Master's thesis

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Norwegian University of Science and Technology
Faculty of Social and Educational Sciences
Department of Psychology

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Development of Audio-Visual «Looming» Perception in Infants Receiving Extra Motor Stimulation and Full-Term Controls: A Longitudinal High-Density Electroencephalography Study

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Abstract

The aim of this longitudinal EEG study was to determine whether early extra motor stimulation, in this case baby swimming, could accelerate the development of visual motion perception in infants. Virtual balls approached on a collision course under three different loom speeds, and electroencephalography was used to measure the looming-related brain responses. Ten extra-stimulated infants and ten full-term healthy controls were tested longitudinally before (3-5 months) and after crawling onset (8-12 months). A VEP peak analysis on a trial-by-trial basis showed that with age, infants showed their looming-related brain responses at significantly shorter values of time-to-collision (TTC), suggesting a more efficient processing of looming visual motion after the onset of self-produced locomotion. Additionally, locomotory extra-stimulated infants showed their looming-responses at significantly shorter values of TTC than locomotory control infants, suggesting that early motor stimulation may contribute to a more rapid development of prospective control for motion perception. It was also observed that when infants were younger, they showed their looming-related brain responses at shorter TTC for faster looms, whereas after the onset of self-produced locomotion infants showed their responses at fixed TTC across loom speeds. Time-frequency analyses revealed induced brain activity in the alpha/beta frequency band for controls, while extra-stimulated infants showed higher-frequency gamma activity during processing of audio-visual looming information. Coherence connectivity analysis revealed that, in frequency bands involved in audio-visual processing identified by TSE analysis, extra-stimulated infants showed more significant connections than controls after becoming mobile. During processing of looming in the second testing, both groups displayed more functional connections compared to non-looming stimuli and processing in the initial testing before self-produced locomotion. Further investigation should explore whether interventions, such as early extra motor stimulation, can facilitate development in developmentally vulnerable infants.

Sammendrag

Formålet med denne longitudinelle EEG-studien var å undersøke om tidlig ekstra motorisk stimulering, spesifikt babysvømming, kunne fremskynde utviklingen av visuell bevegelsesoppfattelse hos spedbarn. Det ble simulert virtuelle baller på direkte kollisjonskurs med tre ulike hastigheter, mens elektroencefalografi (EEG) ble brukt til å måle looming-relaterte hjerneresponser. Ti ekstrastimulerte spedbarn og ti terminfødte friske kontroller ble testet longitudinelt før (3-5 måneder) og etter de begynte å krabbe (8-12 måneder). En peak-analyse på enkeltforsøk avslørte at da spedbarna ble eldre og hadde begynt å krabbe, viste de sine looming-relaterte hjerneresponser betydelig nærere kollisjon, noe som tyder på en mer effektiv prosessering av visuell bevegelse etter starten av egenprodusert bevegelse. Videre viste spedbarn som mottok ekstra stimulering signifikant kortere tid-til-kollisjon (TTC)-verdier sammenlignet med kontrollspedbarn, noe som kan bety at tidlig motorisk stimulering bidrar til en raskere utvikling av prospektiv kontroll for bevegelsesoppfattelse. I første testing viste begge gruppene looming-responser med kortere TTC-verdier for raskere loom, mens spedbarn med krabbeerfaring viste sine looming-relaterte hjerneresponser ved konstante TTC-verdier for ulike hastigheter. Tidsfrekvensanalyser viste indusert hjerneaktivitet i alfa/beta-frekvensbåndet for kontrollspedbarnene, mens de som mottok ekstra stimulering viste gamma-aktivitet under prosessering av audio-visuell looming informasjon. «Coherence connectivity» analyse viste flere signifikante forbindelser for ekstrastimulerte spedbarn enn kontrollgruppen etter at de hadde begynt å krabbe, i frekvensbåndene som er involvert i audio-visuell prosessering identifisert av TSE-analysen. I andre testing viste begge gruppene flere funksjonelle forbindelser under prosessering av looming sammenlignet med ikke-looming stimuli og testingen før krabbeerfaring. Videre forskning burde se på om intervensjoner i form av tidlig ekstra motorisk stimulering av utviklingsmessig sårbare spedbarn kan bidra til en utvikling som følger de friske normalutviklede.

Acknowledgements

It has been an honour to work on my master's thesis in this lab, which stands out for its excellent equipment and good facilities. I would like to extend a heartfelt thank you to my supervisor, Professor Audrey van der Meer, for providing valuable feedback, guidance, and engaging discussions in the lab. I also want to express my immense gratitude to Ph.D. student Silje-Adelen Slydal Nenseth, who has been invaluable in answering countless questions ranging from technical aspects of testing, writing, and analysis to general life matters. Furthermore, I would like to thank my fellow students Ingrid Larsen, Karoline Hatlen, and Jin Wang for creating an exceptional lab environment filled with laughter, bad jokes, and dry lab humour. I appreciate all the support we have provided to each other during challenging times. Lastly, I want to extend a big thank you to my family and friends for their support and interest in my research. Their encouragement has meant a lot to me. I would also like to thank all the participants and their families who have contributed valuable data to this important research. Without their participation, this study would not have been possible.

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Introduction

During the first year of life, several major changes occur in the infant brain. New-born babies transition from being able to perform very few voluntary tasks to being able to produce intentional movements. Despite new-borns' limited action repertoire, their perceptual systems are functional at birth and are capable of processing information (Gibson & Pick, 2000). After birth, there is an overproduction of both neurons and synapses, which over time are reduced through a mechanism called pruning (Mataga et al., 2004; Sakai, 2020). This occurs as a result of learning and a reduction of ineffective connections, where energy is instead allocated towards streamlining synapses and forming of functional networks. The visual cortex undergoes a peak of synapse formation between 4-12 month after birth (Johnson, 2001; Tierney & Nelson, 2009), which is assumed to be connected to the plasticity of the respective region (Tierney & Nelson, 2009). This critical period is regarded as a highly plastic window that holds importance for future fitness, including adaptability and functional development (Reh et al., 2020).

In addition to synaptogenesis, which already begins before the child is born, an important aspect of brain development is to strengthen or weaken the connections between neurons. Myelination of axons and other structural changes in the connections due to a mechanism called LTP (Long-Term Potentiation) also have functional importance for infant brain development. Together with pruning, these mechanisms are important to make the brain as efficient as possible. Through experiences, the stimulated synapses are strengthened. This occurs because both motor, sensory, and cognitive functions require rapid signal transmissions for optimal functioning (Nave & Werner, 2014). Continuous activation of a synapse prompts the glial cells, support cells of nerve cells, to form a fatty layer called myelin around the axons of the activated cells. This myelin sheath results in a drastic increase in conduction velocity by allowing nerve impulses to jump from one nodal point to another, known as saltatory conduction (Nave & Werner, 2014). Myelinisation of occipital areas becomes apparent in the second half of the first year (Johnson, 2001).

As the baby constantly interacts with the environment while its brain is in a highly plastic state, development progresses. For example, significant changes occur in the infant's ability to move around independently during the first year. Such a development, from the baby’s inability to navigate around the room to reaching the crawling stage, will result in structural neural changes. Because a locomotory skill like crawling changes the relationship between the infant and the environment (Borge Blystad & van der Meer, 2022), infants need to develop neural structures that can provide them with the ability to assess potential collision hazards adequately as their mobility increases during the second half of the first year of life (van der Weel & van der Meer, 2009).

Development of visual processing often involves two cortical systems that are assumed to be crucial for visual perception. One, the ventral stream, encompasses ventral occipital and temporal areas and is primarily responsible for detecting “what” the individual perceives (Klaver et al., 2008). The other cortical system, the dorsal stream, includes dorsal occipital and parietal areas and is referred to as the “where” pathway because it processes visual motion, spatial location, and motion direction information in addition to movement planning, timing, and prospective control (Klaver et al., 2008; Zotcheva & van der Meer, 2016). The parietal areas involved in dorsal stream processing are believed to be involved in processing visual information that is important to understand spatial relationships and to control spatially directed actions (Braddick et al., 2003). Infants exhibit a neural response to motion as early as 3 months, and from 3 to 5 months, they display higher sensitivity to motion stimuli than to a static form (Atkinson, 2017). Early development of the extra-striate dorsal stream is linked to infants’ capability to process motion in an efficient and functional way and can thus be a crucial attribute as the infant begins to acquire locomotion. This development has been observed in healthy full-term infants, while it is often associated with a vulnerability to delayed development in premature infants (Zotcheva & van der Meer, 2016).

Initially, infants have limited abilities to understand where and when something is going to occur, because of their limited experience with, among other things, self-produced movement. The ability to perceive what is going to happen soon, is called prospective control (Agyei et al., 2016) and is closely linked to the onset of locomotor abilities. According to Gibson and Pick (2000), locomotion is prospective, meaning that the infant must make constant decisions, such as choosing the right path when moving through the environment. To effectively navigate and reach a destination, it is crucial to first perceive the visual environment accurately. This perception is then used to guide subsequent actions, which involves integration of the perceptual information, cognitive processes, and the execution of motor actions required to achieve the intended goal (Agyei et al., 2016).

As J.J. Gibson in his theory describes, the infant absorbs the information from the environment through its senses and understands that information through the experience and interaction with it (Adolph & Kretch, 2015; Gibson & Pick, 2000). In a longitudinal study by Adolph (1995) it was found that infants' onset of locomotion and crawling could vary from 4.77 to 9.73 months. Implicit motor learning depends on trial-and-error experience with the environment (Hadders-Algra, 2010) and can be accelerated with the appropriate stimulation (Borge Blystad & van der Meer, 2022). Infants perform actions in accordance with their physical and mental abilities, as well as the opportunities in the surrounding environment (Berger & Adolph, 2007). Infants have an urge to move around even before mobility becomes a reality. This motivates them to practice, and after the action is learned, there will be more purpose behind the movements than there was initially when the goal was simply movement itself (Gibson & Pick, 2000).

Therefore, with some assistance and facilitation, infants' development can be accelerated by allowing them to operate at a level appropriate for their abilities while also challenging them. There are several ways to facilitate infant development. For instance, tummy time can stimulate infants to improve their motor development more effectively than if they are simply lying on their backs (Hewitt et al., 2017; van der Meer & van der Weel, 2022). In such a position, the baby can explore and practice holding their head, as well as adopting a crawling posture. More tummy time is positively correlated with parents' knowledge about its positive outcomes (Hewitt et al., 2017). Parents' information and knowledge about facilitating their baby's development, are crucial for making a difference for the baby.

A method that can support infant stimulation, potentially improving their locomotor abilities and fostering the development of prospective control even before they achieve independent mobility, is engaging in baby swimming (Borge Blystad & van der Meer, 2022; Borioni et al., 2022). In line with the theories concerning infant brain development, such exposure could be appropriate to accelerate developmental progress. In the water, the baby can experience self-produced and self-guided movement before reaching the crawling stage. The reduced effect of gravity in the water facilitates movement for the baby despite its young age (van der Meer, 2002). Borge Blystad and van der Meer (2022) showed that infants receiving extra stimulation through baby swimming had a greater improvement in visual perception than control infants who received a traditional Norwegian upbringing which involves spending up to 90% of their awake time in a supine position (van der Meer & van der Weel, 2022). Furthermore, a pilot study by Borioni et al. (2022) has demonstrated the positive influence of baby swimming on early motor learning, and that trial-and-error learning in the environment results in progressively more efficient movement, that, in turn, can influence neural development. Additionally, they propose that early engagement in baby swimming could be beneficial for infants who are predisposed to atypical development, such as preterm infants, who exhibit heightened vulnerability to coordination impairments among other challenges.

One way to investigate infant brain development is to measure their brain responses during presentation of a looming experiment that triggers the collision response. Braddick et al. (2011) stated that visual development is the key area to assess and to understand early brain development. The term “looming” is used to explain the last part of an optical event where an object is coming towards an individual on direct collision course (Kayed & van der Meer, 2000, 2007). When an object or obstacle is approaching, it gets larger and therefore it can be perceived prospectively (Gibson & Pick, 2000). Looming is experienced as a threat to the individual (Vagnoni et al., 2015) and induces the propagation of neural activity waves within the visual cortex and substantial evidence supports the specialization of the human visual system in detecting and responding to approaching as opposed to receding motion (Holliday & Meese, 2005; Ptito et al., 2001; Shirai et al., 2004). For that reason, a collision response in the brain can be an appropriate indicator to look at the baby’s developmental level and abilities to perform everyday movements (Zotcheva & van der Meer, 2016).

An appropriate method to measure looming-related brain activity is through electroencephalography (EEG). Using high-density EEG will give an accurate measurement of the timing of the brain activity, due to the high temporal resolution as well as a direct measure of the electrophysiological activity (Liu et al., 2017). Because of the high-density technique, it gives a better spatial resolution (Liu et al., 2017) that makes it possible to investigate the regions of interest and more precisely investigate how the activity progresses in the brain. This is advantageous when examining timing in brain activity, as it requires the measurement of electrical brain activity in real time, alongside ensuring signal strength accuracy when assessing frequency bands and whether the activity is synchronized or desynchronized.

When an event-related potential (ERP) occurs in the visual cortex, it is called a visual evoked potential (VEP) and it is due to the transient brain activity that is generated by the dendritic postsynaptic activity of synchronously firing neurons as a response to visual information (Luck, 2005). Visual evoked potentials can be seen as a peak in the brain activity at a particular time after onset of the looming stimuli. Therefore, this type of visual evoked potentials, typically arising towards the end of the looming stimulus, can more precisely be referred to as looming-related brain responses (Zotcheva & van der Meer, 2016).

It has been found that looming-related brain responses for full-term infants occurs closer to the virtual collision with age (van der Meer et al., 2012; Zotcheva & van der Meer, 2016). This may be due to the postnatal improvement of the synaptic myelinization and maturation, and is also likely to be associated with locomotor experience and improved prospective control. Interestingly, preterm infants do not show an improvement in the visual looming motion processing from when they were 4-5 month to when they were 12 months (Zotcheva & van der Meer, 2016), which probably reflects impaired myelinisation processes and lack of white matter observed in the brains of preterm infants (Doesburg et al., 2011).

Since it has been observed that the response to looms approaching on a collision course under different speeds, varies depending on both age-related maturation and the participant's motion experience, it has been investigated which timing strategy infants employ when perceiving the approaching ball and timing their defensive responses to it. Kayed and van der Meer (2000, 2007) examined whether infants used a timing strategy based on the looming ball's velocity, visual angle, or time-to-collision. Findings indicate that infants initially used a timing strategy based on the looming object's visual angle or velocity, to time their defensive blink. However, by the age of 6-7 months, they switched to a strategy based on the time left to the collision (Agyei et al., 2016; Kayed et al., 2008; Kayed & van der Meer, 2000, 2007; van der Meer et al., 2012; Zotcheva & van der Meer, 2016). It is suggested that a strategy based on time-to-collision would be more efficient in timing movements, as the use of a timing strategy based on the visual angle led to many delayed responses (Kayed & van der Meer, 2007), which implies that infants using visual angle as a timing strategy are at risk of not responding in time to avoid a collision, especially at fast speeds. The use of timing strategy can be linked to an infant's prospective control, as the infant learns to navigate the surroundings and handle obstacles to avoid collisions. Transitioning to a more effective timing strategy after the onset of locomotion, will be crucial for successful interaction with the environment.

In the infant's brain, when watching looming balls approach on a collision course, processing will occur in various frequency bands. This can contribute to explain the efficiency of processing and provide an indicator of the importance and complexity of the information that is being processed. A method that can contribute to further understanding of what happens in the infant brain during looming, is through time-frequency analysis that aims to investigate induced brain activity within a given frequency band (Morales & Bowers, 2022; Paul-Jordanov et al., 2021). During presentation of visual motion, event-related oscillatory activity in the different frequency bands can either be synchronized or desynchronized (Pfurtscheller, 1992; Pfurtscheller et al., 1994).

Event-related desynchronization (ERD) is found both during and before visual stimulation (Pfurtscheller et al., 1994). During ERD, the rhythms in the alpha bands get blocked. When larger portions of the brain are active simultaneously, such as through synchronized low-frequency activity in the alpha band, it can be interpreted that the active modules are not ready to receive and process information. Therefore, when the brain shifts from widespread synchronized alpha to desynchronized activity, it signifies a transition from a resting to an active state (Pfurtscheller et al., 1994). The cortical visual areas in the occipital cortex exhibit less interaction with other brain regions and reduced synchrony just before a visual scene to prepare for processing the visual information (Pfurtscheller et al., 1994). Then, desynchronization moves towards parietal areas, while occipital low-frequency alpha waves shift towards greater synchronization when the visual event commences (Pfurtscheller, 1992; Pfurtscheller et al., 1994). Hence, desynchronization may be observed prior to a visual event to prepare the brain to receive and process stimuli, characterized by a greater degree of desynchronized activity in the lower frequency bands. Subsequently, increased synchrony in neural oscillations in the visual areas is observed when the stimulus is presented, particularly in higher frequency bands such as gamma (Pfurtscheller & Lopes da Silva, 1999).

Being able to focus attention on the most relevant aspects of a visual scene is crucial for completing the given task and is important for survival. Gregoriou et al. (2015) found that synchronized oscillation is linked with attention. A looming stimulus, with symmetrical growth, creates a scenario where an approaching object is coming on a direct collision course. Infants need to perceive that something is moving towards them and direct their attention towards the approaching ball to time and execute an appropriate response and avoid being hit. Research has suggested that synchronization of neural oscillations contributes to mechanisms that promote perception, cognition, and motor control (Doesburg et al., 2011), all important factors to be able to act appropriately in critical situations. Additionally, synchronized neural activity promotes efficient processing and enhances communication between neural populations (Gregoriou et al., 2015) which can also be crucial in timing the appropriate action according to the situation. This means that synchronization of neural oscillations contributes to managing a critical event in terms of focusing attention, appropriate motor execution, and efficient processing of information.

It is also crucial which frequency bands are active during the synchronization of oscillations. The processing of different stimuli will be influenced by the frequency band in which it occurs. When discussing various frequency bands in relation to information processing in the brain, the main ones are delta, theta, alpha, beta, and gamma frequencies. During an active, awake state, the major rhythms include theta, beta, and gamma waves, which occur at approximately 4-8 Hz, 14-18 Hz, and 40-100 Hz, respectively (Zheng & Colgin, 2015). It was found that synchronized induced gamma oscillations were a functional frequency-band in the processing of visual motion stimuli (Başar et al., 2001; Hoogenboom et al., 2006; Jensen et al., 2007; Pfurtscheller & Lopes da Silva, 1999) and that they increased with the strength of the stimulus (Siegel et al., 2006). Increased synchrony in the induced high-frequency gamma activity, arises from populations of active neurons firing simultaneously in response to the sensory event (Siegel et al., 2006). Therefore, a ball on a collision course may be an appropriate approach to create a visual stimulus that can elicit a strong visual brain response in addition to capture and focus the participant's attention. Gupta and Chen (2016) suggested that low-frequency synchronized activity contributes to long-range interactions, while high-frequency synchronized gamma oscillations are associated with local activity such as visual processing. Therefore, one can assume that mature visual motion processing may involve synchronized gamma activity in the visual areas.

According to earlier findings, processing in the dorsal stream should be apparent after the onset of locomotion (Atkinson, 2017; Braddick et al., 2003; Klaver et al., 2008; van der Meer et al., 2012). A coherence connectivity analysis can reveal the connections between brain regions within a given frequency band. Hence, the network or the intercommunication among brain regions operating within the same frequency-band can be revealed, allowing us to determine the maturation of the dorsal stream. This can be achieved by examining whether the frequency bands identified through TSE analysis, exhibit significant connections within the brain regions implicated in the dorsal stream.

The present study aimed to investigate infants' development in brain responses to an audio-visual loom approaching on a direct collision course, in a longitudinal design where infants were tested twice during the first year, namely before and after the onset of self-produced locomotion, using high-density EEG. Additionally, the aim was to explore whether extra stimulation in the form of baby swimming could accelerate brain development. Assumptions were made that looming-related neural responses would take place significantly closer to the virtual collision for the extra-stimulated infants compared to the control infants in the second session, where the participation of baby swimming classes had yielded an effect. Another hypothesis was that there would be decreased TTC values for all loom speeds in both infant groups from the first to the second session, where infants had achieved prospective control and increased myelination. Additionally, it was expected that all infants in both groups had changed their timing strategy from visual angle to one based on time, showing more fixed TTC across loom speeds in session two, due to locomotor experience. It was expected that both infant groups would process the audio-visual information in higher frequency bands after becoming mobile, but additionally, that the extra-stimulated infants exhibited even more synchronized high-frequency activity than the controls in session two. It was also assumed that all infants, after the onset of locomotion, would process the audio-visual looming information higher up the dorsal stream than in the initial session, and that the extra-stimulated infants would show more functional connections in the second session than the control infants.

Methods

Participants

Ten healthy extra-stimulated babies that participated in organised baby swimming classes, and 10 healthy controls (non-swimmers), were recruited for testing through birth announcements or contact with parents present during swimming classes in Pirbadet in Trondheim. The group of baby swimmers comprised of 6 girls and 4 boys, and the control babies consisted of 3 girls and 7 boys.

All included baby swimmers started their participation in swimming classes between 5 and 14 weeks of age. A typical swimming session involved various exercises in the form of lots of interaction with peers, parents, and the swimming instructor as well as every part of the environment around them. Infants experienced different forms of balance exercises depending on their level of motor development, ranging from lying on their backs in the water, where they had to control their own body and use their muscles to avoid spinning around their body-axis, to sitting or crawling on a mat on the water, and swimming around in the water. During these baby swimming sessions, infants could explore and experiment with their surroundings without the risk of harming themselves. Additionally, the water facilitates and makes it easier for the baby to move their own body, and the mat on the water provides better friction for practicing crawling or overall movement.

This study followed a longitudinal design where all infants were tested twice, in different test sessions and at different ages to measure brain development. In the first testing session, the baby swimmers had a mean age of 4 months and 18 days (*SD* = 8 days), and the full-term control babies had a mean age of 4 months and 3 days (*SD* = 26 days). At this age, the babies did not have much experience with self-produced movements, but 8 out of 10 baby swimmers were able to roll over, while 7 out of 10 of control infants were able to roll over, either from stomach to back or both ways at the first test session. In the second testing session, the mean age of the baby swimmers was 9 months and 24 days (*SD* = 44 days), and control babies had a mean age of 10 months (*SD* = 31 days). The requirement for the second included test session was dependent on the infants' locomotion experience. That means that some infants had three test sessions, but the one included as session two in the present study, was the one where the infant was able to crawl. All infants were able to both crawl and pull to stand at the second testing. The baby swimmers started to crawl on average at 7 months (*SD* = 46 days) and the control infants at 7 months and 27 days (*SD* = 43 days).

Prior to the experiment, the parents were informed and given a brief introduction about the experimental procedure and the electroencephalography (EEG) going to be used. They were ensured that EEG is a physiological procedure that causes no harm or pain to the infant. They also gave their informed consent to the study and were made aware of the opportunity to withdraw at any time. Projects at the lab have been reported to the Norwegian Social Science Data Services and have been assessed and approved by the Regional Committee for Medical Research Ethics, Region Central Norway.

Stimuli

To simulate a looming ball approaching the infant's face on a direct collision course, a black 2D circle appeared at eye height on a large screen, containing four smaller rotating circles with the colours blue, red, yellow, and green (see Figure 1). The black circle was presented on a white background and was rotating with a constant angular velocity of 300 degrees/s. The aim was to create a virtual collision where the looming object hit the infant's face. The loom was presented at three different speeds (fast, medium, and slow) that approached under three constant accelerations: -21.1, -9.4 and -5.3 m/s^2 before it hit the baby's face. Regardless of the duration and acceleration of the looming object, the size and visual angle of the ball was the same at the beginning and end of each trial. The ball had a visual angle of 5° and a diameter of 6.5 cm at the beginning of each trial and a visual angle of 131° and a diameter of 350 cm at the end of the trial. As illustrated in Figure 1, the ball appeared at its minimum before it expanded over the screen in one of the three speeds. In each trial, a corresponding "whoop" sound was played together with the visual stimuli. This sound was sampled at 44.1 kHz, with a constant intensity level of 60 dB, and was programmed to appear as a sound coming directly towards the infant's face. The sound started at a barely audible 140 Hz and increased in pitch up to 460 Hz by stimulus end, loud enough to simulate a virtual collision. Between trials, 1 second of white screen and a mute sound was presented to avoid sensory adaptation.

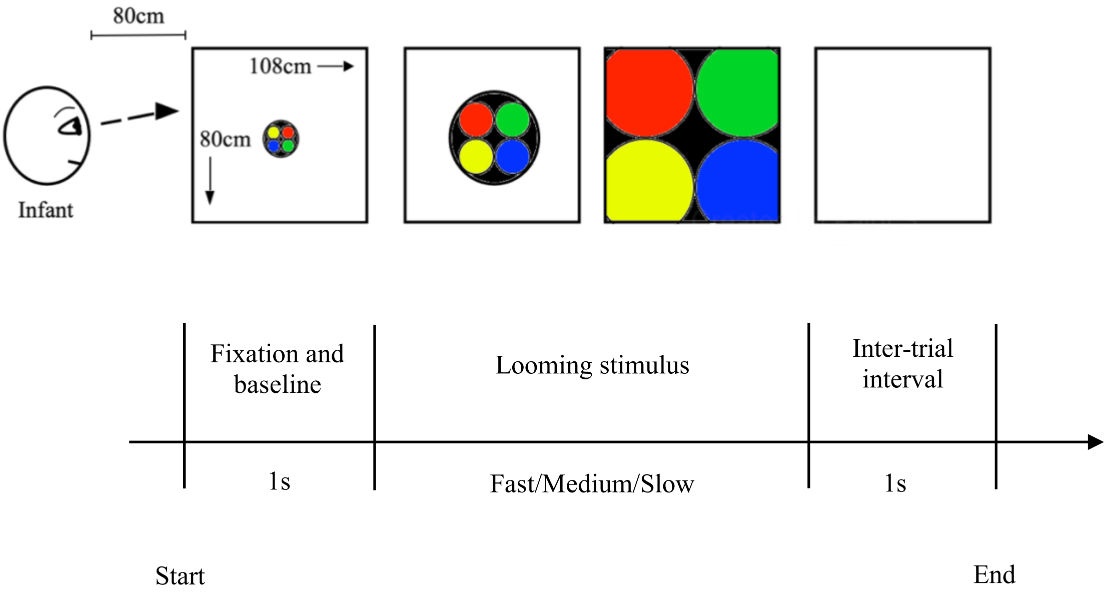


Figure 1. *The experimental setup showing the infant sitting in front of the screen with the 2D virtual loom approaching them on a direct collision course (top row) and the timeline of a single trial from onset to offset, including the time of the fixation, looming stimulus, and inter-trial interval (bottom row).*

Apparatus

The experimental stimuli that created the virtual scene of looming audio-visual motion were generated with E- prime 2.0 (Psychological Software tools) and presented to the infants by projecting the visual looms onto a large screen (108 cm wide, 80 cm high), placed 80 cm in front of the baby. To record EEG activity, a Geodesic Sensor Net (GSN) 200 containing 128 Ag/AgCl sponge sensors, was evenly distributed on the infant's head (Tucker, 1993). For an optimal signal-to-noise ratio, the high-input EGI amplifier was connected to the sensor net to amplify the EEG signals at a maximum impedance of 50 kΩ (Ferree et al., 2001). The amplified EEG signals were recorded with Net Station software on a Macintosh computer. E-Prime was used to communicate triggers for onset and offset of the looming stimuli to Net Station. A Tobii X50-eye tracker was used to control the infants' visual attention and was processed with Clear View software on a HP computer. Additionally, the infant's behaviour was controlled by using two digital cameras to record the participants from different angles during the experiment.

Procedure

The experiments took place at the Developmental Neuroscience Laboratory (NU-lab) at NTNU Campus Dragvoll in Trondheim. When the parents arrived with their infants, they were warmly welcomed by the researchers and the baby got to play and familiarize itself with the lab and researchers before the testing began. An assistant measured the head of the baby to pick the right size of the EEG net and soaked it in saline electrolyte to optimize the electrical conductivity. When putting the net on the infant, an assistant played with toys and blew soap bubbles to distract, while the net was placed gently on the baby's head. After examining the electrodes and ensuring that they were correctly positioned and had good contact with the skull, the baby was placed in a baby car seat in the experimental room. The parent would sit beside the baby to avoid any stress, and the assistant would sit on the other side to ensure that the infant's focus was sufficiently on the screen. When the net was connected to the amplifier, impedance was checked. If needed, the electrodes were adjusted. For data acquisition, two assistants were responsible for the control of the computers responsible for data collection and stimulus generation in a soundproof control room separated from the experimental room by transparent glass.

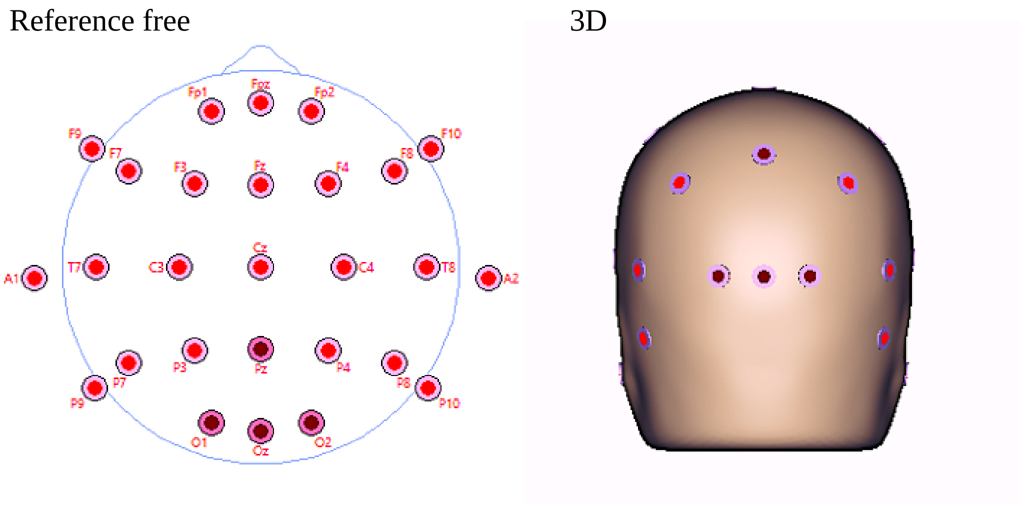
Data acquisition began right after the Tobii eye tracker had been calibrated to the baby's gaze in virtual space. It was carried out in one block, but could be paused if needed, for instance if the baby lost interest or started crying. The experiment could also end prematurely if the lack of interest was clearly high. The three loom speeds were evenly distributed among the trials in a quasi-random order. The looming experiment was consistently presented as experiment number two alongside three other visual motion experiments, each lasting approximately 3-6 minutes. A complete testing session took around 20 minutes in total when all four experiments were included.

Data Analysis

BESA (Brain Electrical Source Analysis) version 7.1 was used to analyse the EEG raw data for both testing sessions. Analyses were carried out in a masked manner, meaning the group assignment of the brain data was undisclosed. The EEG data were segmented in Net Station software and exported as raw files. Standard channel configuration and digitized head surface points were added to the raw data file for each participant. The data material was visually inspected to remove or interpolate bad channels and artifact-contaminated trials caused by head and body movements. The maximum number of channels defined as bad was set at 10%. To remove slow drift in the data, low cut-off filter was set at 1.6 Hz, while high cut-off filter was set at 50 Hz, and the notch filter was set at 50 Hz to remove mainline noise interference from the EEG data.

Peak Analysis

For peak analysis, the work involved processing raw data that had not been cleaned of noise and artifacts, except for eliminating some clearly noisy electrodes to facilitate the identification of peaks in the infant brain activity. To select peaks in the EEG data, the high cut-off filter was changed to 8 Hz and a reference-free montage with 27 standard electrodes was used to simplify the data. The looming-related peaks were found by a trial-by-trial investigation of each infant's EEG recordings. There were mainly four electrodes of special interest when looking for activity in the reference-free montage (see Figure 2).



Reference free

3D

Figure 2. *An illustration of the distribution of the electrodes in the reference free montage. The areas of interest during peak analysis, are marked with electrode Oz, Pz, O1, and O2 in dark red.*

Prominent peaks in the occipital and parietal channels (Oz and Pz) were marked. The annotated peaks represented the looming-related brain activity in the region of interest and marked when it emerged within a trial. To ensure that the selected peak's activity was not caused by a blink or other movements, a 3D mapping of the head, that shows a rise (red) or decline (blue) in voltage activity, had to be thoroughly investigated (see Figure 3). In case of multiple peaks observed in one trial, the peak closest in time to the "collision" was assumed to be more related to a looming-related brain response. Also, the 3D mapping showed which cortical activity was connected to the most functionally looming-related peak. Selecting peaks most likely associated with a looming-related response involved a highly subjective assessment, considering factors such as how the voltage emerged, how it dissipated or moved after emergence, and other nuanced characteristics. For instance, an expectation existed, especially in the second session, that the activity would predominantly shift upward along the dorsal stream rather than downward. It also required evaluating the strength of the voltage to distinguish genuine peaks from potential noise. Additionally, assessing voltage activity in other brain regions was crucial to determine if it could influence the occipital and parietal areas, ensuring that a looming-related response was not mistakenly chosen. Over time, distinct patterns in how activity or peaks behaved became apparent for each participant, particularly in the second session. Observing recurrent activation patterns, both for each participant and across participants, emerged as a method for selecting the correct peaks. For every marked peak, the time left to collision, or “time-to-collision” (TTC), was gathered in an Excel sheet to calculate the mean TTC for each looming-related response, per loom speed and for every participant.

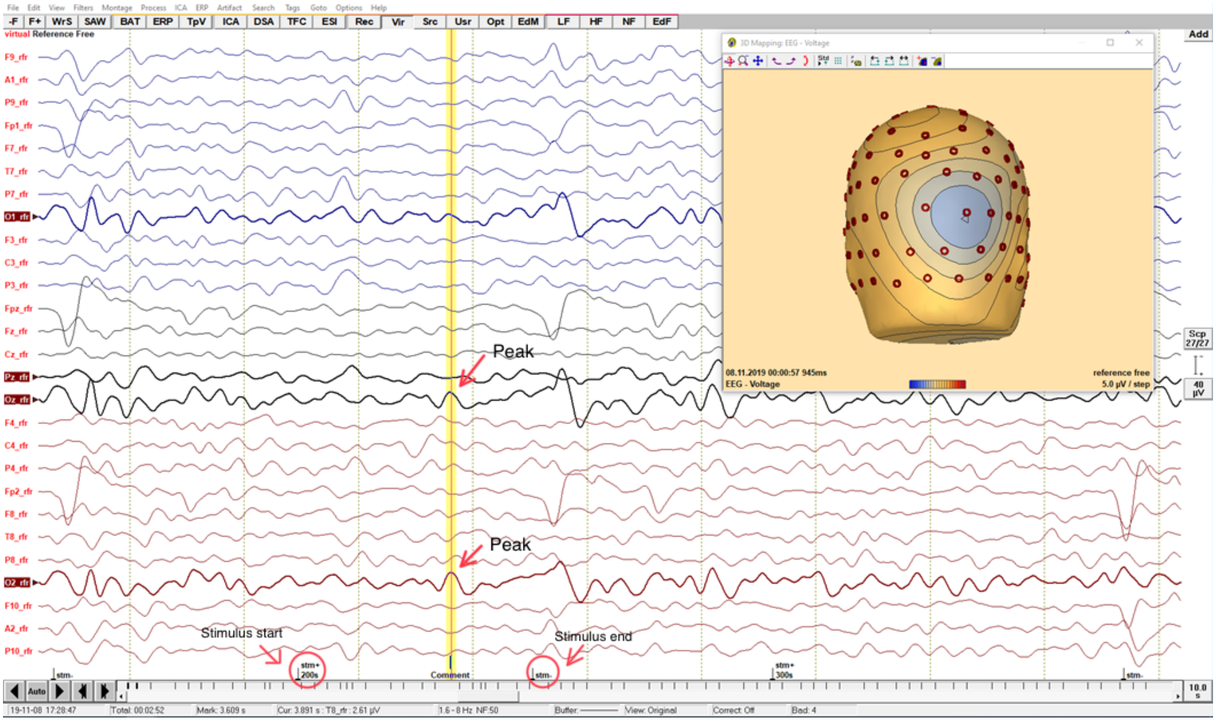


Figure 3. *Illustration of a looming-related peak in response to a fast loom in electrodes O1, Oz and O2 of a 4-month-old infant's raw data in the reference-free montage. Inserts shows 3D mapping of the voltage build-up in the brain during a looming-related response in the occipitoparietal area.*

Timing Strategies

The timing of infants' looming-related brain responses will vary depending on the timing strategy they employ. This encompasses which characteristics of the loom the baby focuses on, whether it is the loom's visual angle, or time before collision. If the baby utilizes the visual angle timing strategy, the time to collision will increase if the visual angle is held constant and the looming loom's acceleration decreases. In other words, the response time will become shorter as the speed of the loom is getting faster (Kayed et al., 2008; Kayed & van der Meer, 2000, 2007, 2009; van der Meer et al., 2012; van der Meer et al., 1994).

If the infant employs a timing strategy based on time, the visual angle will increase if the time to collision is held constant and the loom's acceleration decreases. That means that the baby will have a more fixed time where the response occurs, irrespective of the speed of the approaching loom (Kayed et al., 2008; Kayed & van der Meer, 2007, 2009; van der Meer et al., 1994).

After onset of crawling, infants have been observed to shift their timing strategy from visual gearing their brain responses to a certain angle to the time left before the collision (van der Meer et al., 2012). In this context, such a transition would occur between their two test sessions in this study (Kayed et al., 2008; Kayed & van der Meer, 2007).

Time-frequency analyses

Time-frequency analyses were carried out on oscillatory activity from the EEG to investigate changes in amplitude over time for each infant. Before conducting the Time Spectral Evolution (TSE) analysis, the data underwent a thorough review to eliminate noise and artifacts, such as blinks or other head movements. Once the data were cleansed, event files were made and added to the infants' raw data for both sessions, so only the selected looming-related peaks were included in the analysis. Multiple source dipoles were employed to model the regions of interest in visual and parietal cortices. To ensure an adequate separation of brain activity, a source montage derived from the multiple source model was utilized. The source montage comprised 17 sources that modelled activity in the visual pathways and other relevant areas. Figure 4 shows the regions of the visual cortex that were of particular interest in this study, specifically Visual Cortex lateral Left (VClL), Visual Cortex lateral Right (VClR), Visual Cortex ventral Midline (VCvM), Visual Cortex radial Left (VCrL) and Visual Cortex radial Right (VCrR), as these regions are believed to be actively involved in the visual processing of motion (Probst et al., 1993; Zeki et al., 1991).

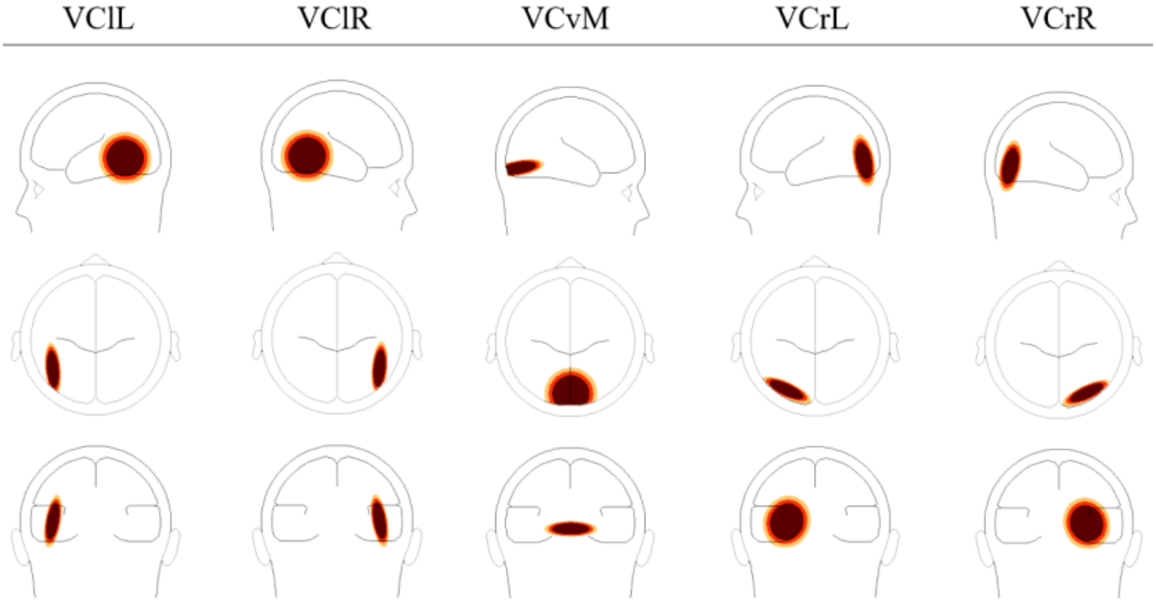


Figure 4. *A head model illustration of brain areas of interest during TSE analysis for motion perception. Visual Cortex lateral Left (VClL), Visual Cortex lateral Right (VClR), Visual Cortex ventral Midline (VCvM), Visual Cortex radial Left (VCrL) and Visual Cortex radial Right (VCrR).*

In order to analyse the information from the chosen sources, a 4-shell ellipsoidal head model (Berg & Scherg, 1994; Hoechstetter et al., 2004; Scherg et al., 2002) was generated for each infant. Source dipoles were inserted into the head model concurrently with the inclusion of the artifact-corrected coordinate files. For infants under one year of age, a recommended template including settings for bone thickness and conductivity at 3.0 mm and 0.02 σ, was selected (Grieve et al., 2003). The settings for filters and average parameters used in peak analyses remained unchanged.

To enable the measurement of induced oscillatory activity specifically during the looming-related response, epochs were set from -300 to 300 ms around the marked looming peaks. All looming responses for fast, medium, and slow looms were aggregated into a common "looming" condition. To examine how oscillatory activity changed during looming motion, it was compared with a "non-looming" condition, where the rotation ball remained stationary on the screen without moving toward the participant (see Figure 1, fixation and baseline), with the same epochs as for looming motion. The frequency and time sampling parameters for the displays were set at 1.0 Hz and 50 ms, respectively. Activity within the range of 2.0 Hz (lower frequency cut-off) to 80 Hz (higher frequency cut-off) was presented in the TSE plots and probability maps. TSE plots and probability maps revealed changes in amplitude over time and significant differences, respectively, for each participant between looming and non-looming. Following the visualization of activity in frequency bands in TSE plots, a visual inspection of relevant brain regions was conducted for each participant to determine which bands were active during the processing of looming. It also revealed if it was desynchronized or synchronized activity.

After individual analyses of participants' respective TSEs, BESA Statistics 2.1 was used to investigate whether there were any significant differences in amplitude values and frequency ranges between looming and non-looming. A paired t-test was conducted for all participants in each group in both test sessions. To address the multiple comparison problem when analysing EEG data, a combination of data clustering and permutation testing was used (Bornfleth et al., 2020). This was done with the idea that if a statistical effect is found over an extended period of time in multiple neighbouring channels, it is unlikely that this effect occurred randomly (Bornfleth et al., 2020).

The permutation number was set at 1024, given the presence of two conditions and one group, thus representing the total number of potential permutations. The cluster alpha, that is the significance level for building clusters in time or frequency, was set at 0.05 with epochs ranging from -300 to 300 ms. The statistics were performed on an average across all channels because all activity not related to induced oscillatory activity associated with a looming response had already been removed during artifact correction. Additionally, looming-related brain activity consisted only of the marked peaks observed in the brain regions of interest, indicating that the activity in “looming” originated solely from the occipital lobe and visual areas during the time frame of the looming-related brain response. Following this, the significant time-frequency ranges from the average of all infants in each session could also be used as a guide when looking back at each of the individual TSE plots.

Coherence Connectivity Analysis

Data from the time frequency analysis were further investigated in BESA Connectivity 2.0 to identify networks and investigate the functional connectivity in areas of interest in the extra-stimulated and control infants during processing of looming motion. In the connectivity analysis, the coherence method was used to measure the linear relationship between two signals at a specific frequency band (Rosenberg et al., 1989). The chosen examined frequency bands originated from the statistically significant clusters from the TSE analysis. Again, a combination of data clustering and permutation testing was used to deal with the multiple comparison problem. The analyses were conducted separately for each infant group in both sessions. The areas of interest in the connectivity analysis are shown in Figure 5. TSE displays from TSE-analysis remained the same, with the display set at 2-80 Hz, and time samples were set at 1-50 ms. Coherence describes the sum of in-phase components of two signals at a specific frequency, and measures the strength of the association from 0-1, where zero means absence of a linear time-invariant relationship (Rosenberg et al., 1989).

T-tests were conducted using BESA Statistics 2.1 to measure the probability of significant coherence clusters for the looming condition, followed by permutation tests. Paired t-tests were conducted for each group in both sessions to compare the connectivity in the brain during looming to the connectivity during non-looming. Unpaired sample t-tests were conducted to evaluate the probability of significant connectivity between the extra-stimulated infants and the control infants in each session independently.

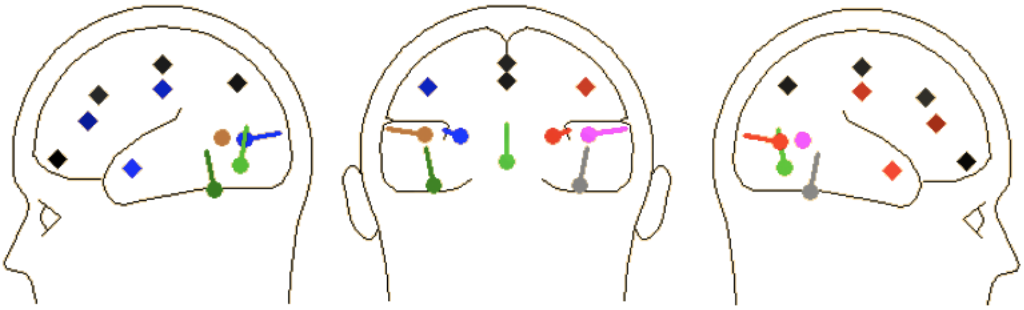


Figure 5. *An illustration of the head model with the source dipoles of interest during connectivity analysis. Visual Cortex lateral Left (VClL), Visual Cortex lateral Right (VClR), Visual Cortex ventral Midline (VCvM), Visual Cortex radial Left (VCrL), Visual Cortex radial Right (VCrR) and Parietal Midline (PM). The approximate Talairach coordinates of the sources are x=0.56 , y=-0.40 , z=0.12 for VClL; x=0.56 , y=-0.40 , z=0.12 for VClR; x=0.00 , y=-0.52 , z=-0.06 for VCvM; x=-0.32, y=-0.55 , z=0.11 for VCrL; x=0.32 , y=-0.55 , z=0.11 for VCrR; and x=0.00 , y=-0.50 , z=0.49 for PM.*

Results

Peak Analysis

The peak analysis provided TTC values for all participants in both sessions (see Figure 6). For extra-stimulated infants, out of 109 annotated peaks, an average looming-related brain response was observed 944 ms (*SD* = 183) before the virtual collision in the first session, with a corresponding TTC value of 343 ms (*SD* = 43), based on 104 peaks, in the second session. Infants with a normal upbringing serving as controls, showed their looming-related responses at an average TTC value of 957 ms (*SD* = 164), based on 122 annotated peaks in the first session, and at 507 ms before collision (*SD* = 51), based on 111 peaks in the second session.

At the first session, preceding the onset of self-produced locomotion, extra-stimulated baby swimmers showed their looming-related brain responses at values of TTC of 743 ms (*SD* = 111), 1013 ms (*SD* = 110), and 1086 ms (*SD* = 82) for fast, medium, and slow looms, respectively. The control infants with normal upbringing showed similar corresponding TTC values of 784 ms (*SD* = 115), 986 ms (*SD* = 92), and 1101 ms (*SD* = 89). For the second testing, after the attainment of self-generated locomotion, extra-stimulated infants exhibited a looming-related response at greatly reduced and rather fixed values of TTC of 320 ms (*SD* = 51), 333 ms (*SD* = 26), and 375 ms (*SD* = 30) for fast, medium, and slow looms, respectively. The controls also reduced their looming-related responses to fixed, but higher values of TTC of 471 ms (*SD* = 53), 524 ms (*SD* = 25), and 526 ms (*SD* = 52) for fast, medium, and slow looms, but they showed their responses around 150 ms earlier in the looming sequence, i.e. further from the virtual collision, than the extra-stimulated infants.

A 2 x 3 x 2 repeated measures ANOVA was used to analyse differences in TTC values between Session (prelocomotor, postlocomotor), Loom speed (fast, medium, slow), and Group (extra stimulated, controls). Findings indicated a two-way interaction between Session and Loom speed. Regardless of Group, infants varied their looming responses based on loom speed in the first session, whereas in the second test session, infants showed their looming-related responses at more consistent values of TTC across different loom speeds *F*(2,36) = 37.16, $p < 0.001$. In the first session when infants were young and had not become mobile yet, both extra-stimulated and control infants showed their looming-related responses at higher values of TTC for slow looms than for faster looms. This suggests that in the first test session, infants employed a timing strategy based on visual angle, whereas in the second session, where the looming-related brain responses occurred at much shorter and more constant TTC values, infants shifted timing strategy to one based on time, thus showing their looming-related brain responses at a relatively fixed time-to-collision. Further, a significant two-way interaction effect for Session and Group was observed, *F*(1,36) = 34.56, $p < 0.001$, revealing that extra-stimulated infants showed their looming-related responses at significantly lower values of TTC than control infants in the second session only.

Additionally, a main effect of session, *F*(1,18) = 1584.91, $p < 0.001$, showed that as infants gained self-produced locomotor experience, both extra-stimulated and control infants exhibited their looming-related brain responses at smaller values of TTC, in other words, later in the looming sequence and closer to the virtual collision.

Finally, main effects were found for Loom speed, *F*(2,36) = 64.92, $p < 0.001$, and for Group, *F*(1,18) = 36.09, $p < 0.001$, but these were most likely a result of the two two-way interactions reported above.

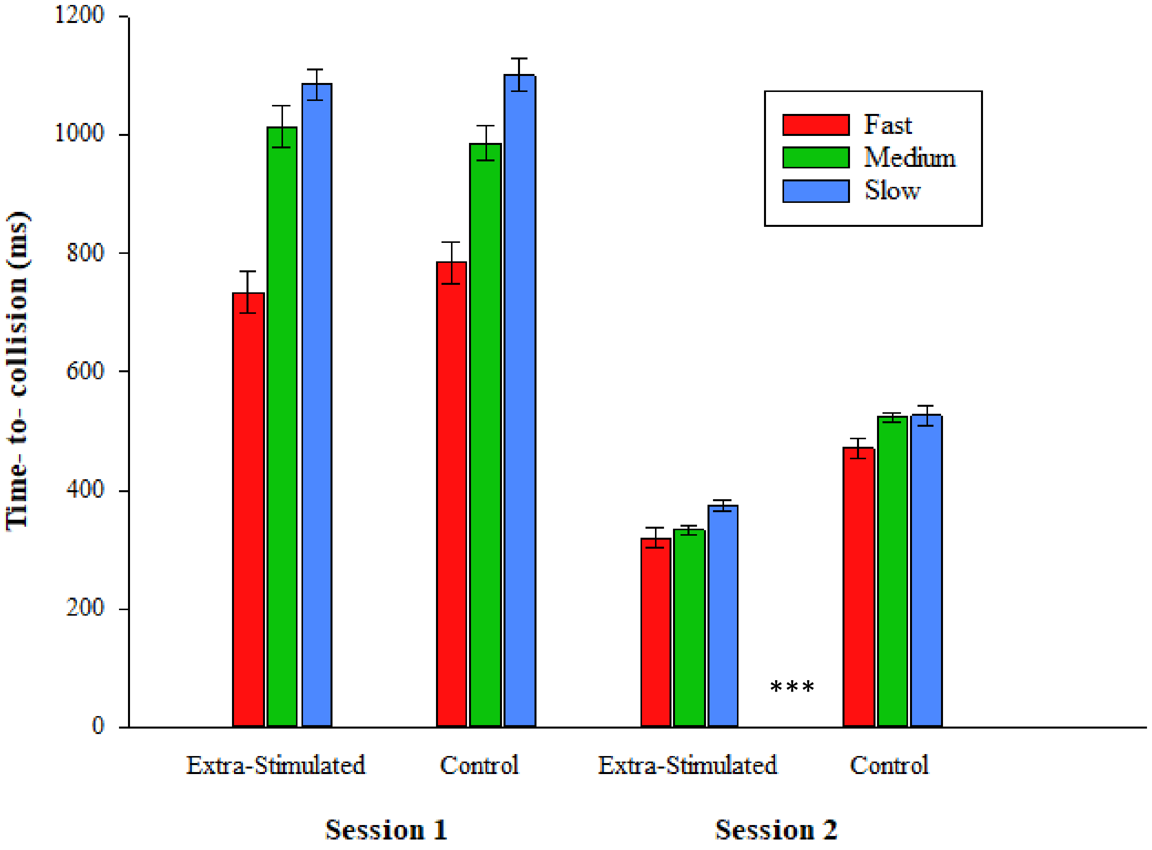


Figure 6. *Bar graph, including error bars representing standard error, of the average looming-related brain responses for extra-stimulated and control infants before (Session 1) and after (Session 2) they gained self-produced locomotor experience. The graphs illustrate TTC values for fast, medium, and slow looms in both sessions. A significant decrease in TTC values was observed in all infants after they started crawling, yet extra-stimulated babies showed their looming-related responses significantly closer to the virtual collision. Also, all infants varied their looming-related brain responses with loom speed (compatible with a timing strategy based on visual angle) in the first session, while they showed their responses at a relatively fixed TTC after onset of crawling (compatible with a timing strategy based on time).*

Timing Strategies

In the analysis of the looming-related peaks, during the initial testing session, it was observed across all infants that the brain responses occurred closer to the virtual collision as the speed of the looming stimulus increased (see Figure 6). According to the timing strategy based on visual angle, this corresponds to the time to collision increasing if the visual angle remains constant and the loom's acceleration decreases, meaning that the infants gear their brain responses to a fixed visual angle of the approaching loom. In the second session after the onset of locomotion, all infants exhibited more consistent TTC values across varying loom speeds. This is also consistent with the alternative timing strategy, based on time, which posits that if the time before collision remains constant, the visual angle will increase as the speed of the approaching object decreases. This suggests that from the first to the second testing session, infants transitioned from the visual angle timing strategy to the more effective timing strategy based on time.

TSE Analysis

The TSE analysis extracted the neural activity and showed how the oscillations varied in the different frequency bands over time. Figures 7 and 8 show the increase or decrease in the spectral amplitude for a representative extra-stimulated and control infant when comparing looming to non-looming. In the first session, extra-stimulated infants showed most induced synchronized activity in the lower frequency bands (theta, alpha and lower beta), but also some activity in higher frequencies during looming. Induced desynchronized activity was also observed in the alpha and theta bands. Control infants showed similar oscillatory activity to the extra-stimulated infants in the first session, namely induced synchronized activity in the lower frequency bands together with desynchronized activity in the theta band.

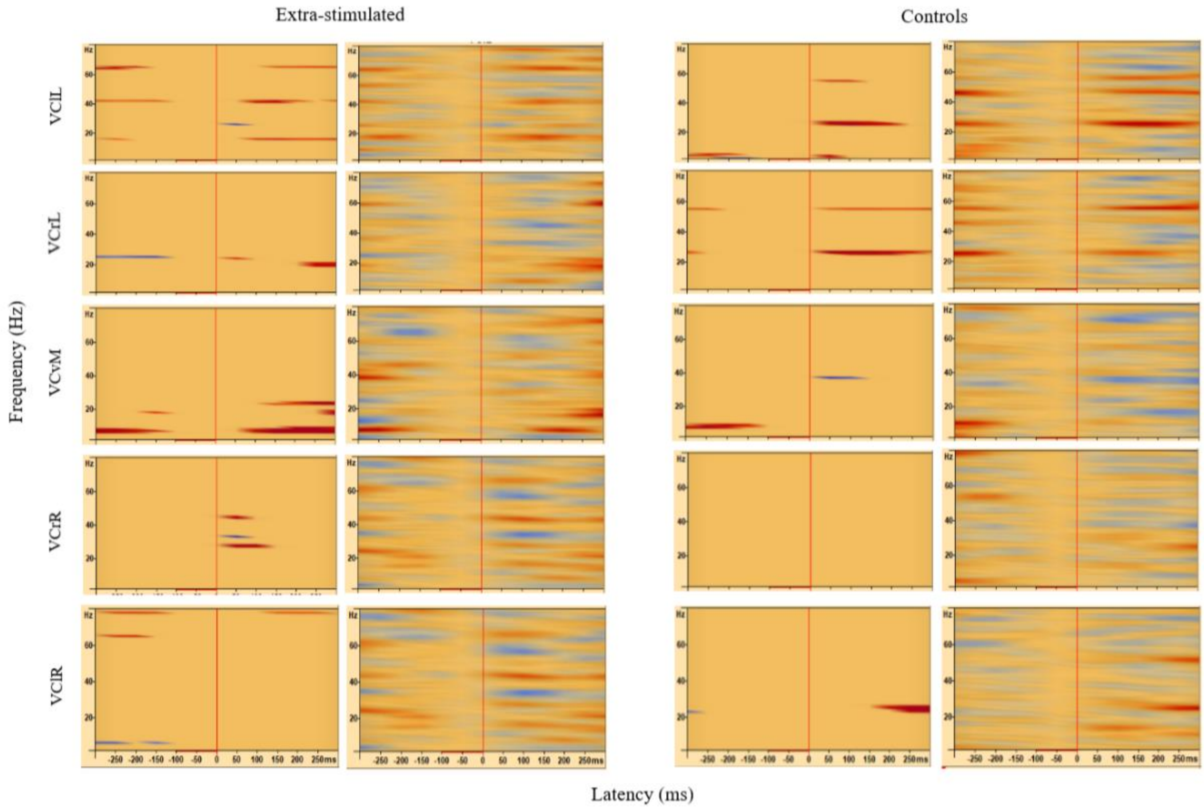


Figure 7. *Probability maps (left panels) and TSE plots (right panels) of the regions of interest in a typical extra-stimulated (4.6 months) and control infant (3.1 months) for visual sources VClL, VCrL, VCvM, VCrR and VClR. The plots show oscillatory brain activity during looming compared to non-looming. The red vertical line shows the peak of the marked looming-related brain response (-300 to 300 ms). Increased spectral amplitude represents induced synchronized activity and is marked in red, while decreased spectral amplitude represents induced desynchronized activity and is marked in blue. TSE probability maps ($p<0.05$) for the first session showed both synchronized and desynchronized activity in the lower frequency bands. Lower alpha-band synchronisation and theta-band desynchronisation was recurrent among both extra-stimulated and control infants.*

In the second session, all extra-stimulated infants showed induced synchronized activity in the gamma frequency band. The most prevalent frequency band for processing looming motion for control infants was the beta band, both as desynchronized and synchronized activity, in addition to some synchronized activity in the theta- and the higher gamma-band.

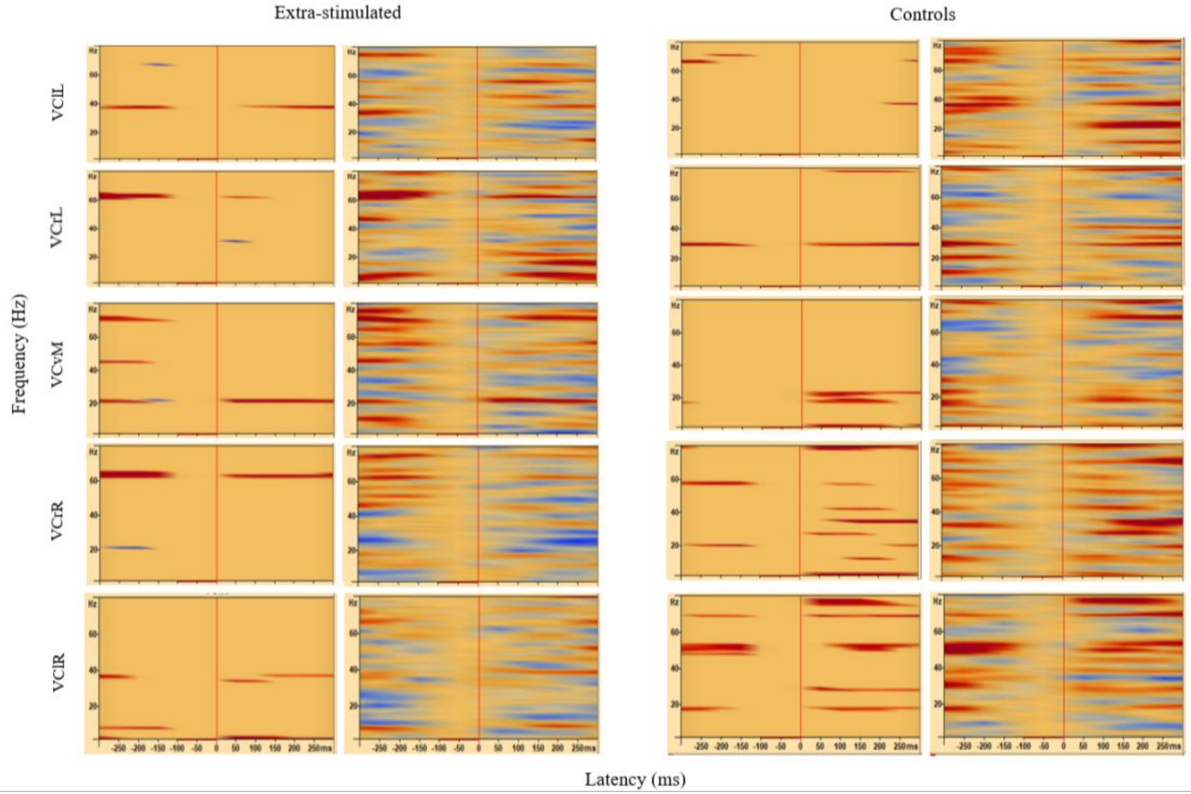


Figure 8. *TSE maps (right) and probability plots (left) of the regions of interest in a typical extra-stimulated (9.9 months) and control (10.3 months) infant: VClL, VCrL, VCvM, VCrR and VClR. The plots show oscillatory brain activity during looming motion compared to the non-looming control condition. The red vertical line shows the peak of the marked looming-related brain response (-300 to 300 ms). Increased spectral amplitude represents induced synchronized activity and is marked in red, while the decreased spectral amplitude representing induced desynchronized activity, is marked in blue. TSE probability maps ($p<0.05$) for the second session showed induced synchronized activity in the gamma frequency band for all extra-stimulated infants. The most prevalent frequency band for processing looming motion in the group of control infants was the beta band, as both desynchronized and synchronized activity. It was also observed some activity in the theta band and the higher gamma band.*

Paired t-tests and permutation tests for all infants in both testing sessions were conducted in BESA Statistics 2.1. Figure 9 shows a significant data cluster when comparing looming to non-looming for both the extra-stimulated and the control infants in the second testing session, after onset of locomotion and after receiving the extra stimulation through participation in baby swimming classes. The results showed oscillatory activity in the higher gamma frequency band for the extra-stimulated infants, while the control infants showed processing in the alpha-beta band in the second testing session.

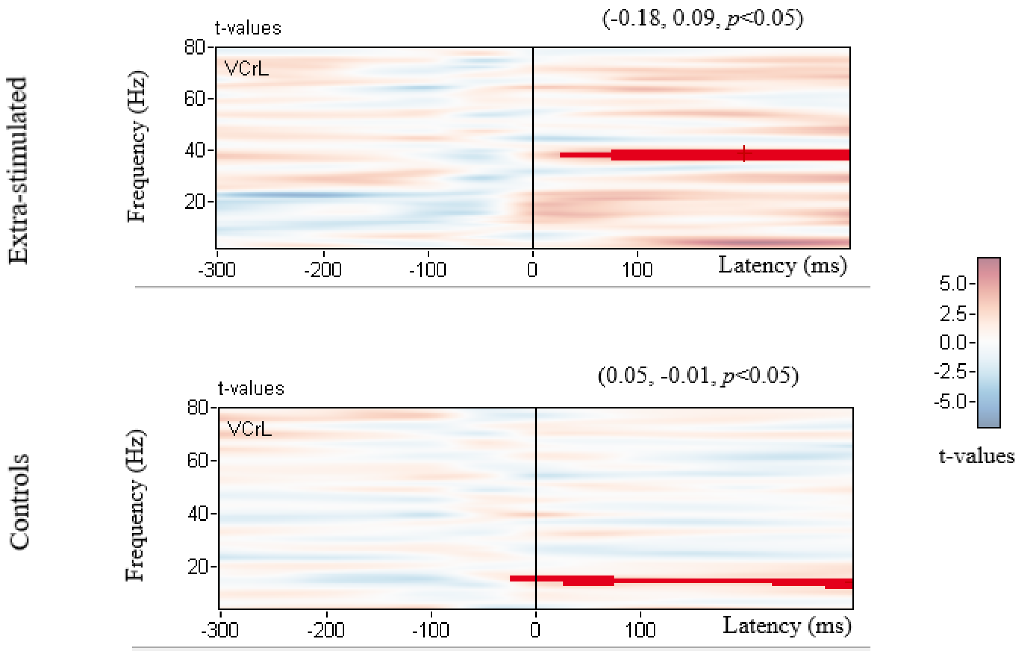


Figure 9. *Significant positive data clusters when comparing looming to non-looming control condition, showing oscillatory activity in the higher gamma frequency band for the extra-stimulated infants, while the control infants showed processing in the alpha-beta band in the second testing session. The positive clusters are marked with light red, and the negative clusters are marked with light blue. The cluster marked with stronger red colour shows the significant positive cluster, meaning the looming condition had significantly larger t-values than the non-looming control condition in both groups' second testing session.*

Coherence Connectivity Analysis

Connectivity analysis for looming motion revealed that extra-stimulated infants and control infants showed less functional connections before the onset of locomotion than after (see Figure 10). In addition, extra-stimulated infants showed more functional network connectivity in the second session compared to controls, during processing of audio-visual looming stimuli. Figure 10 also shows that both infant groups exhibited greater connectivity between sources during the processing of looming compared to non-looming. However, these differences were larger after the onset of locomotion. Among the regions of interest, extra-stimulated infants in the second testing session showed four significant connections between VCvM and VCrR, VCrR and VClR, VCrR and VCrL, VCrL and PM. Control infants, on the other hand, exhibited significant connections only between VCvM and VCrR, and between VClR and PM. In the first session, when all infants were still non-locomotory, both infant groups displayed a relatively similar activation pattern, with considerably fewer connections than observed in the second testing session.

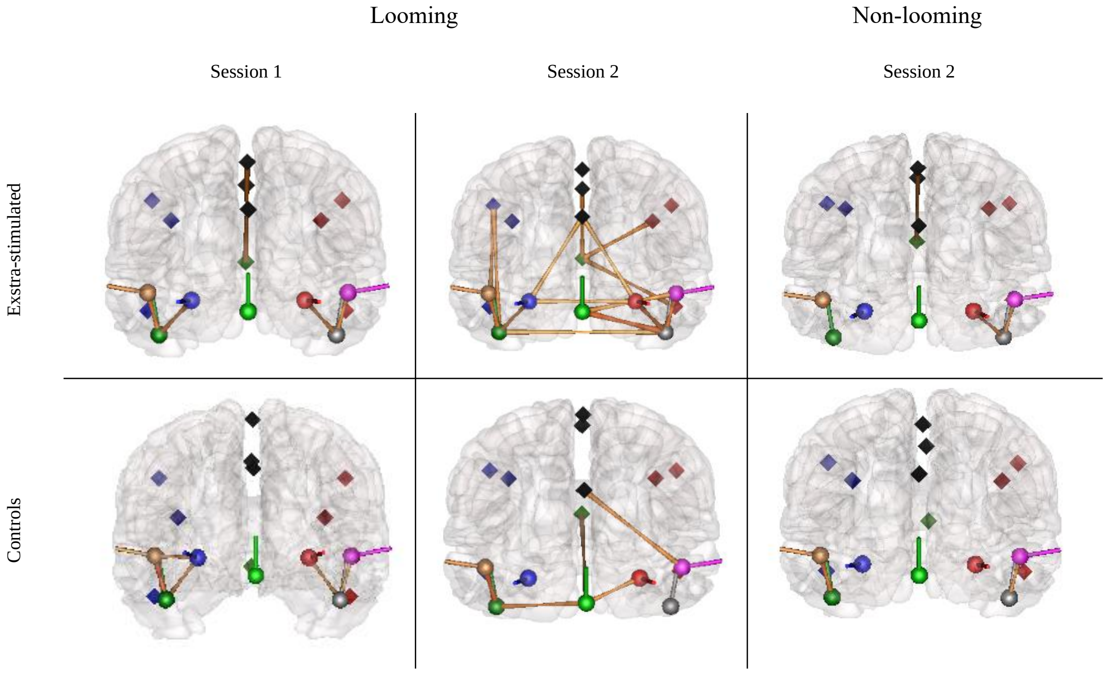


Figure 10. *Connectivity analysis during looming showing connections between brain regions for extra-stimulated and control infants, before and after becoming mobile. It also displays the connectivity in the infant brain during non-looming. Both infant groups showed fewer functional connections before the onset of locomotion than after. Also, extra-stimulated infants showed more functional network connectivity in the second session compared to controls during processing of audio-visual looms. In the second testing session and after infants had become mobile, extra-stimulated infants showed four significant connections between VCvM and VCrR, VCrR and VClR, VCrR and VCrL, and between VCrL and PM, while the control infants exhibited significant connections only between VCvM and VCrR, and between VClR and PM. In the first testing session, before the onset of locomotion, both infant groups displayed a relatively similar activation pattern, with considerably fewer connections than observed in the second testing session. Additionally, connectivity analysis showed greater connectivity between sources during the processing of looming motion compared to non-looming for both groups. However, after the onset of locomotion these differences were more pronounced.*

Paired t-tests revealed that the extra-stimulated infants, after onset of locomotion, showed significantly stronger clusters in connections between VClR and PM (0.42, 0.21, *p*=0.008) (see Figure 11) and between VCrR and VClL (0.39, 0.19, *p*=0.009), during looming compared to non-looming control condition. The control infants showed significantly stronger connections between VCrR and PM (0.41, 0.21, *p*=0.013), when comparing looming to non-looming (see Figure 11). Figure 12 shows an unpaired t-test that revealed significant clusters showing that extra-stimulated infants displayed stronger connections between VCrL and VCbR (0.53, 0.28, *p*=0.010) than control infants in the second testing session. VCbR is not in the listed regions of interest, but it is a part of the area involved in visual processing.

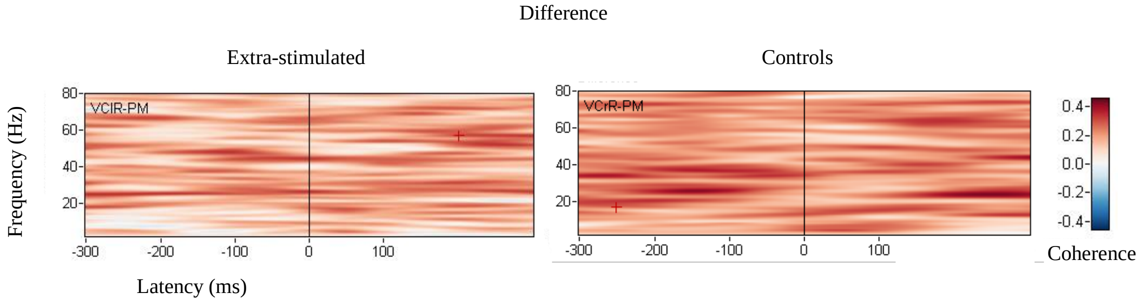


Figure 11. *An illustration of the statistically significant differences in connectivity in extra-stimulated and control infants after the onset of locomotion when comparing looming condition to the non-looming control condition. Extra-stimulated infants showed statistically significant stronger connections between VClR and PM (0.42, 0.21, p=0.008), while control infants showed statistically significant stronger connections between VCrR and PM (0.41, 0.21, p=0.013).*

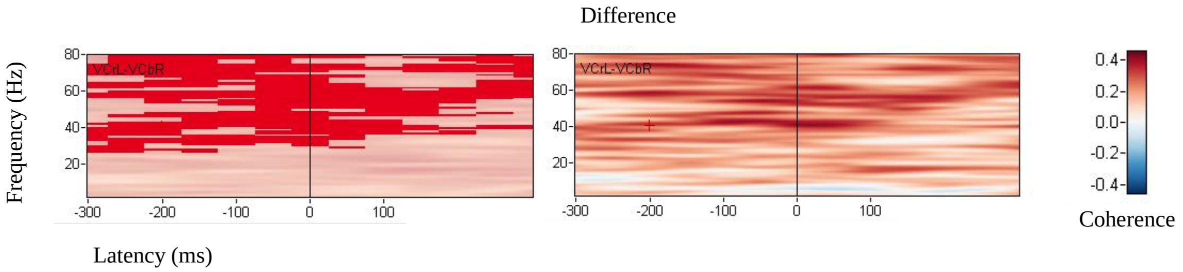


Figure 12. *Illustration of significantly different clusters between extra-stimulated infants and controls in the second testing session, after onset of locomotion, during looming (0.53, 0.28, p=0.010) showing that extra-stimulated infants had stronger connections between VCrL and VCbR than control infants.*

Discussion

In the present longitudinal study, high-density EEG was used to examine the brain activity of extra-stimulated infants and control infants aged 3-5 months and 8-12 months during exposure to audio-visual looming stimuli. A trial-by-trial analysis of the raw EEG data to identify looming-related peaks was used to investigate the moving pattern of the electrical visual evoked activity and timing in the brain. In addition, time-frequency analysis was used to investigate induced brain activity between the two infant groups and to discover differences in oscillatory activity when processing looming and non-looming audio-visual motion. A connectivity analysis was used to investigate the development of functional networks involved in processing audio-visual looming information. Together, the brain analyses aimed to investigate whether extra motor stimulation during early infancy was associated with enhanced brain development and improved audio-visual motion perception.

The peak analysis revealed that during the first year of life, all infants showed improvement in visual motion processing due to the significant changes and maturation of the brain the first year of life. Both extra-stimulated and control infants exhibited their looming-related responses at shorter time to collision in the second session compared to the first, following the onset of locomotion. However, extra-stimulated baby swimmers showed the looming-related brain responses even closer to collision than control infants after crawling onset. This developmental pattern is consistent with prior research indicating that healthy, typically developing infants tend to exhibit a looming-related brain response closer to collision after reaching the crawling stage and gaining the ability to move freely with self-directed motion (Zotcheva & van der Meer, 2016).

The reason for this improvement in brain function after the baby has reached the crawling stage and is able to move around independently, may be attributed to several factors. Both the infant's age and its experiences with the surrounding environment have evolved from the first to the second session. When the baby reaches the crawling stage, its relationship with the surroundings shifts (Borge Blystad & van der Meer, 2022). It will now be more vulnerable to collisions, thus requiring more considerations and decision-making to navigate the room smoothly. During this inter-session interval, the brain will undergo substantial neurodevelopmental advancements, in line with the infant's locomotory level. Strengthening of synapses and formation of networks along with the development of the dorsal stream and prospective control (Agyei et al., 2016), are all important aspects of the development that occur between the first and second sessions, and which may help explain the observed enhancements in infants' processing of impending looming motion.

As a baby accumulates new experiences and engages in activities, like those involved in early movement, the activated synapses undergo repeated activation. Over time, this process demands enhanced and more efficient signal transmission, prompting myelination to occur. When an axon is myelinated, it improves conductivity 20-100 times without occupying much additional space, hence neural activity is facilitated (Nave & Werner, 2014). From the first to the second session, the baby would have received a significant amount of stimulation of various kinds, and with the onset of locomotion, this would trigger the myelination process of networks and communicating cells. The improvement in the overall conductivity within systems involved in motor- and audio-visual motion processing caused by infants' increased experiences between the two test sessions, would also help explain why infants in session two exhibited a shorter TTC compared to session one. With responses closer to the collision, it suggests that processing must occur rapidly to allow the infant to execute an adequate defensive response to the impending loom. A short TTC value thus suggests that the infant possesses the ability to react and act within a relatively brief timeframe, signifying efficient processing.

When babies begin to navigate their surroundings independently, it also requires, in addition to faster signal transmission, that they eventually learn to interact with the environment to a greater extent than before. The establishment of a heightened level of prospective control during locomotor development in the first year of life, could help explain the findings from the peak analysis. As infants acquire a greater degree of prospective control, they demonstrate a more mature interaction with the environment. Consequently, this enhanced prospective control enables them to exhibit improved and more adaptive responses to impending virtual collisions by looming motion. Studies have indicated that locomotor experience plays a crucial role in shaping individuals' abilities to perceive and respond to various forms of visual information regarding spatial relations, including aspects of optic flow (Anderson et al., 2001; Berger & Adolph, 2007)

Development of prospective control can be linked to the maturation of the dorsal stream, which is believed to commence around the age of 3-5 months, when infants show greater sensitivity to motion compared to static scenes (Atkinson, 2017). Once infants gain an increased level of prospective control after they begin navigating their surroundings, it also implies processing within the dorsal stream. This can be explained because prospective control involves the ability of individuals to execute and plan precisely calculated movements adapted to our changing environment (Zotcheva & van der Meer, 2016). It is assumed that in the parietal areas of the dorsal stream, information necessary for understanding spatial relations and controlling spatial actions is processed (Braddick et al., 2003; Klaver et al., 2008). This suggests that if infants have attained prospective control and are capable of effective interaction with their environment, it is likely that the dorsal stream has commenced its establishment and engagement in processing, providing explanation of shorter TTC values observed after reaching the crawling stage.

During peak analysis, it was observed through trial-by-trial investigation by studying how the electrical voltage moved across the skull, that after the activity originated in occipital areas, it shifted more towards parietal areas in the second session. This shift implies that, following the onset of locomotion, infants processed the visual looming information to a greater extent in the dorsal stream compared to the first session. Such findings suggest that locomotion fosters heightened prospective control and increased processing within dorsal stream regions, leading to better and more efficient processing of looming motion.

Since extra-stimulated infants demonstrated accelerated development in their response to incoming audio-visual looms compared to controls, it suggests that there are factors beyond the physiological development and maturation of the brains of normally developing babies due to age. Infants who received extra stimulation through baby swimming began crawling one month earlier than control infants, in addition to exhibit smaller TTC values in response to looming stimuli. This may indicate that additional stimulation in the form of extra motor activity and interaction in environments where they more easily can move their own bodies before they have become locomotory, will facilitate brain development. Previous research provides supportive evidence with findings showing that baby swimmers have accelerated brain development with improved processing of visual motion stimuli compared to controls (Borge Blystad & van der Meer, 2022), in addition to the benefits of earlier motor learning (Borioni et al., 2022).

During baby swimming, infants were exposed to various forms of stimulation, including interactions with peers, parents, and swim instructor, as well as extensive motor and sensory stimulation. Additionally, babies were often placed on their stomachs on floating mats in the water, incorporating the aspect of tummy time (Hewitt et al., 2017). The positive outcome, demonstrated by the results of infants who received extra stimulation in the looming experiment, is likely due to the comprehensive stimulation they received. This stimulation facilitated earlier development of prospective control and locomotor abilities by allowing young infants to use their bodies in facilitating environments favourable to their development.

During the first year of life, infants undergo synaptogenesis, characterized by a burst in the formation of synapses and new connections. A period within this phase is termed a critical period, during which stimulation is crucial for further development (Reh et al., 2020; Tierney & Nelson, 2009). It has been suggested that the critical phase of synaptogenesis in the visual cortex occurs at around 4 to 8 months (Tierney & Nelson, 2009). In this context, the additional stimulation infants receive from baby swimming may potentially capitalize on this critical phase because the infant brain is highly receptive and plastic during this time. It has been observed that plasticity during this period is influenced by experiences, and that neural circuits and connections are shaped by these experiences, allowing the individual to adapt behaviour to the surrounding environment (Reh et al., 2020). Perhaps the optimal timing of the additional stimulation could further enhance the outcome of its associated benefits. Given that baby swimming took place during a critical phase of infant brain development, this could explain why baby swimmers exhibited significant better audio-visual processing compared to control infants after crawling onset. This could be because they maximized the benefits of all the training, exposure, and stimulation when their brain was in an extremely plastic state, contributing to accelerating the developmental process by shaping, strengthening, and streamlining the involved cortical areas.

Not only the visual system has such critical periods. Infants also display sensitivity to differentiation of speech sounds and recognition of monkey faces (Tierney & Nelson, 2009), indicating that exposure during sensitive periods can have a significant impact on development (Reh et al., 2020). Thus, extra stimulation during critical periods may contribute to accelerated development because the visual system and other parts of the brain are highly plastic during this timeframe. Baby swimmers were approximately 4 months old at the first session and 10 months old at the second, indicating that the extra stimulation of the participating infants occurred during the period of peak synapse formation in the visual cortex. This may support and help explain how extra stimulation early on in infants' lives contributed to improved processing of the audio-visual looming motion.

Peak analysis also showed that infants after onset of locomotion shifted their timing strategy based on time from a strategy based on visual angle. In the first session, it was observed that the infants used the less sophisticated timing strategy based on visual angle to deal with the oncoming audio-visual looms. The fastest loom gave the shortest TTC, meaning the response occurred closest to the collision, while the slowest loom resulted in the highest TTC values, meaning that the response occurred farthest from the collision. This is because the infants used the visual angle of the approaching loom as a reference to determine the timing of the looming-related brain response. Therefore, in the first session, TTC differed between slow, medium, and fast looms. As the loom approaches, it increases in size and alters the perceived visual angle, so if the infant relies on the looms visual angle, it may lead to more misjudgements, which can be critical when making its defensive response. Previous findings also showed that infants who did not switch to a timing strategy based on time, may encounter difficulties when an object rapidly approaches them while accelerating (Agyei et al., 2016; Kayed et al., 2008; Kayed & van der Meer, 2000, 2007; Zotcheva & van der Meer, 2016). Locomotory infants that employed the more efficient timing strategy involving specialized mechanisms, were better equipped to successfully manage perceptuo-motor tasks (Kayed & van der Meer, 2007), for instance avoiding a ball on collision course.

When TTC values in the second session was investigated, it seemed that all infants at a group level transitioned to a time-based strategy, because looming-related brain responses occurred at a more specific time-to-collision, regardless of loom speed. This was observed for both extra-stimulated and control infants, although extra-stimulated infants displayed their looming-related responses, on average, at lower values of TTC than the control infants. This could be due to the fact that in the first session, much of the visual system is not as well-developed as in the second session. Additionally, infants in the second session may engage in more complex and matured information processing, involving processing in the dorsal stream, as evidenced by the investigation of voltage maps of the electrical activity of looming-related brain responses. Thus, this developmental shift in timing strategy may be associated with both locomotion and the development of prospective control, as well as the natural maturation of brain systems, specializations, and processing efficiency.

Changes in the brain electrical activities related to the processing of audio-visual motion stimuli during the first year could also be observed when analysing the induced oscillatory activities from the EEG in TSE analysis. When TSE from the combined audio-visual looming was compared with a non-looming control condition, both synchronized and desynchronized induced activity was observed in the lower frequency bands in both infant groups. Synchronized alpha and theta and desynchronized theta were seen in both extra-stimulated infants and control infants. Despite the dominance of alpha and theta frequencies, the activity during the first session appeared to be quite scattered.

Desynchronization observed during the first testing may be associated with the fact that desynchronization often occurs in conjunction with sudden or novel events to prepare the processing of the stimuli (Pfurtscheller et al., 1994). An oncoming object could represent a new experience for some of the infants during the first session, as they lack experience with both locomotion and prospective control. Thus, desynchronization may occur as a result of a shift in active brain regions, allowing low frequency synchronized oscillatory activity over wide cortical areas to transition to desynchronized activity to focus processing of the new information. In the second testing, looming motion will not be processed to the same extent as new information, as the infants have become accustomed to handling obstacles in their environment and have more experience with self-generated movement. Consequently, processing looming in the second testing session will be more advanced, exhibiting a more complex and synchronized processing of the audio-visual looming information, needing less energy. When discussing synchrony in relation to audio-visual processing during the second testing session, it will not be associated with the widespread low-frequency synchronization across the brain, typically linked to a resting state. Instead, it will entail a functional processing characterized by synchronized oscillations in frequencies in visual areas.

It is found that gamma-band oscillations reflect local activities, whereas the lower frequencies are engaged in long-range interactions (Gupta & Chen, 2016). With this in mind, the processing evident in young, non-locomotory infants that occurs in the lower frequency bands, might suggest that larger groups of nonspecialized neurons are involved. When infant EEG data are dominated by large amplitudes of low-frequency activity, it is a sign of immaturity (Agyei et al., 2016), since a more adult-like processing of motion in either local or distributed network often involves high-frequency oscillatory activity.

However, in the second session, when TSEs during looming were compared to non-looming, considerable synchronized gamma oscillations in the extra-stimulated baby swimmers were observed. Among the controls, on the other hand, the most prevalent observation of induced oscillatory brain activity was synchronized beta activity, which also has been found in earlier research (Agyei et al., 2016). Additionally, some activity was also observed in both lower frequency bands and in the gamma band for control infants. This indicates that both groups have experienced an improved processing of audio-visual looming motion. Less observed desynchronized activity indicates more specialized processing for both groups. Together with processing in higher frequency-bands after becoming locomotory, the processing in the second testing session indicates that there has been a transition from having larger immature cell assemblies with less specialized neurons to cell assemblies with fewer but more specialized neurons processing visual motion information (Agyei et al., 2016).

This finding may also suggest that the extra-stimulated infants have developed an even greater degree of specialized neural groups contributing to the processing of visual looming motion, because their synchronized processing in high-frequency bands is already present. Previous studies have shown that gamma frequency is observed in the visual cortex related to visual perception of motion stimuli (Başar et al., 2001; Hoogenboom et al., 2006; Jensen et al., 2007; Pfurtscheller & Lopes da Silva, 1999; Siegel et al., 2006). The increased induced oscillatory activity in higher frequency bands observed in infants who received extra stimulation at an early age compared to control infants, may indicate a more matured and specialized processing of visual motion. This could be attributed to the early exposure and stimulation of visual and perceptual systems that can contribute to development of prospective control and strengthen the specialisation of neural assemblies even before the onset of locomotion (Johnson, 2001).

Further, statistical analysis in BESA statistics revealed that extra-stimulated baby swimmers exhibited significantly more activity in the high-frequency gamma band when looming was compared with non-looming after onset of locomotion. Meanwhile, the controls showed a significant increase in activity in the alpha-beta band after locomotory onset, when looming was compared non-looming. This finding demonstrates significant differences in infants' oscillatory brain activity when processing looming motion compared to observing a non-looming ball, for both extra-stimulated baby swimmers and control infants. Such findings support the results of the individual TSE plots and probability maps, reinforcing the presence of differences between infant groups and indicating that significant differences in processing looming compared to non-looming occur in different frequency bands for extra-stimulated and control infants. This is yet another indication that extra early stimulation leads to accelerated development and more mature processing of visual motion within the first year.

The significant differences observed in the induced brain activity in this analysis are solely derived from the peaks manually selected and included in the peak analysis. This implies that the activity included in the TSE analysis originates solely from participants' evoked looming-related brain responses, primarily from visual cortex or areas involved in visual processing. This means that findings from TSE and peak analysis thus mutually supported each other, because after the onset of locomotion and improved prospective control, infants who received extra stimulation processed information in visual areas in higher frequency bands at the group level than their age-matched controls. This implies that processing of the audio-visual looms in extra-stimulated infants occurred more rapidly than in controls, in accordance with the significant clusters observed post-peak (see Figure 9). Therefore, it makes sense that the evoked looming-related brain response was observed closer to the collision in extra-stimulated infants than in controls, because they require less time for processing due to having developed a more mature and efficient processing of the audio-visual looming information.

Connectivity analysis revealed that both infant groups exhibited connections up to PM in the second session, following the onset of locomotion, indicating involvement higher up the dorsal stream in processing of looming motion. In the statistical analysis of the second testing session, it was demonstrated that connections from lower areas in the visual cortex to the PM were significantly stronger when comparing processing of looming motion to non-looming. This indicates engagement of the dorsal stream in motion processing (Atkinson, 2017; Braddick et al., 2003; Klaver et al., 2008; Zotcheva & van der Meer, 2016) after onset of locomotion, whereas there were fewer connections up the dorsal stream during initial testing, prior to locomotion onset. This can be explained by limited experience with self-generated movement and limited prospective control, consistent with a less mature dorsal stream before infants receive more exposure and experiences with motion. However, it was observed that extra-stimulated infants exhibited more functional connections in the second testing session than control infants, suggesting a more developed network associated with visual processing. The additional exposure and stimulation received by the baby swimmers have contributed to the formation of a more specialized network and initiated an earlier and more advanced development of the dorsal stream than control infants. The processing in gamma-frequency in the dorsal stream could help explain the improved visual motion processing in extra-stimulated infants, because of the rapid coupling between spatially separated brain regions, due to the high frequency.

Taken together, this longitudinal EEG study demonstrated that extra stimulation in early infancy, particularly during the first year of life, enhances both infant locomotor and brain development, accelerating the processing and perception of audio-visual motion. Infants who received extra stimulation started to crawl on average one month before infants that received normal Western upbringing. After onset of locomotion, the infants showed a shift in the timing strategy used to handle audio-visual looming motion information. Before onset of locomotion, when infants have less developed prospective control, they relied on a strategy based on the visual angle of the loom, resulting in responses with higher TTC values for faster looms. In contrast, during second testing after onset of locomotion, the strategy shifted to one based on time-to-collision, leading to more consistent TTC values. Peak analysis revealed that both infant groups exhibited shorter TTC values after the onset of locomotion. Furthermore, extra-stimulated infants showed a looming-related brain response closer to the virtual collision than control infants after the onset of locomotion, indicating a more efficient developed and mature processing. Extra-stimulated infants also showed processing of looming motion information in higher frequency bands than the controls in the second testing, in addition to more significant connections between brain regions, indicating more functional, specialized and matured networks involved in audio-visual processing.

These findings may suggest the importance of facilitating early stimulation of infants' motor skills and sensory system through various activities, such as baby-swimming, as demonstrated by the positive outcomes in brain development observed in this study. Additionally, it could serve as an encouragement for parents to engage their babies in activities and dare to challenge their development. Since early stimulation can accelerate the development of healthy full-term infants, it would be valuable to investigate whether early stimulation could lead to a more typical development in vulnerable groups, such as premature infants. Premature infants often deviate from the typical developmental trajectory and are at increased risk for delayed development, impaired coordination, and visual processing difficulties (Doesburg et al., 2011; Zotcheva & van der Meer, 2016). When early stimulation accelerates the development of looming-related brain responses, along with processing in higher frequency bands and the extension of functional connections between brain regions, it suggests that such exposure may induce structural and functional changes in infants, leading to more efficient and complex processing. Alongside the finding that baby swimming also yields motor development benefits (Borioni et al., 2022), it could be valuable for future research to investigate whether an extra-stimulating intervention for premature infants can mitigate the weakened motor outcomes associated with preterm birth. Additionally, the extra stimulation may lead to earlier brain development, myelination, and structural changes, which may have beneficial implications for the vulnerability in visual processing. It could also be valuable to include several countries to look at the differences in upbringing across cultures and if other cultures stimulate their infants in a beneficial way in accordance with advanced brain development.

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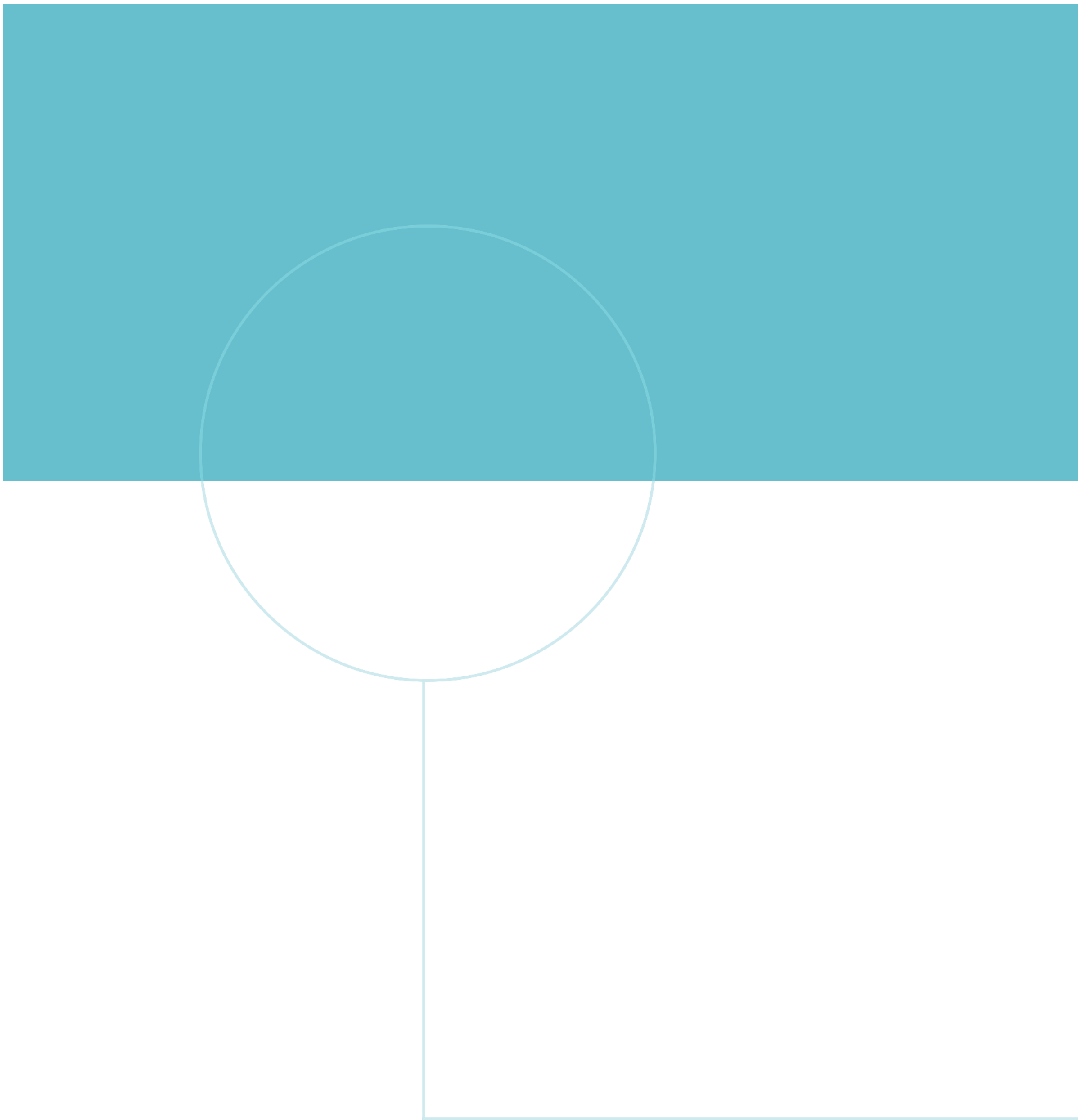

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