Auditory Motion Capturing Ambiguous Visual Motion. *Frontiers in Psychology*. doi:10.3389/fpsyg.2011.00391
- Alkac,U., Kedzior,K., & Keskindemirci,G. (2007). Event related potentials to visual, auditory, and bimodal (combined auditory-visual) stimuli. *Intern. J. Neuroscience*, *117*: 259-273.doi: 10. 1080/0020745000534118
- Allison, T., Wood, C. C., & McCarthy, G. M. (1986).The central nervous system. In M. G. H. Coles, E. Donchin& S. W. Porges (Eds.), *Psychophysiology: Systems, processes, and applications* (pp. 5-25). New York: Guilford
- Anderson, A. L., & Thomason, M. E. (2013). Functional plasticity before the cradle: A review of neural functional imaging in the human fetus. *Neuroscience and Biobehavioral Reviews*. doi:10.1016/j.neubiorev.2013.03.013
- Anderson, A. W., Marois, R., Colson, E. R., Peterson, B. S., Duncan, C. C., Ehrenkranz, R. A., ... Ment, L. R. (2001). Neonatal auditory activation detected by functional magnetic resonance imaging. *Magnetic Resonance Imaging*, *19*, 1–5. doi:10.1016/S0730-725X(00)00231-9
- Assmus, A., Marshall, J. C., Ritzl, A., Noth, J., Zilles, K., & Fink, G. R. (2003). Left inferior parietal cortex integrates time and space during collision judgments. In *NeuroImage* (Vol. 20). doi:10.1016/j.neuroimage.2003.09.025
- Bach, D. R., Neuhoff, J. G., Perrig, W., & Seifritz, E. (2009). Looming sounds as warning signals: the function of motion cues. *International Journal of Psychophysiology: Official Journal of the International Organization of Psychophysiology*, *74*(1), 28–33. doi:10.1016/j.ijpsycho.2009.06.004
- Bahrack, L. E., Lickliter, R., & Flom, R. (2004). Intersensory redundancy guides the development of selective attention, perception, and cognition in infancy. *Current Directions in Psychological Science*. doi:10.1111/j.0963-7214.2004.00283.x
- Ball, W., & Tronick, E. (1971). Infant responses to impending collision: optical and real. *Science (New York, N.Y.)*, *171*, 818–820. doi:10.1126/science.171.3973.818

- Bendor, D., & Wang, X. (2005). The neuronal representation of pitch in primate auditory cortex. *Nature*, *436*, 1161–1165. doi:10.1038/nature03867
- Billington, J., Wilkie, R. M., Field, D. T., & Wann, J. P. (2011). Neural processing of imminent collision in humans. *Proceedings. Biological Sciences / The Royal Society*, *278*, 1476–1481. doi:10.1098/rspb.2010.1895
- Bower, T. G. R., Broughton, J. M., & Moore, M. K. (1971). Infant responses to approaching objects: An indicator of response to distal variables. *Perception & Psychophysics*. doi:10.3758/BF03212627
- Braddick, O., Birtles, D., Wattam-Bell, J., & Atkinson, J. (2005). Motion- and orientation-specific cortical responses in infancy. *Vision Research*, *45*, 3169–3179. doi:10.1016/j.visres.2005.07.021
- Brooks, A., van der Zwan, R., Billard, A., Petreska, B., Clarke, S., & Blanke, O. (2007). Auditory motion affects visual biological motion processing. *Neuropsychologia*, *45*, 523–530. doi:10.1016/j.neuropsychologia.2005.12.012
- Burton, H., Snyder, A. Z., Diamond, J. B., & Raichle, M. E. (2002). Adaptive changes in early and late blind: a fMRI study of verb generation to heard nouns. *Journal of Neurophysiology*, *88*, 3359–3371. doi:10.1152/jn.00129.2002
- Cappe, C., Thelen, A., Romei, V., Thut, G., & Murray, M. M. (2012). Looming signals reveal synergistic principles of multisensory integration. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *32*(4), 1171–82. doi:10.1523/JNEUROSCI.5517-11.2012
- Cheng, K., Fujita, H., Hanno, I., Miura, S., & Tanaka, K. (1995). Human cortical regions activated by wide-field visual motion: An H<sub>2</sub><sup>15</sup>O PET study. *Journal of Neurophysiology*, *74* (1), 413-427.
- Cappe, C., Thut, G., Romei, V., & Murray, M. M. (2009). Selective integration of auditory-visual looming cues by humans. *Neuropsychologia*, *47*, 1045–1052. doi:10.1016/j.neuropsychologia.2008.11.003
- Conrad, V., Bartels, A., Kleiner, M., & Noppeney, U. (2010). Audiovisual interactions in binocular rivalry. *Journal of Vision*, *10*, 27. doi:10.1167/10.10.27
- Conrad, V., Kleiner, M., Bartels, A., Hartcher O'Brien, J., Bülhoff, H. H., & Noppeney, U. (2013). Naturalistic Stimulus Structure Determines the Integration of Audiovisual Looming Signals in Binocular Rivalry. *PLoS ONE*, *8*. doi:10.1371/journal.pone.0070710
- Coull, J. T., Vidal, F., Goulon, C., Nazarian, B., & Craig, C. (2008). Using time-to-contact information to assess potential collision modulates both visual and temporal prediction networks. *Frontiers in Human Neuroscience*, *2*, 10. doi:10.3389/neuro.09.010.2008
- Dougherty, R. F., Koch, V. M., Brewer, A. A., Fischer, B., Modersitzki, J., & Wandell, B. A. (2003). Visual field representations and locations of visual areas V1/2/3 in human visual cortex. *Journal of Vision*, *3*, 586–598. doi:10.1167/3.10.1



- Dubois, J., Dehaene-Lambertz, G., Soarès, C., Cointepas, Y., Le Bihan, D., & Hertz-Pannier, L. (2008). Microstructural correlates of infant functional development: example of the visual pathways. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *28*, 1943–1948. doi:10.1523/JNEUROSCI.5145-07.2008
- Elul, R. (1972). The Genesis of the Eeg. *International Review of Neurobiology*, *15*, 227–272. doi:10.1016/S0074-7742(08)60333-5
- Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, *415*, 429–433. doi:10.1038/415429a
- Evans, K. K., & Treisman, A. (2010). Natural cross-modal mappings between visual and auditory features. *Journal of Vision*, *10*, 6.1–12. doi:10.1167/10.1.6
- Falchier, A., Clavagnier, S., Barone, P., & Kennedy, H. (2002). Anatomical evidence of multimodal integration in primate striate cortex. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *22*, 5749–5759. doi:20026562
- Ferree, T. C., Luu, P., Russell, G. S., & Tucker, D. M. (2001). Scalp electrode impedance, infection risk, and EEG data quality. *Clinical Neurophysiology*, *112*, 536–544. doi:10.1016/S1388-2457(00)00533-2
- Field, D. T., & Wann, J. P. (2005). Perceiving time to collision activates the sensorimotor cortex. *Current Biology*, *15*, 453–458. doi:10.1016/j.cub.2004.12.081
- Foxe, J. J., Morocz, I. A., Murray, M. M., Higgins, B. A., Javitt, D. C., & Schroeder, C. E. (2000). Multisensory auditory-somatosensory interactions in early cortical processing revealed by high-density electrical mapping. *Cognitive Brain Research*, *10*, 77–83. doi:10.1016/S0926-6410(00)00024-0
- Freeman, E., & Driver, J. (2008). Direction of Visual Apparent Motion Driven Solely by Timing of a Static Sound. *Current Biology*, *18*, 1262–1266. doi:10.1016/j.cub.2008.07.066
- Fu, K.-M. G., Johnston, T. A., Shah, A. S., Arnold, L., Smiley, J., Hackett, T. A., ... Schroeder, C. E. (2003). Auditory cortical neurons respond to somatosensory stimulation. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *23*, 7510–7515.
- Gebhard, J. W., & Mowbray, G. H. (1959). On discriminating the rate of visual flicker and auditory flutter. *The American Journal of Psychology*, *72*, 521–529. doi:10.2307/1419493
- Getzmann, S. (2007). The effect of brief auditory stimuli on visual apparent motion. *Perception*, *36*(7), 1089–1103. doi:10.1068/p5741
- Gibson, J. J. (1966). *The senses considered as perceptual systems*. Boston: Houghton Mifflin Company.

- Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston: Houghton Mifflin Company.
- Ghazanfar, A. a, Maier, J. X., Hoffman, K. L., & Logothetis, N. K. (2005). Multisensory integration of dynamic faces and voices in rhesus monkey auditory cortex. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *25*(20), 5004–12. doi:10.1523/JNEUROSCI.0799-05.2005
- Ghazanfar, A. A., & Maier, J. X. (2009). Rhesus monkeys (*Macaca mulatta*) hear rising frequency sounds as looming. *Behavioral Neuroscience*, *123*, 822–827. doi:10.1037/a0016391
- Ghazanfar, A. A., Neuhoff, J. G., & Logothetis, N. K. (2002a). Auditory looming perception in rhesus monkeys. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 15755–15757. doi:10.1073/pnas.242469699
- Ghazanfar, A. A., Neuhoff, J. G., & Logothetis, N. K. (2002b). Auditory looming perception in rhesus monkeys. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 15755–15757. doi:10.1073/pnas.242469699
- Gingras, G., Rowland, B. A., & Stein, B. E. (2009). The differing impact of multisensory and unisensory integration on behavior. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *29*, 4897–4902. doi:10.1523/JNEUROSCI.4120-08.2009
- Gomes, H., Molholm, S., Christodoulou, C., Ritter, W., & Cowan, N. (2000a). The development of auditory attention in children. *Frontiers in Bioscience* *5*, d108–120. doi:10.1093/toxsci/kfs057
- Gomes, H., Molholm, S., Christodoulou, C., Ritter, W., & Cowan, N. (2000b). The development of auditory attention in children. *Frontiers in Bioscience* *5*, d108–120. doi:10.1093/toxsci/kfs057
- Graven, S. N., & Browne, J. V. (2008). Auditory Development in the Fetus and Infant. *Newborn and Infant Nursing Reviews*, *8*, 187–193. doi:10.1053/j.nainr.2008.10.010
- Graziano, M. S. A., & Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior (DOI:10.1016/j.neuropsychologia.2005.09.009). *Neuropsychologia*. doi:10.1016/j.neuropsychologia.2005.09.011
- Greenfield, P. M. (1991). Language, tools and brain: The ontogeny and phylogeny of hierarchically organized sequential behavior. *Behavioral and Brain Sciences*. doi:10.1017/S0140525X00071235
- Grieve, P. G., Emerson, R. G., Fifer, W. P., Isler, J. R., & Stark, R. I. (2003). Spatial correlation of the infant and adult electroencephalogram. *Clinical Neurophysiology*, *114*, 1594–1608. doi:10.1016/S1388-2457(03)00122-6

- Hackett, T. A., Preuss, T. M., & Kaas, J. H. (2001). Architectonic identification of the core region in auditory cortex of macaques, chimpanzees, and humans. *Journal of Comparative Neurology*, *441*, 197–222. doi:10.1002/cne.1407
- Hall, J. W. (2000). Development of the ear and hearing. *Journal of Perinatology : Official Journal of the California Perinatal Association*, *20*, S12–S20. doi:10.1038/sj.jp.7200439
- Hershenson, M. (1962). Reaction time as a measure of intersensory facilitation. *Journal of Experimental Psychology*, *63*, 289–293. doi:10.1037/h0039516
- Hidaka, S., Manaka, Y., Teramoto, W., Sugita, Y., Miyauchi, R., Gyoba, J., ... Iwaya, Y. (2009). Alternation of sound location induces visual motion perception of a static object. *PLoS ONE*, *4*. doi:10.1371/journal.pone.0008188
- Hidaka, S., Teramoto, W., Sugita, Y., Manaka, Y., Sakamoto, S., & Suzuki, Y. (2011). Auditory motion information drives visual motion perception. *PLoS ONE*, *6*. doi:10.1371/journal.pone.0017499
- Holliday, I. E., & Meese, T. S. (2005). Neuromagnetic evoked responses to complex motions are greatest for expansion. *International Journal of Psychophysiology*, *55*, 145–157. doi:10.1016/j.ijpsycho.2004.07.009
- Huttenlocher, P. R. (1990). Morphometric study of human cerebral cortex development. *Neuropsychologia*, *28*, 517–527. doi:10.1016/0028-3932(90)90031-I
- Jaekl, P., Soto-Faraco, S., & Harris, L. R. (2012). Perceived size change induced by audiovisual temporal delays. *Experimental Brain Research*, *216*(3), 457–62. doi:10.1007/s00221-011-2948-9
- Johnson, M. H. (1990). Cortical Maturation and the Development of Visual Attention in Early Infancy. *Journal of Cognitive Neuroscience*. doi:10.1162/jocn.1990.2.2.81
- Johnson, M. H. (2000). Functional Brain Development in Infants : Elements of an Interactive Specialization Framework, *71*(1), 75–81.
- Kayed, N. S., & van der Meer, A. L. H. (2007). Infants' timing strategies to optical collisions: a longitudinal study. *Infant Behavior & Development*, *30*(1), 50–9. doi:10.1016/j.infbeh.2006.11.001
- KC, A., & RM, S. (1999). Optic flow selectivity in the anterior superior temporal polysensory area, STPa, of the behaving monkey. *The Journal of Neuroscience*, *19*, 2681–2692.
- Kushnerenko, E., Ceponiene, R., Balan, P., Fellman, V., Huotilaine, M., & Näätäne, R. (2002). Maturation of the auditory event-related potentials during the first year of life. *Neuroreport*, *13*, 47–51.
- Kushnerenko, E. V, Van den Bergh, B. R. H., & Winkler, I. (2013). Separating acoustic deviance from novelty during the first year of life: a review of event-related potential evidence. *Frontiers in Psychology*, *4*, 595. doi:10.3389/fpsyg.2013.00595

- Lakatos, P., O'Connell, M. N., Barczak, A., Mills, A., Javitt, D. C., & Schroeder, C. E. (2009). The Leading Sense: Supramodal Control of Neurophysiological Context by Attention. *Neuron*, *64*, 419–430. doi:10.1016/j.neuron.2009.10.014
- Lee, D. (1998a). Guiding Movement by Coupling Taus. *Ecological Psychology*. doi:10.1207/s15326969eco103&4\_4
- Lee, D. (1998b). Guiding Movement by Coupling Taus. *Ecological Psychology*. doi:10.1207/s15326969eco103&4\_4
- Leo, F., Romei, V., Freeman, E., Ladavas, E., & Driver, J. (2011). Looming sounds enhance orientation sensitivity for visual stimuli on the same side as such sounds. *Experimental Brain Research*, *213*, 193–201. doi:10.1007/s00221-011-2742-8
- Lewkowicz, D. J. (1992). Infants' response to temporally based intersensory equivalence: The effect of synchronous sounds on visual preferences for moving stimuli. *Infant Behavior and Development*. doi:10.1016/0163-6383(92)80002-C
- Lewkowicz, D. J. (2008). Perception of dynamic and static audiovisual sequences in 3- and 4-month-old infants. *Child Development*, *79*, 1538–1554. doi:10.1111/j.1467-8624.2008.01204.x
- Li, C., McLennan, H., & Jasper, H. (1952). Brain waves and unit discharge in cerebral cortex. *Science*, *116*(3024), 656-657.
- Luck, S. J. (2005). *An Introduction to the Event-Related Potential technique*. USA: Bradford
- Maier, J. X., Chandrasekaran, C., & Ghazanfar, A. A. (2008). Integration of Bimodal Looming Signals through Neuronal Coherence in the Temporal Lobe. *Current Biology*, *18*, 963–968. doi:10.1016/j.cub.2008.05.043
- Maier, J. X., & Ghazanfar, A. A. (2007). Looming biases in monkey auditory cortex. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *27*, 4093–4100. doi:10.1523/JNEUROSCI.0330-07.2007
- Maier, J. X., Neuhoff, J. G., Logothetis, N. K., & Ghazanfar, A. A. (2004a). Multisensory integration of looming signals by rhesus monkeys. *Neuron*, *43*, 177–181. doi:10.1016/j.neuron.2004.06.027
- Maier, J. X., Neuhoff, J. G., Logothetis, N. K., & Ghazanfar, A. A. (2004b). Multisensory integration of looming signals by rhesus monkeys. *Neuron*, *43*, 177–181. doi:10.1016/j.neuron.2004.06.027
- Meredith, M. A., Nemitz, J. W., & Stein, B. E. (1987). Determinants of multisensory integration in superior colliculus neurons. I. Temporal factors. *The Journal of Neuroscience*, *7*, 3215–29. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/3668625>
- Meyer, G. F., & Wuerger, S. M. (2001). Cross-modal integration of auditory and visual motion signals. *Neuroreport*, *12*, 2557–2560. doi:10.1097/00001756-200108080-00053

- Meyer, G. F., Wuerger, S. M., Röhrbein, F., & Zetsche, C. (2005). Low-level integration of auditory and visual motion signals requires spatial co-localisation. In *Experimental Brain Research* (Vol. 166, pp. 538–547). doi:10.1007/s00221-005-2394-7
- Meyer, M., Baumann, S., Marchina, S., & Jancke, L. (2007). Hemodynamic responses in human multisensory and auditory association cortex to purely visual stimulation. *BMC Neuroscience*, 8, 14. doi:10.1186/1471-2202-8-14
- Morrone, M. C., Tosetti, M., Montanaro, D., Fiorentini, A., Cioni, G., & Burr, D. C. (2000). A cortical area that responds specifically to optic flow, revealed by fMRI. *Nature Neuroscience*, 3 (12), 1322-1328.
- Neuhoff, J. G., & McBeath, M. K. (1996). The Doppler illusion: the influence of dynamic intensity change on perceived pitch. *Journal of Experimental Psychology. Human Perception and Performance*, 22, 970–985. doi:10.1037/0096-1523.22.4.970
- Neuhoff, J. G., McBeath, M. K., & Wanzie, W. C. (1999). Dynamic frequency change influences loudness perception: a central, analytic process. *Journal of Experimental Psychology. Human Perception and Performance*, 25, 1050–1059. doi:10.1037/0096-1523.25.4.1050
- Newell, F. N., Ernst, M. O., Tjan, B. S., & Bühlhoff, H. H. (2001). Viewpoint dependence in visual and haptic object recognition. *Psychological Science : A Journal of the American Psychological Society / APS*, 12, 37–42. doi:10.1111/1467-9280.00307
- Nunze, P. L., & Srinivasan, R. (2006). *Electric fields of the brain: The neurophysics of EEG* (2<sup>nd</sup> edition). Oxford University Press.
- Parton, S., & Marler, P. (1999). Communication goes multimodal. *Science*, 283, 1272-1273. doi:10.1126/science.283.5406.1272
- Paus, T., Collins, D. L., Evans, A. C., Leonard, G., Pike, B., & Zijdenbos, A. (2001). Maturation of white matter in the human brain: A review of magnetic resonance studies. *Brain Research Bulletin*. doi:10.1016/S0361-9230(00)00434-2
- Pfurtscheller, G., & Lopes Da Silva, F. H. (1999). Event-related EEG/MEG synchronization and desynchronization: Basic principles. *Clinical Neurophysiology*. doi:10.1016/S1388-2457(99)00141-8
- Piaget, J. (1952). *The origin of intelligence in children*. New York: International University Press.
- Picton, T. W., Bentin, S., Berg, P., Donchin, E., Hillyard, S. A., Johnson, R., ... Taylor, M. J. (2000). Guidelines for using human event-related potentials to study cognition: recording standards and publication criteria. *Psychophysiology*, 37, 127–152. doi:10.1111/1469-8986.3720127
- Romanski, L. M., & Hwang, J. (2012). Timing of audiovisual inputs to the prefrontal cortex and multisensory integration. *Neuroscience*, 214, 36–48. doi:10.1016/j.neuroscience.2012.03.025

- Romei, V., Murray, M. M., Cappe, C., & Thut, G. (2009). Preperceptual and stimulus-selective enhancement of low-level human visual cortex excitability by sounds. *Current Biology : CB*, *19*(21), 1799–805. doi:10.1016/j.cub.2009.09.027
- Rosander, N., Nyström, P., Gredebäck, G., & von Hofsten, C. (2007). Cortical processing of visual motion in young infants. *Vision Research*, *47*, 1614-1623.
- Rowe, C. (1999). Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour*, *58*, 921–931. doi:10.1006/anbe.1999.1242
- Ruff, H. A., and Rothbart, M.K. (1996). Attention in Early Development: Themes and Variations. New York, NY: Oxford University Press
- Röder, B., Stock, O., Bien, S., Neville, H., & Rösler, F. (2002). Speech processing activates visual cortex in congenitally blind humans. *European Journal of Neuroscience*, *16*, 930–936. doi:10.1046/j.1460-9568.2002.02147.x
- Schiff, W., Caviness, J. A., & Gibson, J. J. (1962). Persistent fear responses in rhesus monkeys to the optical stimulus of “looming”. *Science (New York, N.Y.)*, *136*, 982–983. doi:10.1126/science.136.3520.982
- Schiff, W., & Oldak, R. (1990). Accuracy of judging time to arrival: effects of modality, trajectory, and gender. *Journal of Experimental Psychology. Human Perception and Performance*, *16*, 303–316. doi:10.1037/0096-1523.16.2.303
- Schroeder, C. E., Lakatos, P., Kajikawa, Y., Partan, S., & Puce, A. (2008). Neuronal oscillations and visual amplification of speech. *Trends in Cognitive Sciences*, *12*, 106–113. doi:10.1016/j.tics.2008.01.002
- Schroeder, C. E., Lindsley, R. W., Specht, C., Marcovici, A., Smiley, J. F., & Javitt, D. C. (2001). Somatosensory input to auditory association cortex in the macaque monkey. *Journal of Neurophysiology*, *85*, 1322–1327.
- Seifritz, E., Neuhoff, J. G., Bilecen, D., Scheffler, K., Mustovic, H., Schächinger, H., ... Di Salle, F. (2002). Neural processing of auditory looming in the human brain. *Current Biology : CB*, *12*, 2147–2151.
- Shams, L., & Kim, R. (2010). Crossmodal influences on visual perception. *Physics of Life Reviews*. doi:10.1016/j.plrev.2010.04.006
- Shipley, T. (1964). Auditory flutter driving of visual flicker. *Science (New York, N.Y.)*, *145*, 1328–1330. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/14173429>
- Shirai, N., & Yamaguchi, M. K. (2004). Asymmetry in the perception of motion-in-depth. *Visual Research*, *44*, 1003-1011.
- Stein, B. E., & Meredith, M. A. (1993). *The Merging Senses. Cognitive Neuroscience Series* (p. 221).

- Sumby, W. H. (1954). Visual Contribution to Speech Intelligibility in Noise. *The Journal of the Acoustical Society of America*. doi:10.1121/1.1907309
- Summerfield, Q. (1979). Use of visual information for phonetic perception. *Phonetica*, 36, 314–331. doi:10.1159/000259969.
- Teder-Sälejärvi, W. A., Di Russo, F., McDonald, J. J., & Hillyard, S. A. (2005). Effects of spatial congruity on audio-visual multimodal integration. *Journal of Cognitive Neuroscience*, 17, 1396–1409. doi:10.1162/0898929054985383
- Teramoto, W., Manaka, Y., Hidaka, S., Sugita, Y., Miyauchi, R., Sakamoto, S., ... Suzuki, Y. (2010). Visual motion perception induced by sounds in vertical plane. *Neuroscience Letters*, 479, 221–225. doi:10.1016/j.neulet.2010.05.065
- Tramo, M. J., Cariani, P. A., Koh, C. K., Makris, N., & Braida, L. D. (2005). Neurophysiology and neuroanatomy of pitch perception: auditory cortex. *Annals of the New York Academy of Sciences*. doi:10.1196/annals.1360.011
- Tucker, D. M. (1993). Spatial sampling of head electrical fields: The geodesic sensor net. *Electroencephalography and Clinical Neurophysiology*, 87, 154–163. doi:10.1016/0013-4694(93)90121-B
- Tyll, S., Bonath, B., Schoenfeld, M. A., Heinze, H.-J., Ohl, F. W., & Noesselt, T. (2013). Neural basis of multisensory looming signals. *NeuroImage*, 65, 13–22. doi:10.1016/j.neuroimage.2012.09.056
- Van Der Meer, A. L. H., Svantesson, M., & Van Der Weel, F. R. R. (2013). Longitudinal study of looming in infants with high-density EEG. *Developmental Neuroscience*, 34, 488–501. doi:10.1159/000345154
- Van der Weel, F. R. R., & van der Meer, A. L. H. (2009). Seeing it coming: infants' brain responses to looming danger. *Die Naturwissenschaften*, 96(12), 1385–91. doi:10.1007/s00114-009-0585-y
- Von Hofsten, C. (2004). An action perspective on motor development. *Trends in Cognitive Sciences*. doi:10.1016/j.tics.2004.04.002
- Von Hofsten, C. (2007). Action in development. *Developmental Science*. doi:10.1111/j.1467-7687.2007.00564.x
- Webb, S. J., Long, J. D., & Nelson, C. A. (2005). PAPER A longitudinal investigation of visual event-related potentials in the first year of life, 6, 605–616.
- Wilkie, R., & Wann, J. (2003). *Controlling steering and judging heading: retinal flow, visual direction, and extraretinal information*. *Journal of experimental psychology. Human perception and performance* (Vol. 29, pp. 363–378). doi:10.1037/0096-1523.29.2.363
- Yonas, A., Bechtold, A., Frankel, D., Gordon, F., McRoberts, G., Norcia, A., et al. (1977). Development of sensitivity to information for impending collision. *Attention, Perception, & Psychophysics*, 21(2), 97-104.

