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# A Longitudinal Study Investigating Brain Responses to an Audio-Visual Loom in Extra-Stimulated Infants Using High-Density EEG

Master's thesis in Psychology

Supervisor: Audrey van der Meer

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### **Abstract**

The present study investigated cortical responses to an audio-visual looming stimulus approaching at three different velocities in infants who had received extra motor-stimulation and infants who had received a traditional Western upbringing, using high-density electroencephalogram (EEG). 20 infants participated in the study, 10 (4 girls) of whom received extra motor-stimulation (baby swimming lessons) and 10 (4 girls) being traditionally-raised control infants. Infants were tested first when they were, on average, 20 weeks and again when they were, on average, 43 weeks. The aim of the study was to examine whether extra motor-stimulation facilitated audio-visual motion perception by analysing auditory and visual evoked potentials (AEP and VEP) as well as induced brain activity through frequency-analyses (temporal spectral evolution, TSE). Results showed AEP and VEP peaks to appear closer to collision with increasing age. Extra-stimulated infants showed responses later in the looming sequence than controls at the first session, but not at the last. For VEPs, all infants displayed longer times-to-collision (TTC) for slow looms, and shorter for medium and fast approaching looms at the first session, while more or less time-fixed responses (-0.6 s) were seen in all speeds at the last session, suggesting a shift to a more efficient timing strategy in response to the loom. AEPs also occurred closer to collision with age but were not seen at fixed times like the VEPs at the last session. Time-frequency analyses revealed low-frequency activity (delta-band and theta-band) at an early age and activity in higher frequency-bands (alpha-band and beta-band) later in the first year of life in all infants in both visual and auditory areas, suggesting more mature processing of the audio-visual loom. Additionally, extra-stimulated infants also showed more sophisticated, less widespread, activity at the first testing session than controls. Findings suggests that receiving extra motor-stimulation may possibly facilitate development of multisensory motion perception. To develop possible interventions for infants with abnormal development in motion perception, further research investigating the relationship between additional motor-stimulation and motion perception is required.

## Sammendrag

Tre ulike hastigheter av en audio-visuell looming (voksende) stimulus (roterende sirkel) ble brukt for å undersøke kortikale responser registrert med elektroencefalogram (EEG) i spedbarn som hadde fått ekstra motorisk stimulering og spedbarn som hadde en tradisjonell oppvekst uten ekstra motorisk stimulering. 20 spedbarn deltok i studien hvorav 10 (4 jenter) mottok ekstra motorisk stimulering i form av babysvømming og de resterende 10 (4 jenter) hadde en tradisjonell norsk oppvekst. Spedbarna ble testet første gang da de var, i gjennomsnitt, 20 uker gamle og igjen da de var, i gjennomsnitt, 43 uker gamle. Studiens hensikt var å undersøke om ekstra motorisk stimulering kunne fremme audio-visuell bevegelsespersepsjon gjennom analyser av auditive og visuelt fremkalte potensialer (AEP og VEP), samt analyser av hjerneaktivitet gjennom frekvensanalyse (TSE). Resultatene viste at AEP og VEP responser oppsto nærmere den audio-visuelle kollisjonen med økende alder. Ekstrastimulerte spedbarn viste også responser nærmere den virtuelle kollisjonen enn kontroll-spedbarna ved første testing. Alle spedbarn viste lengre tid-før-kollisjon (TTC) i sakte looms, og kortere TTC for medium og raske looms ved første testing. Spedbarna viste imidlertid VEP ved et mer eller mindre fiksert tidspunkt (-0.6 s) ved siste testing, noe som tyder på en endring av timing-strategi fra en strategi som var mindre effektiv til en strategi som var bedre egnet for å oppfatte stimulusen. AEP oppsto også nærmere kollisjonen ved siste testing, men viste ikke den samme tidspunktfikseringen som VEP. TSE viste lav-frekvens-aktivitet (i delta- og theta-band) ved tidlig alder, og aktivitet i høyere frekvenser (som i alpha- og beta-band) i både visuelle og auditive områder ved slutten av spedbarnas første leveår. Det kan tyde på mer modne hjernerresponser i prosesseringen av den audio-visuelle loomen. Ekstrastimulerte spedbarn viste også mer sofistikert, og mindre spredning, i aktivitet enn kontrollene allerede ved første testing. Resultatene samlet tyder på at ekstra motorisk stimulering kan være delaktig i utviklingen av multisensorisk bevegelsespersepsjon. Ytterligere forskning er nødvendig for å undersøke koblingen mellom ekstra motorisk stimulering og bevegelsespersepsjon, da det vil kunne være med på å forme intervensjoner og behandlingsmetoder for individer med atypisk utvikling i bevegelsespersepsjon.

## Introduction

Whether it be playing sports or simply crossing the street, perceiving motion is pivotal for avoiding potentially harmful events and navigating the environment efficiently. Avoiding objects approaching on a collision course requires accurate multisensory motion perception and precise judgement of time-to-collision. Important for judging time-to-collision, as well as obstacle avoidance, is the concept of optic flow first introduced by James J. Gibson (Kayed & van der Meer, 2000; Wilkie & Wann, 2003). Gibson described optic flow as the pattern of visual information caused by the individual's own movements (Gibson, 1979). The development of optic flow skyrockets during the first year of life, as does independent movement and development of brain areas responsible for perceiving motion, all seemingly affecting each other.

Visual information from the environment passes through the eyes, the lateral geniculate nucleus (LGN), and then further to the primary visual cortex (V1) in the calcarine sulcus, located in the occipital lobe. Visual motion processing is associated with the dorsal stream, which leads from the occipital lobe, through the medial temporal area (V5/MT), the medial superior temporal (MST) area, and to the parietal lobe (Andersen, 1997; Creem & Proffitt, 2001). Additionally, layer 4B in V1 contains a concentration of direction selective neurons, and is believed to be the starting point of the visual motion processing before the information travels to the higher cortical areas such as MT/V5 and MST for further complex processing (Andersen, 1997; Orban et al., 1995). Neurons in the dorsomedial superior temporal area (MSTd) in monkeys have proven to be particularly sensitive to motion information such as rotating and expanding motion patterns in addition to frontal parallel planar motion (Duffy & Wurtz, 1991), which is important for detecting looming objects. The term looming refers to the last part of the approach of an object accelerating towards the perceiver (Kayed & van der Meer, 2007), and can also be presented auditorily where the sound growing in intensity and/or pitch offers additional information of the approaching event (Neuhoff, 2001).

The brain's ability to combine visual and auditory information is of great importance as vision and audition contribute with distinct, but complimentary, information when localizing stimuli (Knudsen & Brainard, 1995). Although not as well studied as its visual counterpart, auditory looming perception can be interesting to investigate as it serves an auxiliary function to vision in detecting looming objects (Ghazanfar, Neuhoff, & Logothetis, 2002; Seifritz et al., 2002). Sounds travel through the outer and middle ear and towards the hair cells in the basilar membrane in the cochlea that are sensitive to the specific frequency of

that particular sound. The information passes through the auditory nerve and is processed in the primary auditory cortex (A1) located in the temporal lobe (Warren, 2008). When dealing with looming sounds, especially with rising tones, areas like the right superior temporal plane (TP) and superior temporal sulcus (STS) are shown to be involved (Seifritz et al., 2002). Further, the visual motion complex (hMT/V5+) seems to be involved in auditory directional sensitivity (Alink, Euler, Kriegeskorte, Singer, & Kohler, 2012). Multisensory integration is dependent on the interaction between several brain regions (Maier, Chandrasekaran, & Ghazanfar, 2008), and using auditive as well as visual information in studies with looming stimuli offers an opportunity to better understand how different sensory modalities develop and work together.

Previous studies have discovered that infants are capable of combining distinct aspects of modalities and thus understand that some perceptual entities belong together. Kaye and Bower (1994) conducted a study combining tactile and visual information using dummies that showed infants as young as 12 hours were able to match seen shape with orally presented shape. Kuhl and Meltzoff (1982) carried out an experiment on intermodal perception with 18 to 20-week-old infants that showed an ability to detect the auditory-visual correspondence of presented speech sounds. Another study, conducted by Orioli, Bremner, and Farroni (2018) found that when neonates were tested on visual looming and receding objects alongside a rising or decreasing sound, infants were able to match the increasing sound with the correct visual information by looking longer at the looming stimuli congruent with the rising sound. Furthermore, a study of young adults showed that visual stimuli affected the participants' ability to correctly identify the localisation of a sound source, which could be an indication that the brain continuously attempts to match auditory and visual stimuli (Bonath et al., 2014).

Infants' movements have commonly been viewed as reflexes, contrary to wilful actions. However, studies show that infants possess prospective control, i.e. the ability to anticipate events, and are acting upon their environment at a very early age (Lee, Craig, & Grealy, 1999; van der Meer, van der Weel, & Lee, 1995; von Hofsten, 1982; von Hofsten & Rosander, 1997). Following objects with smooth eye movements is an early indication of development of prospective control, which is an ability found to be developed in the first three months of life (von Hofsten & Rosander, 1997). Prospective control is dependent on information acquired through perception and is important in order to respond successfully to the events of everyday life. An appropriate way of examining prospective control is to conduct experiments with objects on collision course and measure brain responses as the object is looming towards and virtually colliding with the infant (Agyei, van der Weel, & van

der Meer, 2016). Studies on visual looming have shown infants to respond to the loom at variable times-to-collision. Some infants have been shown to distinctly differentiate between loom speeds at early ages while no differentiation have been seen in older infants, suggesting the use of different timing strategies when perceiving the loom (Kayed & van der Meer, 2000, 2007; van der Meer, Svantesson, & van der Weel, 2012). Less efficient strategies based on the loom's angle or velocity were seen when infants were young, while a more appropriate and efficient timing strategy based on time was seen towards the end of the first year of life. As infants gain more experience with the surroundings, accurately judging time-to-collision, and thus showing adequate prospective control, is necessary for successful interactions with the environment. The shorter and more fixed time-to-collision (TTC) seen in response to looming stimuli during infants' first year of life has also been attributed to axonal myelination in neurons that increase transmission speed of the electrical signals as well as the maturation of local glucose metabolic rates (Agyei et al., 2016; Chugani, Müller, & Chugani, 1996; Loenneker et al., 2011), and has additionally been linked with self-produced locomotion (Kayed & van der Meer, 2007; van der Meer et al., 2012). Thus, individuals' processing of, and involvement in, their surroundings depend to a large extent on the development and interplay of both cognitive aspects and motor skills.

Cultural traditions may further offer an insight in the relationship between motor and perceptual development. A cross-cultural study by Keller, Yovsi, and Voelker (2002) showed that Cameroonian Nso mothers focused on motor development to a greater extent than their German counterparts. Many African cultures emphasize the importance of early motor-stimulation. Mothers in these cultures are seen to purposefully train their infants to obtain gross motor control at an early age. For the Nso this was seen as necessary as children were expected to aid their parents with various tasks, e.g. farming. Childrearing in Western cultures, on the other hand, is characterized by the infant spending a lot of time on its back. For example, in Norway parents are encouraged not to interfere in infants motor development (Skjæret & Sperstad, 2012), and infants therefore rarely receive deliberate training to rapidly gain motor control or accelerate the development in any way. Nso mothers were reported to view inactivity as a hindrance, and potentially dangerous, for development. Another study investigating motor milestones in several different ethnical groups found that Bangladeshi and Pakistani infants were more likely to show a delay in certain motor and communicative gestures compared to African and Caribbean infants who, in turn, were less likely than white infants to show developmental delays of gross motor skills (Kelly, Sacker, Schoon, & Nazroo,

2006). The motor delay shown in Bangladeshi and Pakistani infants was explained by cultural customs.

The types of motor stimulation provided to many African infants by their caregivers are less common in Western cultures. However, infants partaking in baby swimming programmes have shown certain early motor advancements. A study conducted on baby swimmers in Iceland showed that independent standing, which typically emerges at around 9-16 months of age, was achieved at a much earlier age (3-8 months) when infants participated in deliberate training (Sigmundsson, Loras, & Haga, 2017). Early motor stimulation practices, like baby swimming, are compelling to use in developmental research as it may provide insights into the relationship between motor development and cognitive development.

When studying cognitive development in infants, non-invasive electroencephalography (EEG) has proven a suitable method. In addition to providing accurate temporal information, EEG is also easier to use in studies with infant participants compared to other, more invasive, neurophysiological and imaging techniques. Through EEG recordings it is possible to detect event related potentials (ERP) which represent the summed postsynaptic activity in underlying cortical regions in response to a specific event (Luck, 2005; Nunez & Srinivasan, 2006). For ERPs to be detected in the ongoing EEG, pyramidal cells must be aligned perpendicular to the scalp. With its high temporal resolution, EEG is suitable for examining brain responses happening at the millisecond timescale following the presentation of audio-visual looming information.

Induced oscillatory activity can also be studied from the recordings of EEG. Event-related phenomena represent frequency-specific changes in the ongoing EEG that is comprised of increases or decreases of power in different frequency bands. An increase in spectral amplitude is observed as event-related synchronization (ERS), while a decrease is observed as event-related desynchronization (ERD) (Pfurtscheller & Da Silva, 1999). The different frequency bands range from <1 Hz to >30 Hz. The lowest frequency band being delta (0.5-3.5 Hz), followed by theta (4-7.5 Hz), then alpha (8-13 Hz), and beta (14-30 Hz), and lastly gamma (>30 Hz) (Niedermeyer & da Silva, 2005). While ERPs are phase-locked to the event, ERS and ERD are not (Pfurtscheller & Da Silva, 1999). Instead, they are time-locked to the stimulus and cannot be extracted by methods such as averaging, like ERPs can, but must rather be revealed through frequency analysis (Luck, 2005). Oscillatory activity in relation to visual looming stimuli have shown to be characterized by theta activity in typically developing infants (Agyei et al., 2016; Kahana, Seelig, & Madsen, 2001; van der Weel & van der Meer, 2009). Multimodal stimuli can elicit activity in the lower beta-band (Senkowski,



Molholm, Gomez-Ramirez, & Foxe, 2006; Senkowski, Schneider, Foxe, & Engel, 2008; von Stein, Rappelsberger, Sarnthein, & Petsche, 1999). Additionally, Maier, Chandrasekaran, and Ghazanfar (2008) presented findings of audio-visual looming signals eliciting increased gamma-band activity in the auditory cortex and STS in monkeys, compared to stimuli with unimodal or receding properties, indicating a possible greater sensitivity to approaching looming stimuli than receding ones.

Using high-density EEG, this study aimed to investigate infants' brain responses to an audio-visual loom approaching at three different velocities, and whether extra stimulation could facilitate development of multimodal motion perception. It was hypothesised that there would be significant differences in AEP and VEP responses to the audio-visual loom during the course of the first year of life, and that the extra-stimulated infants would show their looming-related brain responses closer to collision than control infants who received a traditional upbringing. In line with previous studies (van der Meer et al., 2012; van der Weel & van der Meer, 2009), significant differences between loom speeds were expected to be found at the first testing session, when infants had not started crawling yet, but not at the last testing session when infants had at least nine weeks of experience with self-produced locomotion. Additionally, brain responses in the visual cortex were presumed to be more prominent compared to the auditory responses when perceiving the loom. Earlier findings have shown young infants to display induced oscillatory activity in the theta-band (Agyei et al., 2016; Orekhova, Stroganova, Posikera, & Elam, 2006; van der Weel & van der Meer, 2009), while activity in the alpha- and beta-bands has been seen as they get older (Agyei, Holth, van der Weel, & van der Meer, 2015). It was anticipated that oscillatory brain activity would be observed in the same frequency bands as in earlier studies over the course of the first year of life. However, extra-stimulated infants were expected to display more synchronised high-frequency activity than controls, possibly at an earlier age. Furthermore, multimodal stimuli have been shown to elicit activity in the beta- and lower gamma-band, and were thought to be found in both visual and auditory areas in all infants in the present study.

## Methods

### Participants

Twenty-four infants were recruited in the present longitudinal study. Four participants were excluded for not producing sufficient data for analysis at one or both testing sessions. Additionally, two infants were tested a total of three times but only the first and last sessions were included, as a result of no crawling experience at second testing. Infants' second/third session will hereafter be referred to as the last session for the sake of simplicity. The included participants consisted of ten (four girls) infants that had completed at least one course of 10 baby swimming lessons, equivalent to one lesson a week for 10 weeks. The remaining ten (four girls) were controls who had received a traditional Norwegian upbringing. Extra-stimulated infants were recruited through a beginners course at Pirbadet in Trondheim (see Appendix A for recruitment letter). Controls were recruited via birth announcements in the local newspaper, and by word of mouth. Extra-stimulated infants had a mean age of 20 weeks ( $SD = 1.06$ ) at the first test session, while the controls had a mean age of 19 weeks ( $SD = 2.65$ ). At this point, none of the infants in either group had experience with crawling. However, six of the 10 extra-stimulated infants and five of 10 controls were rolling over from back to stomach. Mean age at the last testing session was 43 weeks ( $SD = 7.12$ ) for extra-stimulated infants and 42 weeks ( $SD = 3.82$ ) for controls. All infants had experience with self-produced locomotion (crawling) for 9 ( $SD = 4.23$ ) and 10 ( $SD = 4.11$ ) weeks in extra-stimulated and control infants, respectively. All infants were born to term, displayed typical development, and parents reported no neurological deficits.

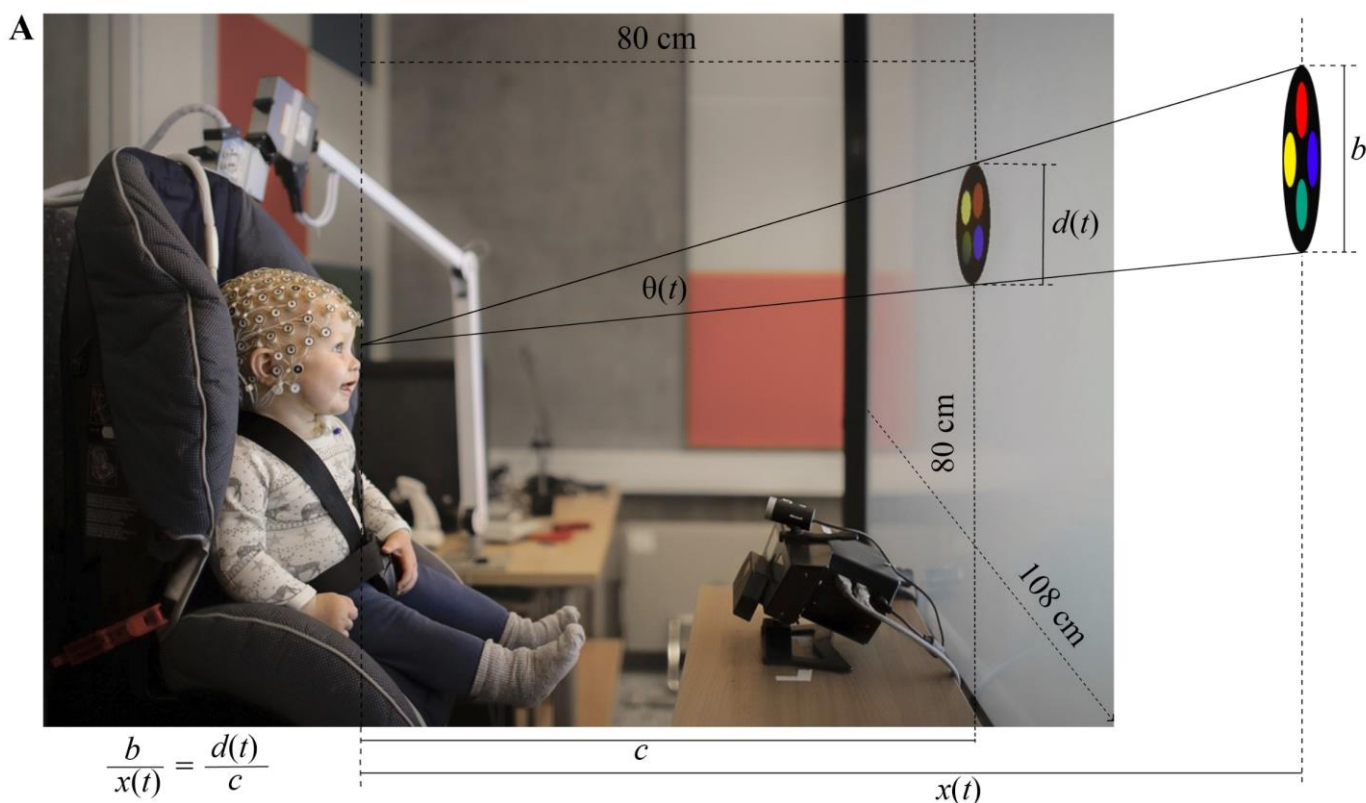
### Equipment and Data Acquisition

EEG activity was recorded with a Geodesic Sensor Net (GSN) consisting of 128 electrodes, and an EGI amplifier was utilized to amplify signals from the net to a Macintosh computer with Net Station software. A maximum impedance of 50 k $\Omega$  was used for optimal signal-to-noise ratio (Ferree, Luu, Russell, & Tucker, 2001). The sampling rate of the amplified signals was set to 500 Hz, the low pass filter being 100 Hz, and the high pass filter was 0.1 Hz. Stimulus onset and offset were controlled through the software E-prime (Psychological Software Tools, Inc), which again communicated with the Net Station program. The stimulus was presented on a large wide screen (108 cm x 80 cm). Infants were seated in a car seat approximately 80 cm from the screen. One infant was too little to sit in the car seat at the first testing session and was therefore placed on the parent's lap before initiating the experiment. The looming sound was presented through Logitech loudspeakers

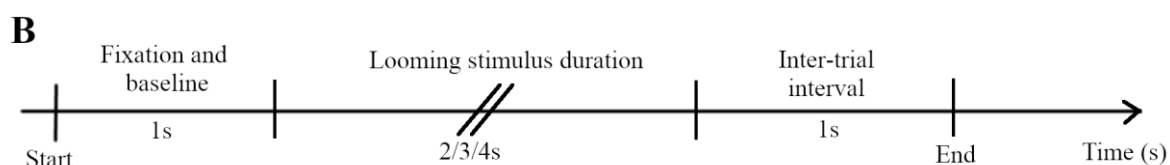
on either side of the screen. Tobii X50 infrared eye camera was used to track infants' eye movements throughout the experiment. Additional digital cameras were also used to record behavioural responses.

### **Experimental Stimuli and Paradigm**

Figure 1A shows the visual stimulus consisting of a two-dimensional disk with colourful (red, blue, yellow, and green) smaller circles within, programmed with E-prime. The four smaller internal disks were 1/3 of the diameter of the outer, larger disk. The disk was approaching at three different speeds while rotating at a constant angular velocity of 300 degrees per second. The three different looms lasted for 2, 3, and 4 seconds with the corresponding accelerations of  $-21.1 \text{ m/s}^2$ ,  $-9.4 \text{ m/s}^2$ , and  $-5.3 \text{ m/s}^2$ . When the visual loom commenced it was held at its smallest (visual angle =  $5^\circ$ , diameter = 6.5 cm, and virtual distance = 43.1 m) for a second before gradually expanding to its maximum (visual angle =  $131^\circ$ , diameter = 350 cm, and virtual distance = 0.0 m). After expanding to its largest size, the visual loom disappeared from the screen, leaving it blank for one second until the next trial started. All visual looms started at the same place on the screen and followed the same trajectory towards the virtual collision. The auditory loom, computed with the Audacity sound software (Audacity 2.0.3, The Audacity Team, 2013), was presented simultaneous with the visual loom. The sound itself was a dynamic “woop” /vɔ:p/ sound and grew in accordance with the visual loom. The frequency of the auditory loom ascended from hardly noticeable 140 Hz, where it was held at one second, before it grew in frequency to its loudest at 460 Hz. Looming sounds were sampled at a rate of 44.1 kHz, and intensity levels were constant at 60 dB.



*Figure 1A.* Display of the experimental setup including a diagram of the stimulus configuration. The mathematical formula in lower left corner of the image represents the increment of the loom. ©Photo by Elin Iversen, NTNU.



*Figure 1B.* A timeline of the approaching loom illustrating start and end of one trial, including duration of loom at 2, 3, or 4 seconds. “Fixation and baseline” represent the loom being held constant for 1 second at the beginning of the trial. “Inter-trial interval” is immediately after the virtual collision when the screen was completely blank (white) for 1 second before the end of the trial.

## Procedure

Parents arrived with their infants to the Developmental Neuroscience Laboratory (Nulab) for testing. Both verbal and written information about the experiment was given to the parents, and they were informed of the possibility of withdrawing from the study at any point. All signed an informed consent sheet prior to the testing (Appendix A). Infants were allowed to familiarise themselves with the lab (especially the toy nook) and get comfortable before the session was initiated. In order to find the right size EEG net, the infant’s head was

measured. The appropriate net was then submerged in a lukewarm saline solution for about ten minutes to ensure optimal connectivity. The next step was placing the net on the infant's head while (s)he was distracted by a lab-assistant blowing soap bubbles and/or shaking a rattle. After making sure the placement of the net was correct, infants, parents, and laboratory staff proceeded to the experimental room. The infant was placed in a car seat in front of the wide screen. The net was connected to the amplifier and connectivity was inspected. The control room, where all the computers for data collection and stimulus generation were located, was separated from the experimental room. A wall with a soundproof glass window connected the two rooms and made it possible for lab personnel to communicate via signs. The experimental room was equipped with sound absorbing materials on the walls. Lights in both experimental and control rooms were turned off for the testing. Testing session was initiated with an eye-calibration, which was followed by the onset of a series of different experiments on visual motion perception. The looming experiment was presented as the second out of four experiments. Infants usually found the looming quite interesting and each would be willing to pay attention for 47 and 43 trials, on average, for extra-stimulated and control infants, respectively. A parent was sitting next to the infant at all time during the session. The experiment was paused or discontinued if the infant showed signs of being uncomfortable or uninterested. The study was approved by the Norwegian Regional Ethics Committee and the Norwegian Data Services for the Social Sciences.

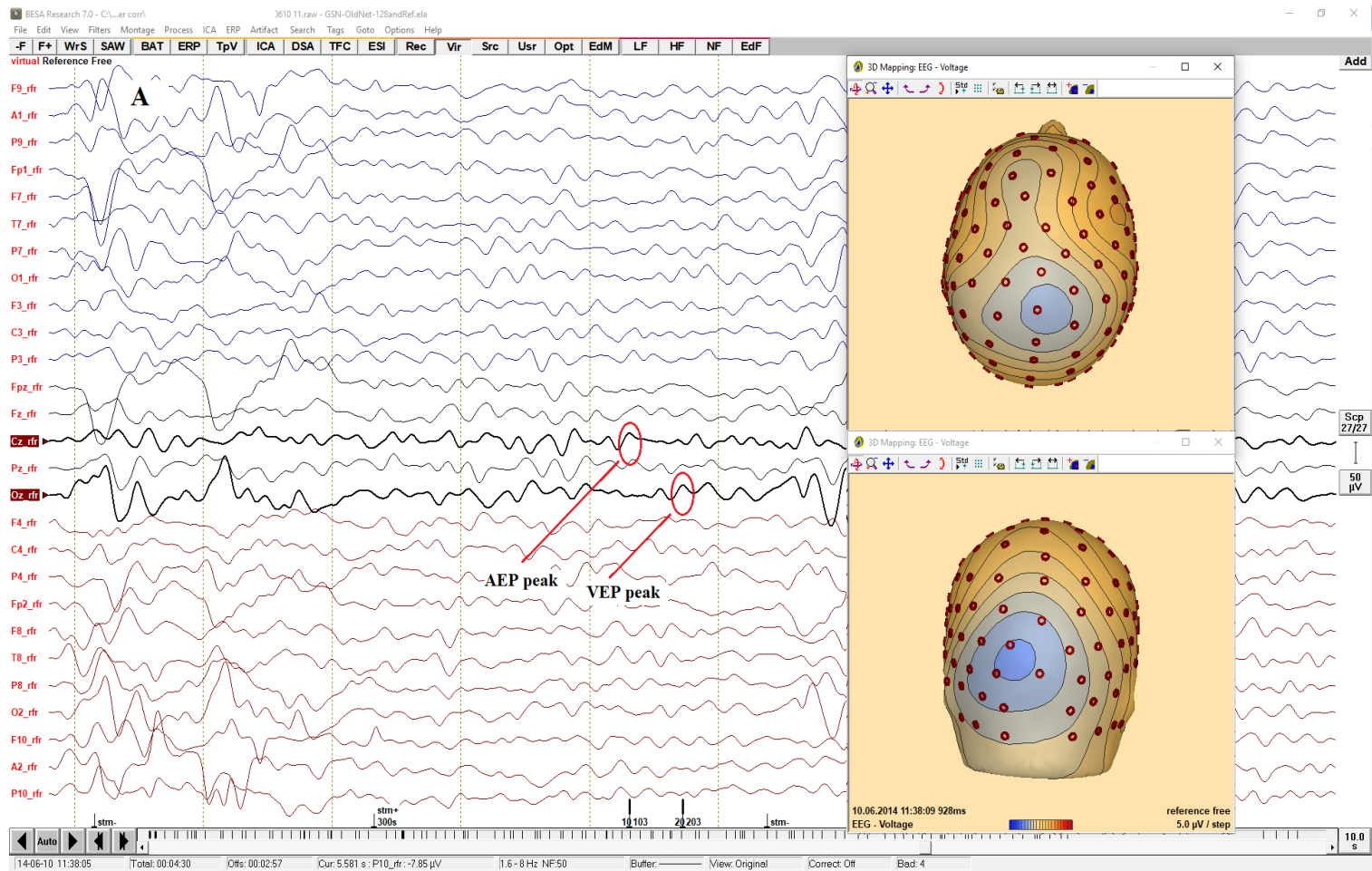
### **Data Analysis**

Recorded data were segmented from Net Station and stored on a hard drive for offline analysis. Brain Electrical Source Analysis (BESA) version 7.0 was used for the analysis of the raw data. At the start of the analysing process, standard channel configuration and digitized head surface points were added to the raw data file of each participant. Filters were set to 1.6 Hz for the low cut-off filter (high band pass) and 8 Hz for the high cut-off filter (low band pass) when registering auditory and visual evoked potentials. Notch filter was set to 50 Hz. These filters contributed to minimise noise in the EEG-data. No more than 10% of electrodes were marked as bad during analysis. A reference-free montage of 27 channels was also applied to make the data more easily accessible for analysis. Trials where infants were not looking at the screen were excluded from analysis.

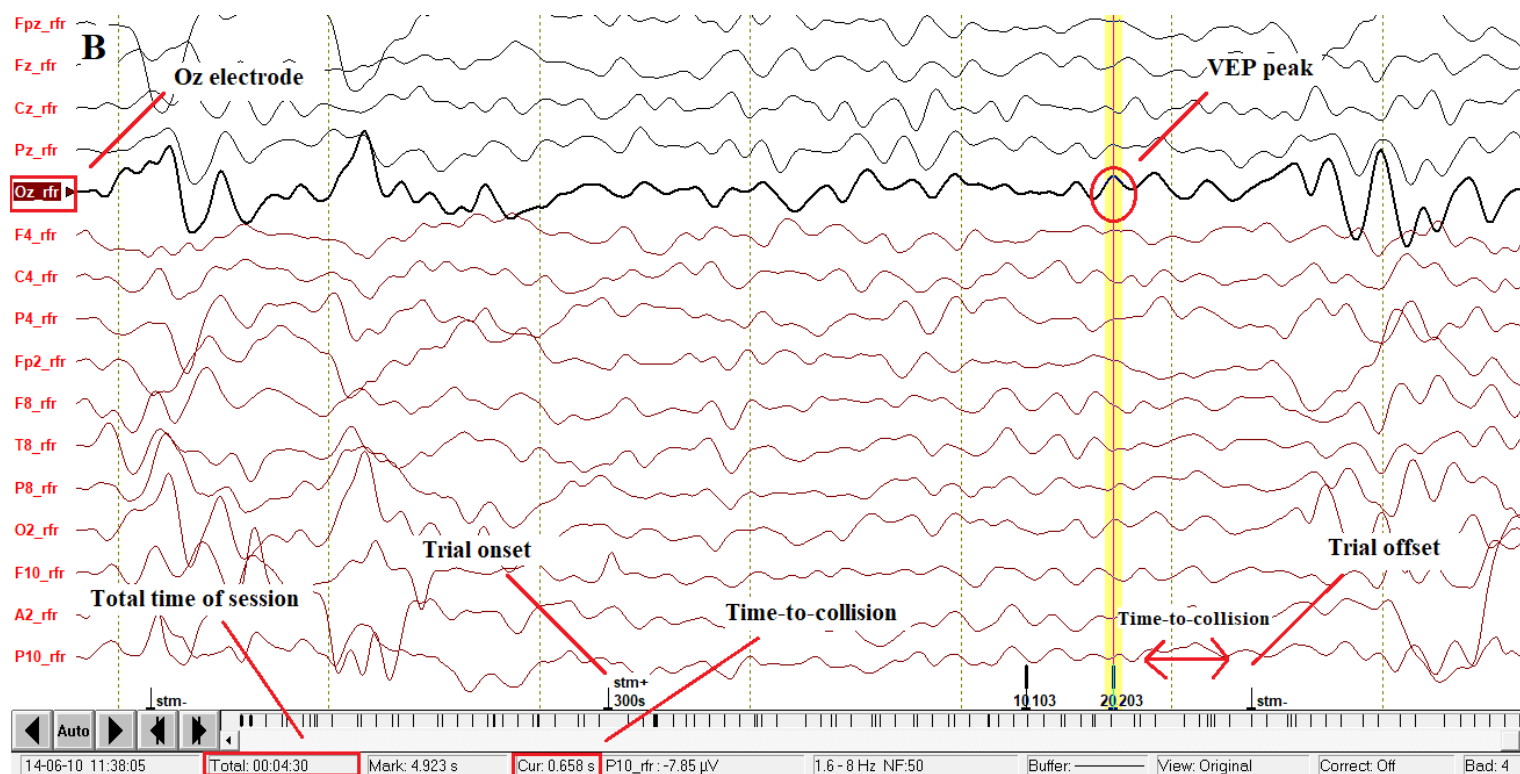
By recording electrical activity that is generated by large numbers of neurons aligned perpendicular to the scalp in a specific area, it is possible to measure event-related potentials (ERP) (Otten & Rugg, 2005). ERPs, such as auditory evoked potentials (AEP) and visual

evoked potentials (VEP), are considered to be responses to auditory and visual external stimuli, and are therefore assumed to represent ERPs of the auditory and visual cortices (Luck, 2005). AEPs and VEPs produce dense activation in the parietal and occipital areas, and central and occipital channels Cz and Oz corresponding to these areas were used when searching for ERPs produced by the audio-visual loom (Figure 2A) (Ellingson, Danahy, Nelson, & Lathrop, 1974; van der Meer et al., 2012). A manual inspection of each trial was conducted to select the correct AEP and VEP peaks, aided by the 3D-mapping (Figures 2A) of a build-up and decline of voltage in the chosen brain areas. ERPs towards the last half of the trial, i.e. closer to the stimulus offset, were assumed to be more closely related to the audio-visual collision. Furthermore, AEPs were always thought to appear further from collision than the VEPs, which was also accounted for when assessing ERPs.

**AEP and VEP analyses.** Average time-to-contact for all AEP and VEP peaks were calculated, including standard deviations, for all extra-stimulated and control infants at both testing sessions. An overview of the distribution of all looming-related responses in all loom speeds at both sessions can be seen in Table 1. Mean amplitude for AEP and VEP peaks were also calculated for both extra-stimulated and control groups (Figures 3 and 4).



*Figure 2A.* The highlighted channels Cz and Oz show the AEP and the VEP, respectively, of a medium loom (3 seconds). Looming-related brain responses of a traditionally-raised 9-month-old boy (control infant) are displayed, from the last testing session. The 3D head models show dense activity around the Cz and the Oz electrodes.



*Figure 2B.* Presentation of an enlarged version of Figure 2A. The highlighted channel (Oz) shows a visual evoked potential (VEP) in a medium loom speed (3 seconds). The chosen infant (same as in Figure 2A) displayed the VEP at 0.658 seconds prior to the collision, the accurate time point can be seen in the bottom toolbar marked with a red box. The total time of the session is also marked by a red box and so is the chosen electrode (Oz). Also marked are the trial onset, and offset, ending in the virtual collision.

Additionally, appropriate statistical analyses were employed to examine differences and interactions between factors. Analyses of time-to-collision of the ERPs, in addition to amplitudes, were conducted.

**Time-frequency analyses.** The oscillatory activity extracted from EEG can be partitioned into different types, namely evoked and induced activity. To better understand brain activity elicited by an audio-visual looming stimulus frequency analyses of the induced activity, alongside analyses of evoked activity, were carried out. Frequency analysis is an appropriate method for extracting induced activity as it is time-locked to the event and cannot be extracted with simple linear methods like averaging, as is possible for evoked activity.

Event files were made for every session and added onto the respective infant's raw file, so that only the chosen looming-related responses would be included in the frequency analysis. To run time-frequency analyses, multiple source dipoles that represented the relevant parietal and visual brain regions were used. Source montages were applied, separately for AEPs and VEPs, for optimal separation of brain activity (Berg & Scherg, 1994; Scherg &



Berg, 1991; Scherg, Ille, Bornfleth, & Berg, 2002). Areas shown to be related to processing motion stimuli were chosen when interpreting the data (Probst, Plendl, Paulus, Wist, & Scherg, 1993; van der Weel & van der Meer, 2009). For the visual areas, visual cortex radial left (VCrL), visual cortex lateral left (VCIL), visual cortex ventral midline (VCvM), visual cortex lateral right (VCIR), and visual cortex radial right (VCrR) were chosen. Corresponding auditory areas, auditory cortex radial left (ACrL), auditory cortex temporal left (ACtL), central midline (CM), auditory cortex temporal right (ACtR), and auditory cortex radial right (ACrR) were also analysed. In order to analyse information from the chosen auditory and visual regions, a four-shell ellipsoidal head model (Berg & Scherg, 1994; Hoehstetter et al., 2004) was generated for every infant. Source dipoles were inserted into the head model with the appending artefact-corrected coordinate files. The appropriate template for infants (0-18 months) was selected in BESA 7.0, with settings for bone thickness and conductivity at 3.0 mm and  $0.02 \sigma$ , respectively, as recommended for infant data (Grieve, Emerson, Fifer, Isler, & Stark, 2003; BESA information). Settings for filters and average parameters were kept as in the AEP and VEP analyses.

Time-frequency displays (Temporal Spectral Evolution, TSE) resulting from analyses, represented the changes in amplitude over time in each infant. Looming speeds were compared individually first, and then combined and compared to a static and non-sounding control condition. Further, time-frequency maps for each infant with corresponding statistical plots were computed and displayed. The frequency- and time-sampling for the displays were set to 1.0 Hz and 50 ms, respectively. Maps and probability plots exhibited activity between 2.0 Hz (lower frequency cut-off) and 50 Hz (higher frequency cut-off). Epochs were set from -300 ms to 300 ms.

## Results

### AEP and VEP Distribution

The visual and auditory responses of the looming stimuli were recorded from channels Oz and Cz. Below, the number and distributions of looming-related responses are illustrated (Table 1), as well as amplitude peaks (Figures 3 and 4) and time-to-collision for AEPs (Figure 5) and VEPs (Figure 6).

**Table 1**

Number and distribution of 1406 looming-related ERPs

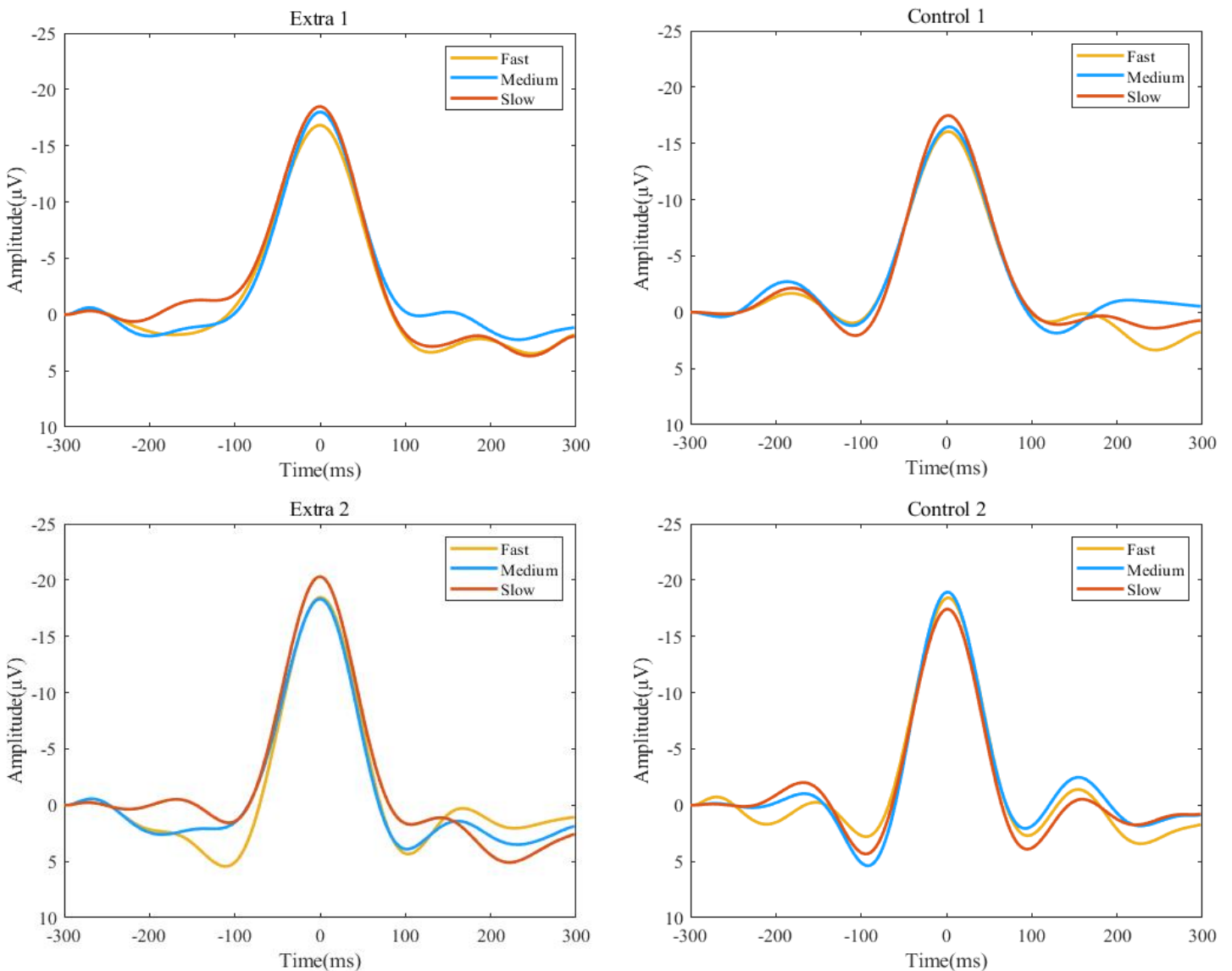
	<u>First session at 4-5 months</u>		<u>Last session at 8-12 months</u>	
	<b>AEP</b>	<b>VEP</b>	<b>AEP</b>	<b>VEP</b>
<b>Extra-stimulated infants</b>				
<b>Fast</b>	39	54	44	66
<b>Medium</b>	38	75	58	79
<b>Slow</b>	55	70	55	77
<b>Sum</b>	132	199	157	222
<b>Control infants</b>				
<b>Fast</b>	39	73	49	67
<b>Medium</b>	34	77	40	71
<b>Slow</b>	45	85	49	67
<b>Sum</b>	118	235	138	205
<b>ERP total</b>	684		722	

Table 1 displays a total of 1406 annotated looming-related ERPs for the infants receiving extra stimulation and control infants, at both testing sessions. AEPs and VEPs were recorded from the Cz and Oz channels, respectively. Extra-stimulated infants contributed on average 44 AEPs and 66 VEPs in each of the loom speeds at the first testing session, and on average 52 AEPs and 74 VEPs in each of the loom speeds at the last session. Control infants contributed on average 39 AEPs and 78 VEPs in each of the loom speeds at the first testing session, while at the last session they contributed on average 46 AEPs and 50 VEPs,

respectively. In every infant, at both testing sessions and in both groups, a larger number of VEPs than AEPs was recorded.

### Amplitude of Peaks

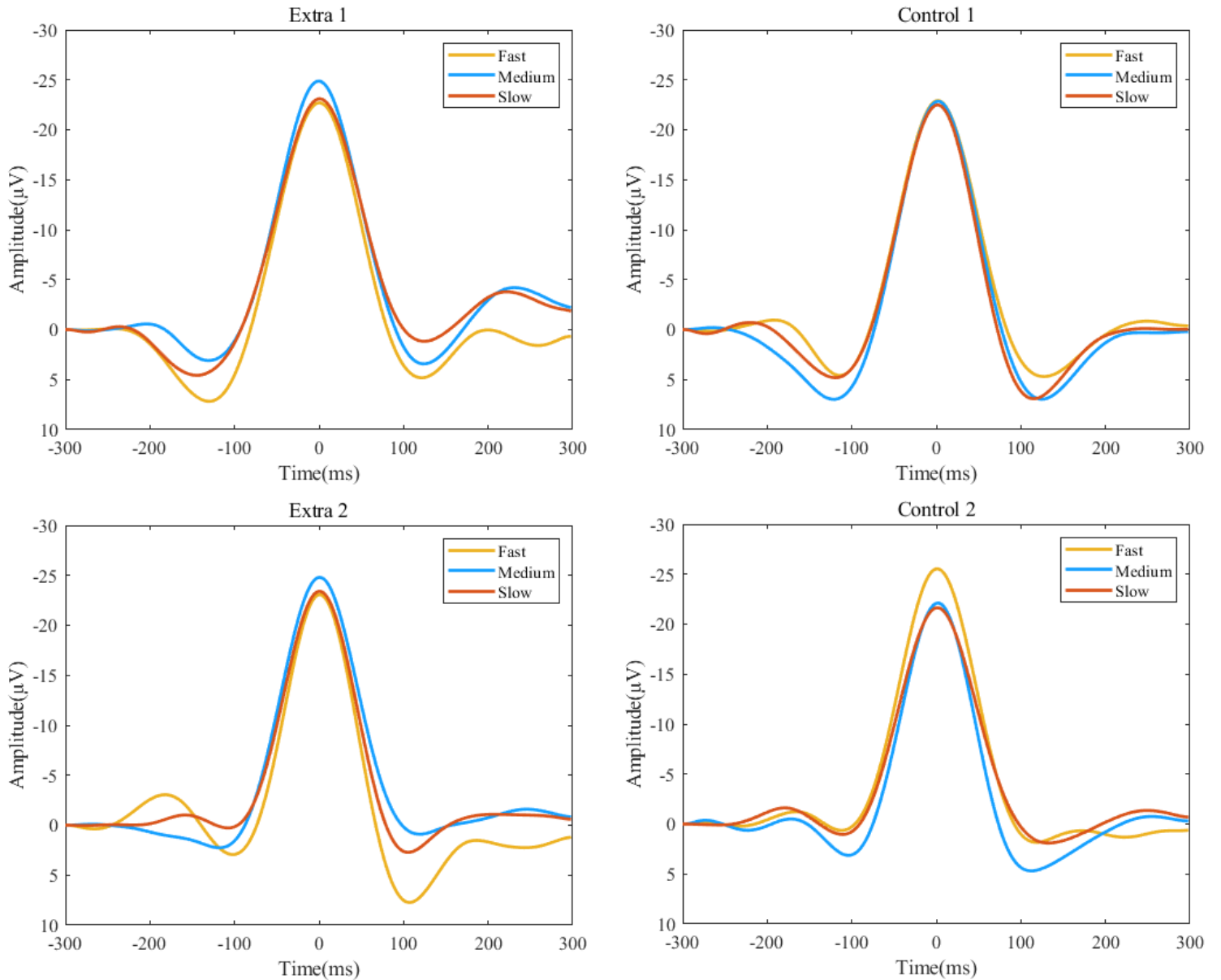
Averages on the amplitudes of looming-related AEP and VEP peaks for each infant were made and interpolated to the standard 81 channel electrodes. Grand averages were then computed combining all infants in their respective groups and sessions, displayed in Figure 3 and 4.



*Figure 3.* Grand averages for looming-related AEP peaks, recorded from electrode Cz. The figure shows the three different lobe speeds in yellow (fast), blue (medium), and red (slow) colours for extra-stimulated infants (Extra) and control infants (Control) at their first (1) and last (2) session. Amplitude is measured in  $\mu\text{V}$  and displayed from 10 to -25, while epochs are displayed from -300 to 300 ms. Peak amplitudes for AEPs are seen as slightly higher at the last testing session compared to the first session, for both groups.

On average, amplitudes of AEPs for the extra-stimulated infants were  $-16.98 \mu\text{V}$  at the first testing session and  $-17.72 \mu\text{V}$  at the last session, while amplitudes of VEPs at the same sessions for the same infants were, on average,  $-23.03 \mu\text{V}$  and  $-24.33 \mu\text{V}$ , respectively. Amplitudes for the AEPs of the control infants were on average  $-16.27 \mu\text{V}$  at the first testing session, and  $-17.72 \mu\text{V}$  at the last session. Control infants' amplitudes of VEPs were, on average,  $-23.87 \mu\text{V}$  at the first testing session, and  $-23.02 \mu\text{V}$  at the last session.

When running two repeated-measures ANOVAs on amplitude peaks separately for AEPs and VEPs no significant differences were found on any of the variables. However, the average amplitudes of VEPs were higher than the average amplitudes of AEPs in both extra-stimulated and control infants at both sessions, illustrated by Figure 3 and 4.



*Figure 4.* Grand averages of looming-related VEP peaks recorded from the Oz-electrode. Loom speeds are distinguished by different colours: yellow (fast), blue (medium), and red (slow) for extra-stimulated infants (Extra) and control infants (Control) at their first (1) and last (2) session. Amplitude is measured in  $\mu\text{V}$  and displayed from 10 to -30, while epochs are displayed from -300 to 300 ms. All looming-related VEP peaks show higher amplitudes than those of AEP peaks in Figure 3.

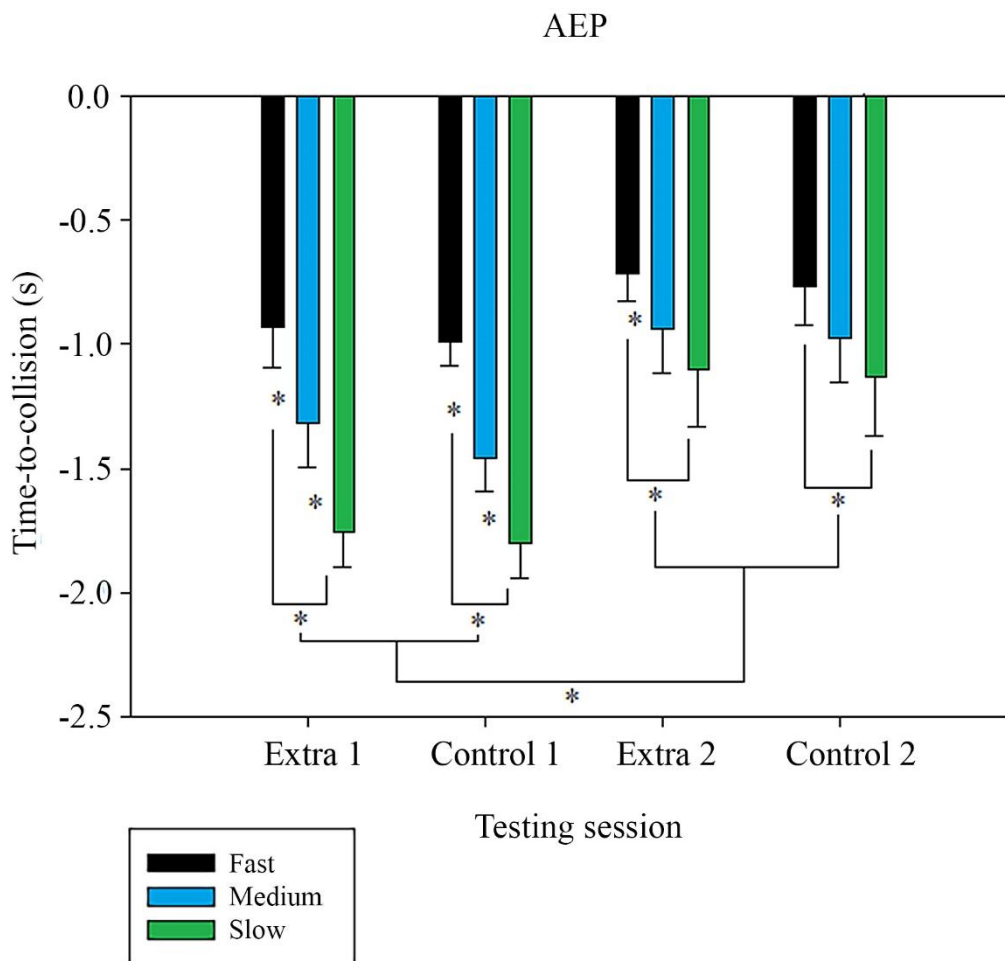
### AEP and VEP Responses

To examine average looming-related peak activation of visual and auditory evoked potentials in extra-stimulated and control infants at the two different testing sessions, two repeated-measures ANOVAs were conducted. The two 2 (groups [early stimulation, controls])  $\times$  2 (session [first, last testing session])  $\times$  3 (loom speed [fast, medium, slow]) repeated-measures ANOVAs were conducted on time-to-collision of the average looming-

related peak activation for AEPs and VEPs separately. Bonferroni correction was employed to adjust for multiple comparisons.

At the first testing session, extra-stimulated infants showed looming-related AEPs on average 1.35 s (SD = 0.48) prior to collision, while infants in the control group displayed responses, on average, 1.43 s (SD = 0.44) prior to collision. At the last testing session, extra-stimulated infants showed responses, on average, 0.89 s (SD = 0.36) prior to collision, while control infants showed responses, on average, 0.95 s (SD = 0.29) prior to collision.

For AEPs, a significant interaction effect of loom speed and session was found,  $F(2,36) = 26.44, p < .001$ , suggesting that in both groups looming-related responses occurred closest to collision for fast looms and further from collision for medium and slow looms, respectively, but only in the first session. A main effect of session was found, showing that, irrespective of loom speed and group, the looming-related AEPs occurred closer to collision in the last session than in the first session,  $F(1,18) = 166.79, p < .001$ . On average, fast speeds occurred at 0.96 s, medium at 1.39 s, and slow at 1.75 s prior to collision, for all infants combined at the first session, while the responses occurred on average at 0.73 s, 0.95 s, and 1.08 s prior to collision for fast, medium and slow looms, respectively, at the last session. Also, a main effect of speed was found, but as the last session did not show significant differences between all loom speeds, it was most likely caused by the underlying interaction effect and therefore not reported. Finally, a main effect of group was found  $F(1,18) = 6.41, p < .05$ , showing that the extra-stimulated infants showed AEPs significantly closer to collision than the control infants across loom speeds and sessions.



*Figure 5.* Bar graph of the average looming-related AEP peaks (including standard deviation bars) for extra-stimulated and control infants at first and last testing session for the three loom speeds, recorded from the Cz electrode. Averaged responses of time-to-collision of the fast, medium, and slow looms are represented by colours black, blue, and green, respectively. 0 on the y-axis represents the collision. For both extra-stimulated and control infants at both testing sessions, looming-related AEPs occurred closest to virtual collision for the fast looms, and earlier in the looming sequence at larger times-to-collision for medium and slow looms, respectively. Both extra-stimulated and control infants showed their looming-related AEP peaks closer to collision in the last session compared to the first session. Significant differences between loom speeds and sessions are marked with asterisks.

\*  $p < .001$

At the first session, extra-stimulated infants displayed looming-related VEP responses on average 1.12 s (SD = 0.41) prior to collision, while infants in the control group showed responses, on average, 1.24 s (SD = 0.44) prior to collision. At the second session, extra-stimulated infants showed VEP responses, on average, 0.59 s (SD = 0.25) prior to collision,

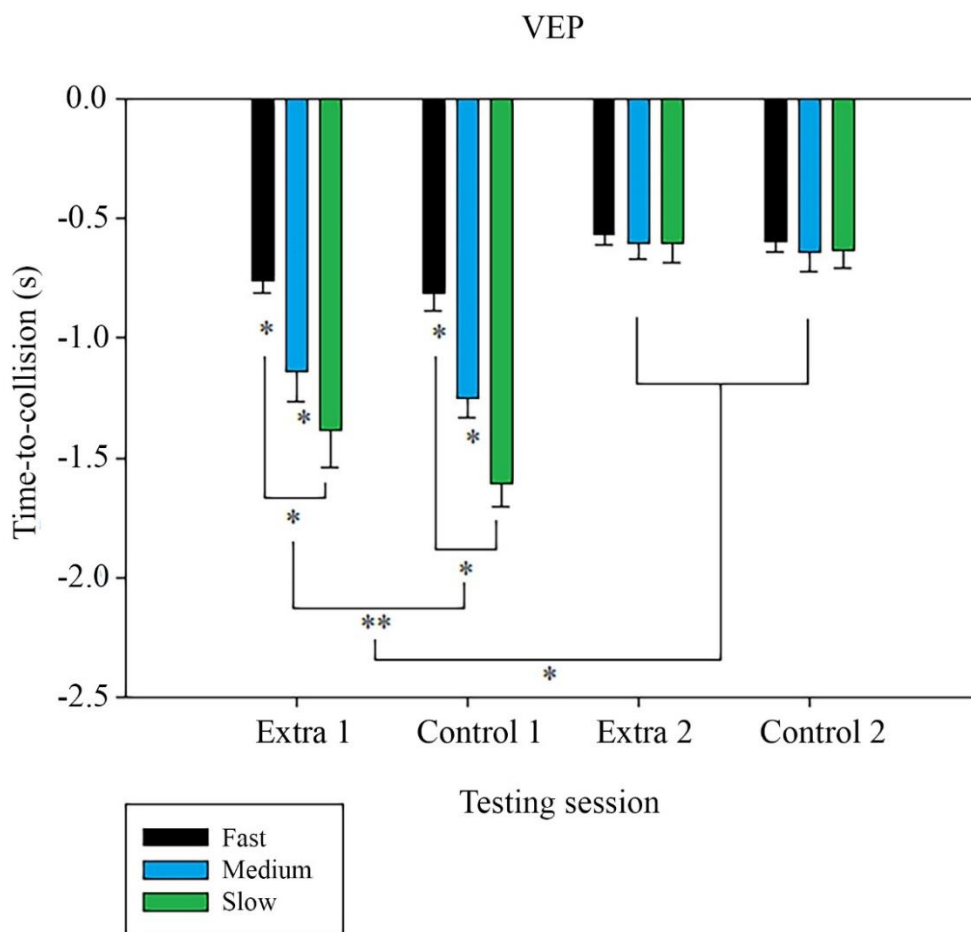
while control infants displayed responses, on average, 0.62 s (SD = 0.25) prior to collision. All looming-related VEPs were found to occur closer to collision than looming-related AEPs.

The repeated-measures ANOVA for VEPs revealed a significant three-way interaction effect of speed, session, and group,  $F(2,36) = 4.25$ ,  $p < .05$ , showing that extra-stimulated infants displayed looming-related responses closer to collision for all loom speeds compared to the controls, but only in the first session. No significant differences between loom speeds at the last session were found for either extra-stimulated (the average time-to-collision for combined speeds was -0.59 s) or control infants (the average time-to-collision for combined speeds was -0.62 s).

A two-way interaction effect was found for session and group,  $F(1,18) = 21.58$ ,  $p < .001$ , indicating that, irrespective of loom speed, the extra-stimulated infants displayed looming-related VEPs closer to collision than controls, but only at the first testing session. However, this finding does not add new information and is most likely a product of the three-way interaction. Results further showed an interaction effect of session and speed,  $F(2,36) = 194.38$ ,  $p < .001$ , suggesting a decrease in time-to-collision from first to last testing session of loom speeds, where slow looms reduced time-to-collision most (on average 0.88 s), medium looms reduced time-to-collision second most (0.57 s), and fast looms had the least reduction in time-to collision (0.20 s), independently of infants having received extra stimulation or not.

A significant main effect of session was found,  $F(1,18) = 9.08$ ,  $p < .001$  showing that both extra-stimulated and control infants showed responses closer to collision at the last session than the first session. Finally, a main effect of group was found,  $F(1,18) = 13.10$ ,  $p < .05$ , showing that the two groups were inherently different from each other as the extra-stimulated infants displayed looming-related responses closer to collision than the controls across sessions and speeds. However, the difference between groups was only seen in the first session and therefore the main effect is most likely a false effect caused by the underlying two- and three-way interaction effects. A main effect of speed was also found but as there were no significant differences between speeds in the last session it was also likely to be caused by the underlying two- and three-way interactions and therefore not reported.





*Figure 6.* Bar graph of the average looming-related VEP peaks (including SD bars) recorded from the Oz electrode. Averaged responses of time-to-collision of the fast, medium, and slow looms are represented by colours black, blue, and green. Looming-related responses to fast looms occurred closer to collision than for medium and slow looms, in the first session. VEPs occurred closer to collision, and at a relatively fixed time-to-collision across loom speeds of about -0.61 s for both groups, at the last session compared to the first session (on average, -0.59 s for fast, -0.62 s for medium, and -0.62 s for slow looms for both groups combined). Significant differences between loom speeds, sessions and groups are indicated by asterisks.

\*  $p < .001$ , \*\*  $< .01$

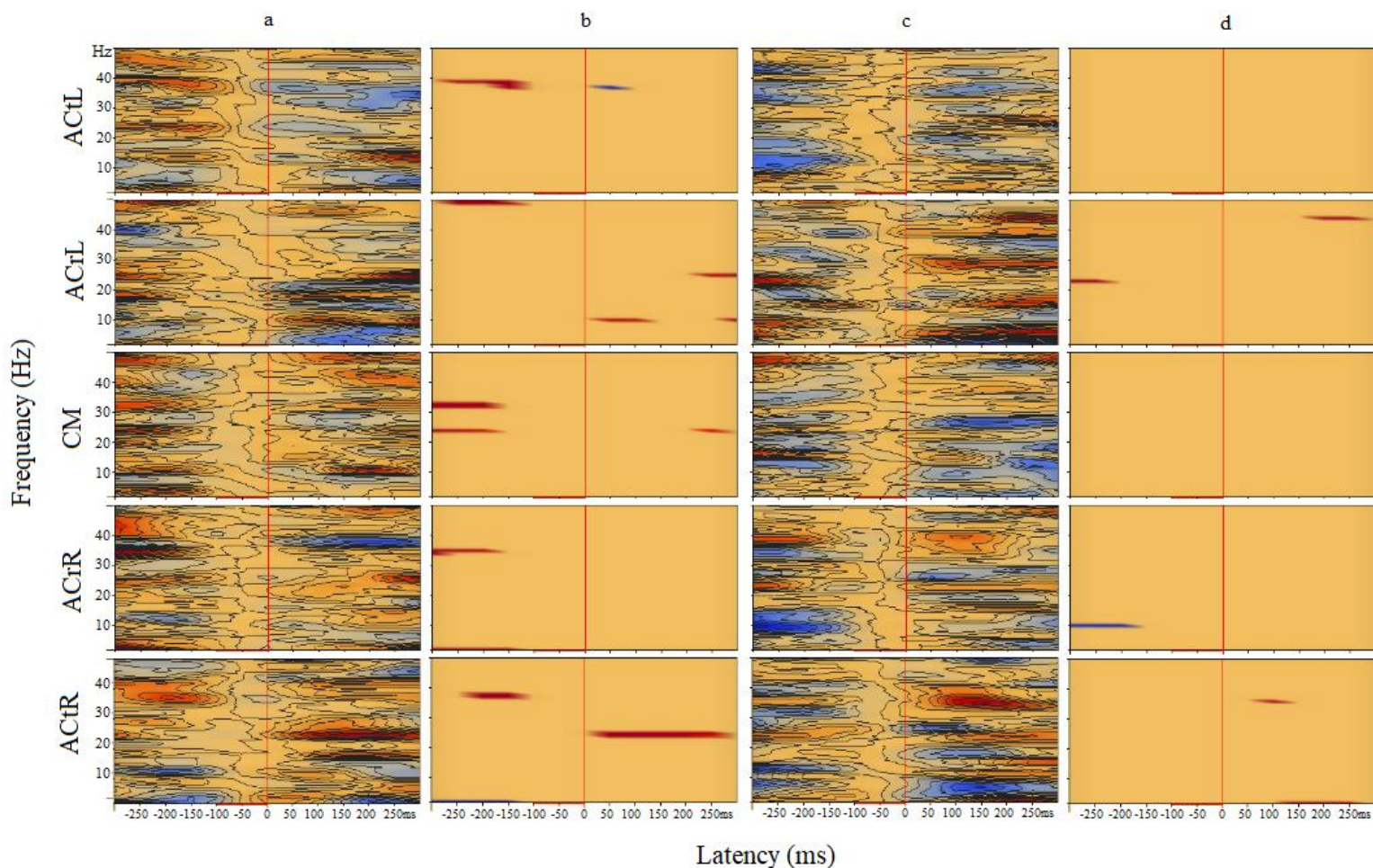
### Time-Frequency Displays

No differences between loom speeds were found when comparing each of the speeds individually to a silent and stationary control condition, they were therefore combined and compared to the control condition when generating the TSE-maps below. Typical infants that represented their respective groups, extra stimulation and control, were chosen to illustrate the induced activity related to the audio-visual loom. The typical extra-stimulated infant is always

displayed to the left in columns a and b of Figures 7, 8, 9, and 10, while the typical control is displayed to the right in columns c and d in the same figures.

At the first testing session, the auditory TSE-maps displayed synchronised activity in the lower alpha-band (8-13 Hz) and beta-band (14-30 Hz) for the extra-stimulated infants. Activity in the lower frequency-bands, such as delta (0.5-3.5 Hz) and theta (4-7.5 Hz), could be observed in both extra-stimulated infants, e.g. in the typical infant in Figure 7a, as well as in control infants, e.g. in Figure 7c. Even though desynchronised activity could be seen at some frequencies, more synchronised activity was displayed in all frequency-bands.

TSE probability plots displaying statistically significant activity were also registered for every infant, showing synchronised and desynchronised activity (represented by red and blue voxels) that was significantly different ( $p < .05$ ) from the silent control condition. Auditory probability plots for extra-stimulated infants at the first testing displayed significant synchronised delta-band activity in multiple areas of interest (ACtL, ACrR, and ACtR). Extra-stimulated infants also showed significant synchronised activity in the beta-band in all areas of interest (ACtL, ACrL, CM, ACrR, and ACtR). Control infants showed significant synchronised activity in the theta-band (in areas ACtL, ACrL, CM, and ACtR) and the beta-band (in areas ACrL, CM, ACrR, and ACtR) in the first testing session.

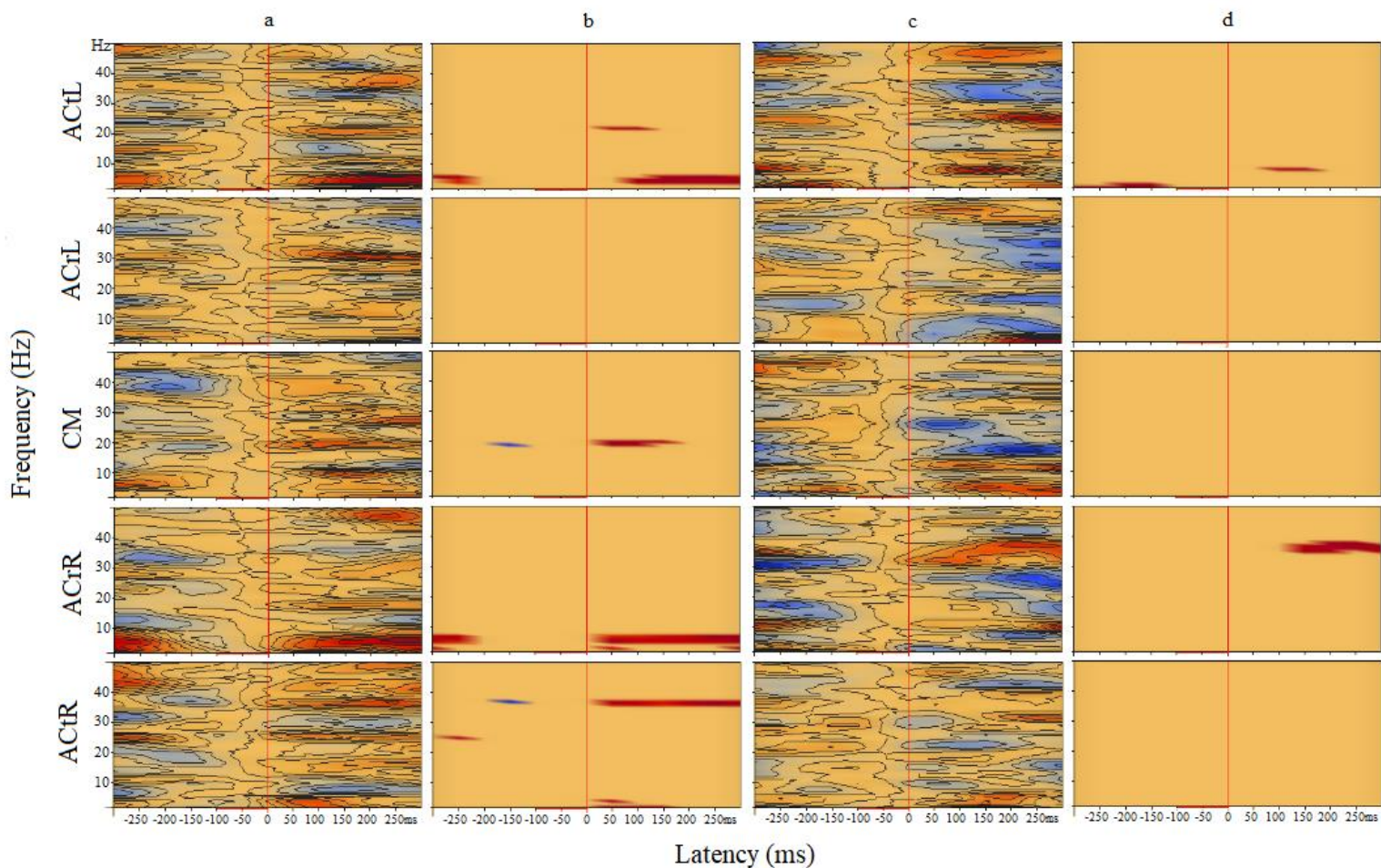


*Figure 7.* TSE maps of combined looming condition compared to a control condition for the auditory areas of interest: auditory cortex temporal left (ACtL), auditory cortex radial left (ACrL), central midline (CM), auditory cortex radial right (ACrR), and auditory cortex temporal right (ACtR). A red vertical line represents the top of the looming-related AEP-peak. Epochs are displayed from -300 to 300 ms on the x-axis. Y-axis displays frequency level measured in Hertz from 0 to 50. **Blue** areas represent decreased spectral amplitude (desynchronised activity), while **red** areas represent increased spectral amplitude (synchronised activity). Column a shows one typical extra-stimulated infant (4-month-old boy) and column c shows one typical control infant (4-month-old boy), while corresponding probability plots are displayed in columns b and d. Contoured lines in columns a and c accentuate the synchronised and desynchronised activity. All maps are from the first testing session.

The auditory TSE-maps for the last testing session (Figure 8), displayed overall less widespread activity than in the first testing for both groups. The extra-stimulated group displayed both desynchronised and synchronised activity in the beta- and early gamma (>30 Hz) frequency-bands. In the same frequency-bands, controls displayed desynchronised activity quite similar as in their first testing session.

Probability plots for the extra-stimulated infants showed more significant synchronised activity in higher frequency-bands, such as alpha- (in areas ACtL, ACrL, and CM) and beta-band activity (in areas ACtL, CM, ACtR, and ACrR), compared to the first testing session. Probability plots for control infants did not show an increase in activity in these frequency-bands. Both extra-stimulated and control infants displayed less activity in low-frequency bands, such as delta, at the last testing session.

The auditory probability plots showed overall more synchronised than desynchronised activity at all frequencies in both groups. However, in the extra-stimulated infants at the last session there was observed more desynchronised activity in the higher frequency-bands, e.g in the beta-band, compared to the first session. Controls displayed a relatively similar distribution of synchronised and desynchronised activity in the last session as in the first session.



*Figure 8.* TSE maps of combined looming condition compared with a control condition for the auditory areas of interest (ACtL, ACrL, CM, ACrR, ACtR). The red vertical line represents the top of the looming-related AEP-peak. Epochs are displayed on x-axis ranging from -300 to 300 ms. Y-axis displays frequency levels from 0 up to 50 Hz. The figure shows the same extra-stimulated infant (at 12 months) and control infant (at 9 months) from figure 7, but at the last testing session. Corresponding probability plots are displayed in columns b and d, respectively for the extra-stimulated infant and control infant. **Blue** areas represent decreased spectral amplitude (desynchronised activity), while **red** areas represent increased spectral amplitude (synchronised activity).

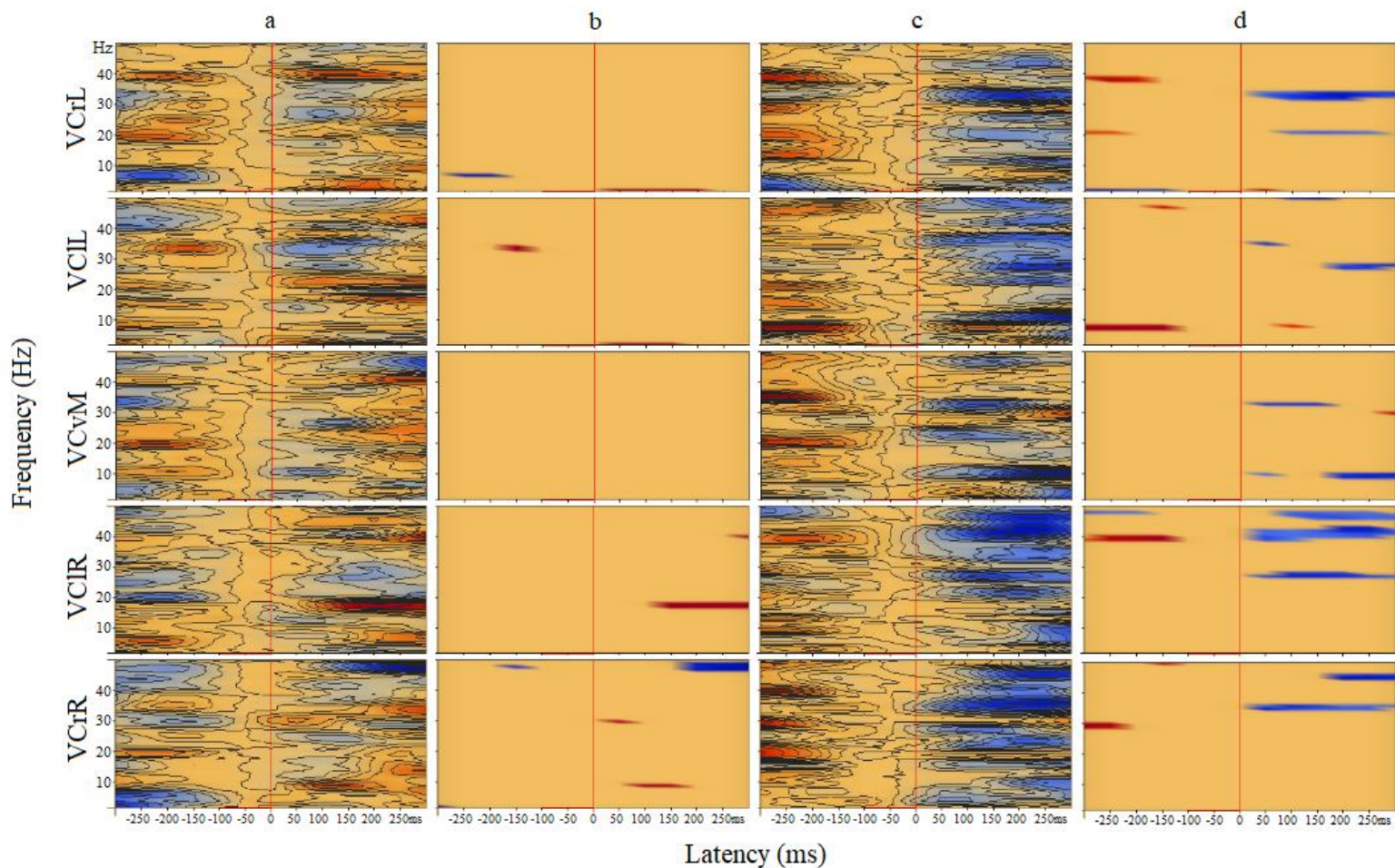
For the visual TSE-maps a typical infant that represented the extra-stimulated group (column a) and a typical infant representing the control group (column c) were displayed in Figures 9 and 10 with corresponding probability plots.

At the first testing session, extra-stimulated infants showed synchronised activity at lower frequency-bands such as theta and lower alpha. Controls showed widespread desynchronised activity, where desynchronised theta- and alpha-band activity were more prevalent in the first session.

Probability plots showed statistically significant synchronised activity in the lower frequency-bands, such as delta (in areas VCrL, VCIL, VCIR, and VCrR) and theta (in areas



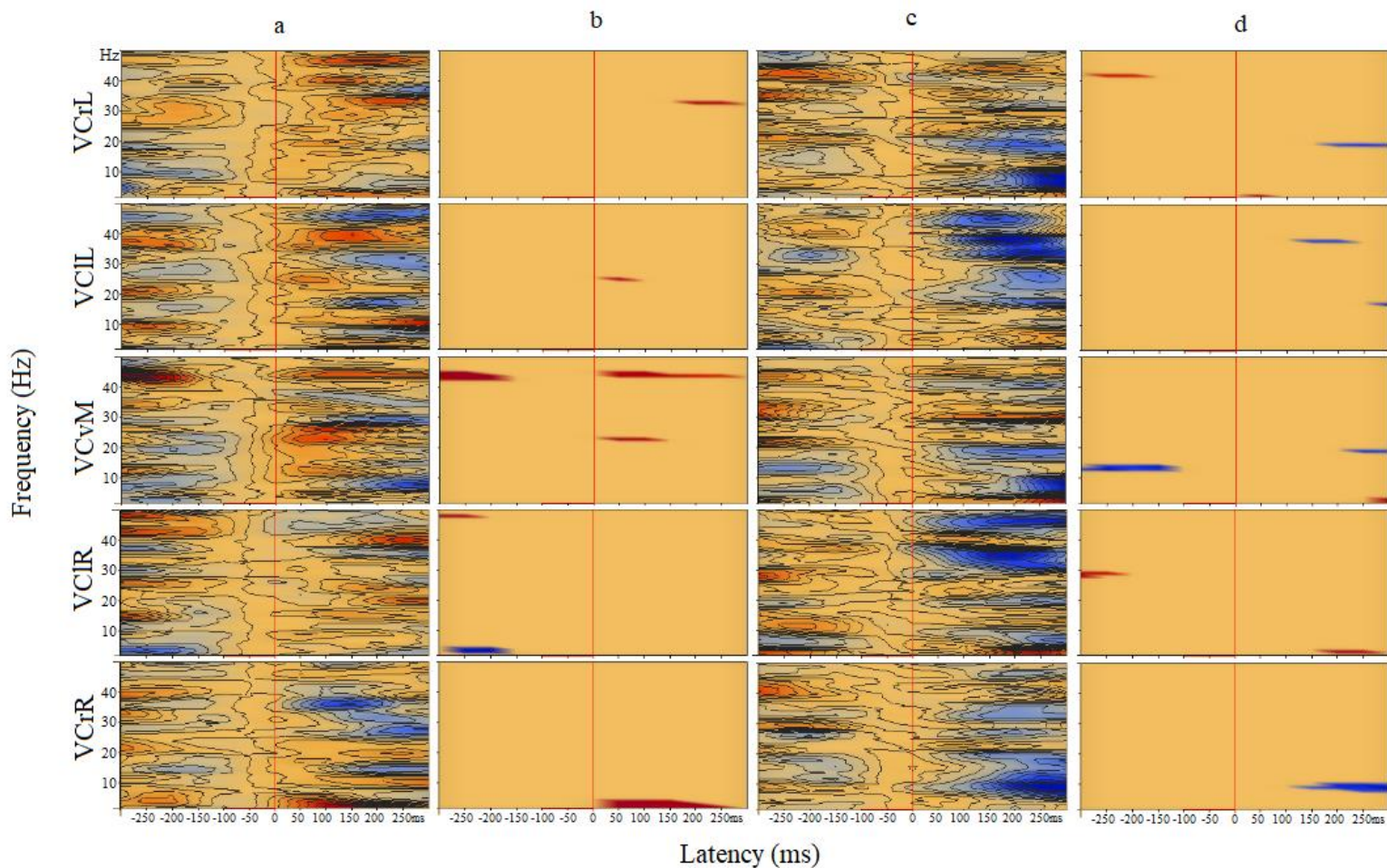
VCrL, VCvM, and VCrR), in the first testing session for extra-stimulated infants. Probability plots also reflected the widespread activity seen in control infants, as statistically significant activity in all frequency-bands could be seen (reflected in the typical infant in Figure 9d).



*Figure 9.* TSE maps show combined looming conditions compared with a control condition for the visual brain regions of interest: visual cortex radial left (VCrL), visual cortex lateral left (VCIL), visual cortex ventral midline (VCvM), visual cortex lateral right (VCIR), and visual cortex radial right (VCrR). Column a displays a typical infant from the extra-stimulated group (4-month-old boy), while column c shows a typical infant from the control group (4-month-old girl). Corresponding probability plots are displayed in column b for the extra-stimulated infant and in column d for the control infant. All maps are from the first session. A red vertical line marks the top of the VEP-peak. Epochs range from -300 to 300 ms on the x-axis, and frequencies on the y-axis are displayed up to 50 Hz. The activity is represented in blue (desynchronised activity) and red (synchronised activity) areas. Contoured lines in columns a and c are used to accentuate the activity.

At the last testing session, extra-stimulated infants (as the typical infant in Figure 10a) showed more upper alpha-band as well as beta-band activity than at the first session (Figure 9a). At the last session, control infants (as the typical infant in Figure 10c) showed more desynchronised activity (Figure 9c) in lower and higher frequencies of the beta-band.

Probability plots for extra-stimulated infants, displayed more activity in the upper alpha-band (in areas VCIL, VCvM, and VCIR) in the last session compared to the first session. Extra-stimulated infants also showed less significant delta-band activity in the last session than at the first session. Controls also displayed less significant activity in the delta-band as well as theta-band activity at their last session. Additionally, controls showed less widespread activity in their last session (illustrated by the typical infant in Figure 10c and d) compared to the first (Figure 9c and d).



*Figure 10.* TSE maps show the combined looming conditions compared with a control condition for the same visual areas of interest as Figure 9. Column a displays the same typical extra-stimulated infant as in Figure 9a, but at the last testing session (9 months). Column c shows the typical control infant at the last session (9 months). Columns b and d display probability plots for the extra-stimulated and control infants, respectively. **Red** areas represent induced synchronised activity, while **blue** areas represent induced desynchronisation. A red vertical line illustrates the top of the looming-related VEP-peak. Epochs range from -300 to 300 ms, and frequencies are displayed up to 50 Hz. Contoured lines are used to accentuate induced synchronisation and desynchronisation in columns a and c.

## Discussion

The present longitudinal study investigated brain responses to audio-visual looming in infants who had received extra motor-stimulation and traditionally raised control infants at two separate testing sessions. EEG recordings registered electrical brain activity in response to the loom appearing as auditory and visual evoked potentials (AEP and VEP). Analyses of AEPs and VEPs were conducted to reveal any differences in time-to-collision (TTC) of the looming-related responses in the two infant groups during the course of the first year of life. Analyses on the amplitudes of the looming-related peaks were also carried out. Furthermore, to investigate induced neuronal oscillatory activity in all infants at both sessions, time-frequency analyses were applied.

Analyses of both AEPs and VEPs revealed that, as infants grew older, brain responses occurred at shorter TTC. Extra-stimulated infants showed looming-related AEPs closer to collision than the control infants at both testing sessions. When combining speeds, AEP peaks occurred on average 1.31 s prior to collision at the first session for extra-stimulated infants and 0.89 s prior to collision at the last session, while controls showed responses on average 1.42 s prior to collision and 0.96 s prior to collision at the same sessions. The decrease in TTC over time is thought to be a sign of more rapid neural processing caused by increased myelination of axons, and fewer, more specialised groups of neurons (Grieve et al., 2003; Picton & Taylor, 2007). All infants showed significant differences between all three loom speeds of the AEPs at the first session, which might be indicative of a timing strategy that depends on pitch. The strategy based on pitch is not particularly accurate when judging precise time-to-collision of the looming sound and can be seen as equivalent to a visual timing strategy based on the angle of the loom presented in Kaye and van der Meer (2007). At the last session, for all three loom speeds, responses occurred closer to collision than in the first testing session for both extra-stimulated and control infants. Results also showed no significant differences between two of the three loom speeds. This may indicate a transition towards a more efficient strategy where responses are based on when the loom is a certain time away from the infant, rather than at a fixed angle. However, a full transformation from one timing strategy to another has yet to be completed which could suggest that auditory information is less salient in a multisensory stimulus. Zhou and colleagues (2007) found that when participants attended to an audio-visual stimulus, their judgment of TTC was far more accurate when the visual stimulus was presented alone or in combination with the auditory stimulus as opposed to when the auditory feature was their sole source of information. Both extra-stimulated and control infants were shown to underestimate TTC of the auditory loom to



a greater extent than the visual loom at both sessions, meaning AEPs occurred earlier in the looming sequence than did VEPs. This underestimation could serve as a warning signal or a “margin of safety” and be vital in aiding infants perceive the stimulus (Maier et al., 2008; Maier, Neuhoff, Logothetis, & Ghazanfar, 2004; Neuhoff, 2001).

For VEPs, differences between the groups in TTC of loom speeds were seen at the first testing session, but not the last. Extra-stimulated infants showed looming-related responses at the first session on average 1.10 s prior to collision (loom speeds combined), while control showed responses on average 1.22 s prior to collision. Even though extra-stimulated infants showed responses closer to collision at the early testing session, the difference between the groups evened out as they grew older. This suggests that the extra stimulation (one baby-swimming class a week) was not enough to produce long-lasting effects. Also, looming-related responses might be closer to collision at the first session for extra-stimulated infants because most of the organized extra-stimulation was completed prior to the first testing session. At the first session, both groups of infants displayed VEPs closest to collision for the fast loom, while VEPs of the medium and slow looms occurred further from collision. This is indicative of a less efficient timing strategy based on the visual angle of the loom and is often seen in younger infants as well as older infants with certain developmental challenges, e.g. as in preterm birth (Kayed, Farstad, & van der Meer, 2008; Kayed & van der Meer, 2000). Synaptogenesis is at its highest in primary visual cortex of infants between 4 and 6 months (Huttenlocher, 1990). However, at this time the neural networks have yet to become specialized and may be partly responsible for the inaccurate responses at the first testing session. At the last session, responses were more or less fixed at 0.6 s prior to collision for both infant groups. In line with earlier studies, this is a sign of development of prospective control and suggests a shift in timing strategy where infants utilise a more efficient strategy based on time instead of the loom’s angle or velocity (Agyei et al., 2016; Kayed & van der Meer, 2007; van der Meer et al., 2012). The standard deviations in the last session (SD = 0.25 for extra-stimulated infants, SD = 0.25 for controls) were also smaller compared to the first session (SD = 0.41 for extra-stimulated infants, SD = 0.44 for controls) which is an additional indication of the use of the more appropriate strategy based on time. Similarly to the changes seen in the auditory responses, this developmental trend can be partly ascribed to the increasing speed of electrical activity resulting in more rapid information transmission that is caused by the increased myelination of axons as well as smaller groups of more specialised neuronal networks working more efficiently throughout

the involved brain areas (Grieve et al., 2003). However, myelination starts earlier in the occipital lobes than the temporal lobes (Lippé, Kovacevic, & McIntosh, 2009), which could further explain the shorter TTC for VEPs than AEPs, especially at the first testing session.

Amplitude of oscillations are related to the number of synchronously firing cells, which means that slowly oscillating assemblies of cells with higher amplitudes consist of more neurons than faster oscillating ones (Pfurtscheller & Da Silva, 1999; Singer, 1993). The larger cortical synchronisation could mediate the multisensory integration of the audio-visual loom, as proposed by Maier, Chandrasekaran, and Ghazanfar (2008). The results in the present study did not reveal any significant differences in amplitudes between groups or sessions, but they did show amplitudes of VEPs (Figure 4) recorded from the Oz-electrode to be, on average, larger than amplitudes of AEPs (Figure 3) recorded from the Cz-electrode, regardless of the loom's speed. This finding could imply more neurons firing in response to the loom in the visual cortex compared to the auditory cortex, which in turn suggests that the visual cortex consists of a network of less specialised cells than the auditory cortex. An explanation of the higher amplitudes of VEPs as opposed to AEPs may be rooted in a greater complexity of the visual system regarding cell morphology, hierarchical organisation, and cortical circuits, among other things (Lippé et al., 2009; Rauschecker, 2015), which could affect communication within and across the visual cortex and other areas. However, it is worth noting that the infant scalp changes in terms of bone thickness during the first year of life (Grieve et al., 2003), which makes it harder to accurately measure the electrical activity, and thus draw appropriate conclusions about the changes – or lack thereof – in amplitude levels.

Time-frequency analyses of the induced brain activity were conducted to investigate changes in neural oscillations as a function of auditory and visual motion perception. When the combined looming conditions were compared to a control condition, analyses of the activity revealed both synchronised and desynchronised activity in different areas of interest in extra-stimulated and control infants at both testing sessions. In both auditory and visual TSE-maps, more activity in low-frequency-bands, like delta, appeared in the first session than the last session, for all infants. In the last session, activity in higher frequency-bands (e.g. upper alpha-band) were more prominent and activity in low-frequency-bands, such as delta and theta, were less prominent than earlier. Activity at lower frequencies, such as theta, are thought to reflect a more immature brain (Orekhova et al., 2006; Thierry, 2005). Neural networks were less specialised at the first testing session, thus making it more difficult for infants to perceive the loom accurately. Synchronised alpha activity is believed to represent

internally controlled attention where irrelevant stimuli are ignored so that attention can be allocated towards the important information in the visual field (Orekhova, Stroganova, & Posikera, 2001). The increase of synchronised activity in higher frequency-bands could represent a rearrangement in the cortical networks allowing for a more efficient processing of the loom in infants as they grew older. Another possible explanation of the change in oscillatory activity over the two testing sessions can also be linked to increasing self-produced locomotion (Agyei et al., 2015; Agyei et al., 2016; van der Meer et al., 2012).

In addition to an increase of activity in higher frequency-bands during the course of the first year of life, auditory TSE-maps also revealed more desynchronised activity for the extra-stimulated infants in their last session compared to their first session, while controls showed more or less the same distribution in both sessions. However, auditory TSE-plots revealed more synchronised than desynchronised activity in all frequency bands. Synchronised activity could be indicative of areas involved in the cross-modal integration of multisensory information (Bauer, Debener, & Nobre, 2020). Visual TSE-plots for extra-stimulated infants showed more synchronised activity in several frequency-bands in the first testing session compared to the controls at the same time, which might be a sign of slightly more sophisticated processing of the loom at the first session for the extra-stimulated infants. This finding coincides neatly with results from the VEP analysis which revealed shorter times-to-collision for the same infants at the same session, also suggesting a more sophisticated detection of the loom. Furthermore, beta-band activity was clearly pronounced in both testing sessions for both groups in both visual and auditory areas, although somewhat more in the visual areas. This finding suggests beta oscillations to be potentially the most common frequency in processing audio-visual stimuli, as supported by earlier multisensory studies (Senkowski et al., 2006; von Stein et al., 1999).

Overall, visual TSE-plots showed more areas of significant activity in all frequency-bands compared to their auditory counterparts, which signifies a visual dominance over auditory perception. Corbetta, Miezin, Dobmeyer, Shulman, and Petersen (1990) demonstrated that only a small amount of sensory information is possible to respond to at any given time by showing that participants who had to divide attention between several attributes of a stimulus performed worse on a discriminatory task than when they were focusing solely on one attribute. Some modalities must yield for others, as is the case for the auditory feature of the bimodal loom. Nevertheless, the auditory modality can serve as a warning-signal for time-to-turn or time-to-jump in looming danger (Guski, 1992), especially when sight is obstructed.

Brain development does not happen in a vacuum. Over the infant's first year of life remarkable changes occur in both psychological and physiological functioning. Infants who have mastered crawling are generally better at perceiving looming stimuli than before the onset of crawling (van der Meer et al., 2012). This is supported in the present study where both extra-stimulated and control infants perceived the audio-visual loom closer to collision after they all had some experience with crawling. Results from AEP and VEP analyses also displayed looming-related responses closer to collision for extra-stimulated infants than controls at the first session, which could result from the additional motor stimulation given. Johansson and Belichenko (2002) showed that rats being reared in a stimulating environment displayed a significant increase in dendritic spines of pyramidal cells compared to those who were not. Even rats with lesions showed a greater growth of dendrites when exposed to the enriched environment. This finding exhibits the brain's plasticity, which would be of the utmost importance in the development of future plasticity-based treatments (Ganguly & Poo, 2013).

Research on neuronal activity and changes directly linked to additional experience with locomotion in humans, is surprisingly scant. Nevertheless, studies investigating the role of motor experience in psychological development have given insight to how these not-so separate aspects relate to each other. A review by Adolph and Hoch emphasises that motor development is enabling, meaning that "new motor skills create new opportunities for exploration and learning that instigate cascades of development across diverse psychological domains" (Adolph & Hoch, 2019, p. 141). Other studies have also investigated the role of locomotion in various psychological processes, e.g. emotional responses (Anderson et al., 2013; Uchiyama et al., 2008). Adolph and Hoch (2019) also describe motor development as enculturated, which simply means that social and cultural customs are instrumental in shaping motor behaviour. Non-western cultures (like the Cameroon Nso) implement customs that commend the rapid onset of self-produced movements because it is necessary for their way of living (Keller et al., 2002). Infants with greater amounts of early motor stimulation are often more skilled at self-navigating (Keller et al., 2002; Kelly et al., 2006). This may also relate to early development of other psychological aspects, like more accurate motion perception, as it is needed for successful exploration and avoiding harmful events in the environment.

Perceiving a stimulus on collision course is vital for the well-being of any individual as the appropriate (re)action can be formed to the oncoming event. At birth, human infants are rather underdeveloped compared to other non-human animals, but in the first year of life the infant brain alone more than doubles in weight (Picton & Taylor, 2007). During this time

remarkable changes in the perceptual systems takes place, and around their first birthday, infants are making more accurate judgements of approaching objects than ever before.

A potential problem with the current study is the lack of experimenter blindness. Although not possible to carry out a blinded study for the present master's thesis, it should be required for articles pending publication. A bigger sample size as well as a greater diversity in respect to ethnicity and socio-economic status of parents are also necessary to ensure a representative sample.

The present study investigated cortical responses to an audio-visual looming stimulus over two separate testing sessions in extra-stimulated and control infants using high-density EEG. Results revealed that auditory evoked potentials and visual evoked potentials were shown closer to collision as infants grew older, suggesting more efficient processing of the audio-visual looming stimulus. Extra-stimulated infants showed responses later in the looming sequence than controls at the first session, which displayed a slightly more accurate perception of the audio-visual loom for the extra-stimulated infants at this time. Analysis of amplitudes showed higher activation of VEPs compared to AEPs, irrespective of infants, sessions, and loom speeds, suggesting more neurons firing in visual than auditory areas in response to the loom. Investigating the induced oscillatory activity through time-frequency analyses revealed indications of more mature brain activity as the infants got older, as well as signs of slightly more sophisticated activity in the extra-stimulated infants at the first session. The observed beta activity present in both auditory and visual areas, showed this frequency to be the most common in integration of the multisensory loom. Changes in neuronal functioning, such as more rapid information transmission caused by axonal myelination and other neurobiological factors, as well as infants increasing experience with self-produced locomotion are thought to be important contributions in successful development of motion perception. Given the importance of experience in advancing development, the present study offers a foundation from which future studies may continue to explore this link. By doing so, potential interventions can be developed aiding infants susceptible of abnormal development in motion perception.

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## Appendix

### Appendix A



Vår dato  
07.07.2020

Vår referanse  
Audrey van der Meer

Fakultet for samfunns- og utdanningsvitenskap  
Institutt for psykologi  
Nevrovitenskapelig utviklingslaboratorium (Nu-Lab)

#### FORESPØRSEL TIL FORESATTE OM FORSKNING PÅ BARN

### EEG-STUDIE AV HJERNEUTVIKLING HOS SPEDBARN

Vi ønsker å finne ut hvordan spedbarn oppfatter omverdenen. Dere som får dette brevet har en baby under 12 måneder. Hensikten med prosjektet er å undersøke hjernens funksjon og dens utvikling ved å registrere elektrisk hjerneaktivitet, mens barnet holder på med enkle visuelle og auditive oppgaver på en skjerm. Vi ønsker å få kunnskap om hvordan en babyhjerne fungerer og hvordan den utvikler seg med alderen hos terminfødte og for tidlig fødte spedbarn. Det forventes at grunnleggende kognitive ferdigheter (sansemotoriske evner, hukommelse, oppmerksomhet) blir kartlagt. Dette kan lære oss å forstå de minste bedre, og på sikt hjelpe barn der hjernen ikke fungerer helt som den skal.

#### HVA INNEBÆRER PROSJEKTET?

Studien innebærer som regel to oppmøter i løpet av det første leveåret ved Nevrovitenskapelig utviklingslaboratorium (Nu-lab) på NTNU Dragvoll. Deltakelsen i prosjektet vil foregå under en times besøk. Barnet vil ha på seg en helt ufarlig hette med små sensorer og ledninger, og se på film mens det sitter på fanget til mor/far eller i en bilstol med en av foreldrene rett ved siden. Prosjektet vil pågå til slutten av 2030.



#### MULIGE FORDELER OG ULEMPER

Opgaven til babyen er å se på bevegelige ting på skjermen mens det har på seg sensorhetten. Undersøkelsen er ufarlig og vil ikke medføre ubehag. Hvis barnet ikke trives med situasjonen blir forsøket avsluttet med en gang. Dersom deltakelse i prosjektet skulle gi mistanke om sykdom eller skade hos barnet, kan dere få henvisning til riktig helsetjeneste. For oppmøte og testing ved Nu-lab på NTNU/Dragvoll dekkes bussbillett eller parkeringsavgift.

**Postadresse**  
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#### FRIVILLIG DELTAKELSE OG MULIGHET FOR Å TREKKE SITT SAMTYKKE

Det er frivillig å delta i prosjektet. Vi tar kontakt og dersom du ønsker at barnet ditt skal delta, undertegner du samtykkeerklæringen på siste side og leverer det ved oppmøte hos oss. Du kan når som helst og uten å oppgi noen grunn trekke ditt samtykke. Dersom dere trekker dere fra prosjektet, kan dere kreve å få slettet innsamlede prøver og opplysninger, med mindre opplysningene allerede er inngått i analyser eller brukt i vitenskapelige publikasjoner. Dersom du senere ønsker å trekke barnet ditt eller har spørsmål til prosjektet, kan du kontakte Audrey van der Meer, tlf. 918 97 522, [audrey.meer@ntnu.no](mailto:audrey.meer@ntnu.no).

#### HVA SKJER MED OPPLYSNINGENE OM BARNET?

Opplysningene som registreres om barnet skal kun brukes slik som beskrevet i hensikten med prosjektet. Dere har rett til innsyn i hvilke opplysninger som er registrert om barnet og rett til å få korrigert eventuelle feil i de opplysningene som er registrert. Dere har også rett til å få innsyn i sikkerhetstiltakene ved behandling av opplysningene.

Alle opplysningene vil bli behandlet uten navn og fødselsnummer eller andre direkte gjenkjenne opplysninger. En kode knytter barnet til dets opplysninger gjennom en navneliste. Det er kun prosjektleder og prosjektkoordinator som har tilgang til denne listen. Det vil ikke være mulig å identifisere barnet når resultatene offentliggjøres. Hvis barnet har deltatt tidligere i denne studien, ønsker vi å sammenholde tidligere og nåværende opplysninger.

#### FORSIKRING

Pasientskadeloven gjelder for barnets undersøkelse ved NTNU Dragvoll.

#### OPPFØLGINGSPROSJEKT

Det kan bli aktuelt å invitere barnet til nye undersøkelser i denne langtidsstudien.

#### ØKONOMI

Prosjektet er delvis finansiert av NTNU og EU, og utstyret er finansiert av Norsk forskningsråd.

#### GODKJENNING

Regional komité for medisinsk og helsefaglig forskningsetikk har vurdert prosjektet, og har gitt forhåndsgodkjenning (Saksnummer [2010/1273](#)).

Etter ny personopplysningslov har dataansvarlig og prosjektleder Audrey van der Meer et selvstendig ansvar for å sikre at behandlingen av deres opplysninger har et lovlig grunnlag. Dette prosjektet har rettslig grunnlag i EUs personvernforordning artikkel 6a og artikkel 9 nr. 2 og ditt samtykke.

Du har rett til å klage på behandlingen av barnets opplysninger til Datatilsynet.

#### KONTAKTOPPLYSNINGER

Dersom du har spørsmål til prosjektet kan du ta kontakt med:

Prosjektleder: Audrey van der Meer                      e-post: [audrey.meer@ntnu.no](mailto:audrey.meer@ntnu.no)                      tlf: 918 97 522  
 Personvernombud ved institusjonen er Thomas Helgesen, [thomas.helgesen@ntnu.no](mailto:thomas.helgesen@ntnu.no).

**JEG SAMTYKKER TIL Å LA BARNET MITT DELTA I PROSJEKTET**

Jeg har lest informasjonsskrivet og er villig til å la min sønn/datter delta i prosjektet.

---

Sted og dato

Signatur

---

Ditt navn med trykte bokstaver

Jeg bekrefter å ha gitt informasjon om prosjektet.

---

Sted og dato

Signatur

---

Rolle i prosjektet

