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Preterm children show different brain connectivity networks compared to their full-term peers during perception of occluded objects: A high-density EEG study.

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Supervisor: Audrey van der Meer
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Abstract

Electroencephalogram (EEG) was used to investigate oscillatory brain activity and timing of prospective responses in relation to a temporarily occluded object in preterm and full-term children at 6 years of age. The experiment consisted of a car which moved from left to right on a horizontal trajectory and was occluded by two tunnels on its way, and the children were asked to stop the car exactly between the tunnels by pressing on a response pad. Brain activities were analysed by using temporal spectral evolution (TSE, time-dependent amplitude changes) and coherence connectivity analysis. TSEs of *before occlusion*, *during occlusion*, correct responses (*HITS*), and incorrect responses (*MISSES*) showed gamma activity in both groups, but the preterm children used desynchronised gamma-band activity, while the full-term children used synchronised gamma-band activity. In addition, theta-band activity was observed in full-term children during both *HITS* and *MISSES*, but only during *MISSES* for the preterms. Coherence connectivity analysis showed a functional reorganisation of the connectivity networks for the preterm children compared to their full-term peers. At the behavioural level, timing errors showed no significant differences between the groups, nor did Movement-ABC scores. The findings suggest that preterm children rely upon different neural systems and oscillatory mechanisms for both visual motion perception and for timing of prospective responses of a temporarily occluded object than full-term control children. Consequently, different brain activity may function as a compensatory mechanism in preterm children so that they can perform the same prospective responses and perceptuo-motor abilities as their full-term peers.

Sammendrag

Elektroencefalografi (EEG) ble brukt for å undersøke oscillatorisk hjerneaktivitet hos 6 år gamle barn. Barna var delt i grupper etter om de var født før termin (premature) eller til termin (terminfødte). Hensikten var å se om det var forskjell i måten barna responderte når de måtte forutse bevegelsene til et objekt som ble midlertidig tildekket underveis. Eksperimentet besto av en bil som kjørte fra venstre til høyre i en horisontal bane og var tildekket av to tunneler på veien. Barna ble instruert til å stoppe bilen nøyaktig mellom tunnelene ved å presse på en stopp-knapp. Hjerneaktiviteten ble analysert ved å bruke “temporal spectral evolution” (TSE, tidsavhengig amplitude endringer) og “coherence connectivity” analyse. TSE-analyse av hjerneaktivitet *før tildekkelse*, *under tildekkelse*, korrekte responser (*TREFF*) og ikke korrekte responser (*BOM*) viste gamma-aktivitet hos begge gruppene, men de premature barna bruke desynkronisert gamma-bånd aktivitet, mens de terminfødte barna brukte synkronisert gamma-bånd aktivitet. I tillegg ble theta-bånd aktivitet observert hos de terminfødte barna under både *TREFF* og *BOM*, men bare under *BOM* hos de premature barna. “Coherence connectivity” analyse viste en funksjonell reorganisering av hjernenettverket for de premature barna sammenlignet med de terminfødte barna. På atferdsnivå viste timing-oppgaven ingen signifikante forskjeller mellom gruppene. Det gjorde heller ikke M-ABC skårene. Resultatene antyder at premature barn bruker forskjellige nevralt systemer og oscillatoriske mekanismer for både visuell bevegelsespersepsjon og timing av prospektive responser av et midlertidig tildekket objekt sammenlignet med terminfødte barn. Forskjellen i hjerneaktiviteten kan fungere som en kompensatorisk mekanisme hos de premature barna slik at de kan utføre samme prospektive responser og perseptuo-motor ferdigheter som de terminfødte barna.

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1. Introduction

Knowledge about the long-term consequences of preterm birth on brain development is of importance due to greatly increased survival rates in recent decades, accompanied by a high risk for brain injury and long-term neurodevelopmental problems in prematurely born individuals (Allen, 2008; Aarnoudse-Moens, Weisglas-Kuperus, van Goudoever, & Oosterlaan, 2009). Cerebral palsy has long been recognised as a frequent outcome of premature birth, and other neurocognitive abnormalities are also being observed at school age and beyond (Aarnoudse-Moens et al., 2009), such as problems with visual perception (Geldof, van Wassenae, de Kieviet, Kok, & Oosterlaan, 2012) and less severe motor impairments (Bracewell & Marlow, 2002; Wocadlo & Rieger, 2008). Combining visual perception and motor abilities is essential for navigating effectively through everyday life and requires accurate predictions of where objects are in relation to one's own body, even when they are temporarily occluded. Insight into the developmental processes which underlie these abilities in preterm individuals is crucial to minimise long-term problems. An important mechanism in brain development is neuroplasticity, which might be a double-edged sword for the premature brain. On the one hand, preterm individuals are vulnerable to brain injury, including in the cortical areas that process visual perception (Agyei, van der Weel, & van der Meer, 2016a; Braddick, Atkinson, & Wattam-Bell, 2003). On the other hand, they benefit greatly from positive environmental conditions (DeMaster et al., 2019), because these conditions may affect the functional brain connectivity and the development of visual perceptual and motor abilities. However, the structural and functional brain networks underlying the development of perception and motor abilities in preterm children remain poorly understood. It is crucial to detect long-term consequences within the preterm population and evaluate if the problems can be resolved at some point.

The ability to prepare and guide actions according to changing environments involve a complex system in which perception, cognition, and action are tightly coupled, an ability that has been called prospective control (van der Meer & van der Weel, 2020). Using perceptual information predictively during an action, e.g., predicting a moving object's future location so that one can grab it, requires prospective control of head, eye, and arm movements. These actions become even more complicated when an object is occluded on its way, e.g., a car that gets occluded by houses, when a child must predict when it is safe to cross the street. Such

everyday actions depend on the correct interpretation of several processes, such as identifying the object (“what”), perceiving the location (“where”), determining where the object is moving (“direction”), and how fast it is moving (“speed”). All of these processes are highly dependent on correct visual motion perception.

Visual perception is commonly divided into two different but interdependent cortical processing pathways known as the ventral and dorsal streams (Perry & Fallah, 2014). The ventral stream is associated with the identification of objects, and it runs from the primary visual cortex (V1) to other visual areas (V2, V3, and V4) and other regions located in the inferotemporal cortex of the brain (van Polanen & Davare, 2015). The dorsal stream is associated with “where” information, and it is proposed to hold an executive function in processing spatial and temporal object information (e.g., speed and path of motion) involved in guiding action, such as in prospective control (Grill-Spector, Kourtzi, & Kanwisher, 2001; Hegde, Fang, Murray, & Kersten, 2008). This stream is also thought to be initiated in V1 and goes through the visual areas V2, V3, and middle temporal cortex (MT/V5+), as well as other regions in the occipital and parietal lobes (van Polanen & Davare, 2015).

Studies have shown altered structural brain development after preterm birth (Atkinson et al., 2008; Counsell et al., 2007; Skiöld et al., 2010). The time between birth and equivalent age represents a critical period for establishing several essential brain structures, including dendritic differentiation, starting of myelinisation, the establishment of thalamocortical connections, and differentiation of cortical regions (Kostovic & Vasung, 2009). If a child is born preterm, many of these processes are established in the neonatal intensive care unit, where environmental conditions might interfere. Hence, structural brain development may be disturbed because of impaired maturation or specific injuries (Counsell et al., 2007; Hart, Whitby, Griffiths, & Smith, 2008; Kesler et al., 2004). Magnetic resonance imaging (MRI) studies have shown that white matter damage is a prevalent pattern of brain injury in this population, and studies into microstructural development have indicated that white matter abnormalities are evident into childhood due to preterm birth, even in the absence of major impairments and brain damage (Constable et al., 2008; Kesler et al., 2004; Miller & Ferriero, 2009). White matter damage may affect the brain areas that process visual perception, especially the dorsal stream pathway (Braddick et al., 2003). In addition to altered structural development, the functional brain networks are essential, specifically in understanding the integration of visual perception and motor performance.

Altered functional brain development has also been observed after preterm birth (Doesburg et al., 2011; Schafer et al., 2009). Functional brain connectivity reflects the brain's abilities to process and integrate information. The premature brain is associated with reduced network integration compared to the full-term brain (Batalle et al., 2017), and this has been quantified by using hubs, nodes and edges in the framework of a functional connectivity network. Hubs mediate a large fraction of signals, nodes mediate a smaller amount of signals, and edges signal the strength of the signal connection (Oldham & Fornito, 2019). Higher network integration, i.e. more hub and node connections over a wide area of the brain, are tightly linked to higher-order cognition (Just & Varma, 2007). Even in the absence of major intellectual or neurological impairments, altered functional connectivity patterns between cortical regions have been reported in children born preterm (Gozzo et al., 2009; Lawrence et al., 2009; Schafer et al., 2009; Shaywitz et al., 2002). Interestingly, different patterns of functional connectivity have been observed in preterm children even when performance does not differ from their full-term peers (Narberhaus et al., 2009; Schafer et al., 2009). This may indicate functional reorganisation, which impacts how communication between brain regions is recruited to support cognitive operations (Chilosi et al., 2005; Just & Varma, 2007). Functional reorganisation of cortical regions has been observed in visual-perceptual learning tasks in adults born prematurely (Narberhaus et al., 2009), but little is known about the functional connectivity networks that underlie the processing of visual motion in school-aged children born preterm.

The large majority of studies concerning functional brain connectivity in preterm children have used fMRI imaging (Gozzo et al., 2009; Narberhaus et al., 2009; Schafer et al., 2009). Although this modality provides high spatial resolution, it does not directly measure neuronal activity and has a limited temporal resolution, preventing the measurement of neurophysiological oscillations and their inter-regional connections. EEG is an imaging technique that offers a combination of spatial and temporal resolution, allowing both for the decomposition of connectivity into time-frequency space and for the measurements of fast neuronal oscillations directly underlying information processing and communication in the brain (Başar, Başar-Eroğlu, Karakaş, & Schürmann, 1999). Frequency analysis detects induced brain activity, which is time-locked to an event and not phase-locked, and the analysis also represents frequency-specific changes in the ongoing EEG activity. The frequencies are either an event-related decrease (desynchronisation: ERD) or an event-related

increase (synchronisation: ERS) of power in the given frequency band compared to a baseline (Pfurtscheller & Lopes da Silva, 1999). ERD and ERS reflect changes in the activity of local interactions between main neurons and interneurons that control the frequency component of the ongoing EEG. ERD is associated with increased task complexity, attention and/or, learning, while ERS is generally associated with efficacy of information processing (Pfurtscheller & Lopes da Silva, 1999). Neural populations that oscillate in synchrony can consistently exchange bursts of action potential fluctuations, thereby increasing the efficacy of information exchange (Fries, 2005).

Neural oscillations have been found in a range of different frequencies, where low frequencies tend to recruit neurons in larger cortical areas and high frequencies tend to recruit neurons that are spatially restricted (Pfurtscheller & Lopes da Silva, 1999). Different classes of oscillations have been distinguished over the years and are thought to reflect neurophysiological processes that exhibit functionally different roles: delta-band (1–4 Hz), theta-band (4–7 Hz), alpha-band (7–13 Hz), beta-band (13–30 Hz), and gamma-band (30–150 Hz) (Agyei, van der Weel, & van der Meer, 2016b). The use of delta frequencies is found in signal detection and decision making processes (Başar, Başar-Eroğlu, Karakaş, & Schürmann, 2000), theta frequencies are essential for neuronal plasticity and coding of perceptual information (Hanslmayr, Volberg, Wimber, Dalal, & Greenlee, 2013; Landau, Schreyer, van Pelt, & Fries, 2015), alpha frequencies are found in tasks which involve the control of inhibition and cortical processing (Klimesch, Sauseng, & Hanslmayr, 2007), beta frequencies are involved in the maintenance of a particular set of cognitive and motor functions when distractions are presented (Engel & Fries, 2010), and gamma frequencies are used in memory-matching and are fundamental for cognitive processes such as attention, language, and object representation (Herrmann, Frund, & Lenz, 2010; Herrmann & Mecklinger, 2001; Kaufman, Csibra, & Johnson, 2003; Solomon et al., 2017).

Several EEG studies of visual motion perception using time-frequency analysis have shown that infants generally show frequencies of 4 to 8 Hz compared to older children and adults, who show frequencies around 10 to 20 Hz (Rasulo, Vilhelmsen, van der Weel, & van der Meer, 2021; Vilhelmsen, Agyei, van der Weel, & van der Meer, 2019). During infancy, preterm infants have shown lower frequencies in response to visual motion stimuli compared to full-term infants. Full-term infants showed frequencies at around 10 Hz at 12 months while preterm infants of the same age showed much lower frequencies at around 4 Hz (Agyei et al.,

2016a). The low-frequency oscillations undergo systematic development from early childhood to adulthood, and low frequencies in infancy are thought to reflect immaturity (Stroganova & Orekhova, 2007). Agyei and colleagues (2016a) also found differences in power within the frequency bands during motion perception. Where full-term infants at 12 months showed synchronised alpha and beta activity, preterm infants at 12 months showed desynchronised theta activity. Differences in ERS/ERD have also been observed in children, when processing a visual short-term memory task. In this case, preterm children showed desynchronised alpha-band activity and the full-term children used synchronised alpha-band activity (Doesburg et al., 2011).

In everyday life situations, objects get temporarily occluded and we need to pick up predictive information for prospective control to act appropriately. This requires fine and gross motor development, as well as prospective control. Van der Meer and her colleagues (1994) investigated the development of prospective control of head, eye, and arm movements in preterm and full-term infants when catching a moving toy that had been temporarily occluded on its way. The results showed that normally developing infants at the age of 40 weeks could adjust their reaching actions skilfully with respect to the prospective time of arrival of the toy at the catching place. Almost all the preterm infants displayed the same catching skills towards the end of the first year, corrected for prematurity, while two preterm infants still showed poor anticipation of the toy's reappearance (van der Meer, van der Weel, Lee, Laing, & Lin, 1995). These two preterm infants were later diagnosed with mild and moderate cerebral palsy at around 2 years of age. Hence, poor development of prospective control in the catching task could potentially serve as an indicator of possible brain damage, and EEG could be a potential tool for identifying abnormal developmental trajectories of neuromotor control in preterm infants (Nishiyori, Xiao, Vanderbilt, & Smith, 2021). Further, a recent study of normally developing full-term and preterm infants between 22 and 48 weeks of age showed little difference between the groups in catching a moving toy (Kayed & van der Meer, 2009). These studies indicate that many infants born preterm catch up with their peers during the first year of life, but there are still some preterm infants with long-lasting perceptuo-motor impairments (Moreira, Magalhães, & Alves, 2014). Hence, it is essential to understand the underlying developmental process so that children at risk for developmental perceptuo-motor problems can be identified (van der Weel, van der Meer, & Lee, 1996). Additionally, explore if enriching environmental conditions could enhance their perceptuo-motor development. Little is known about whether preterm children at school age catch up with their full-term

peers with regard to timing of prospective responses in tasks involving temporarily occluded moving objects.

In previous studies about occlusion, gamma-band (< 40 Hz) activation during the occlusion period of stationary objects in infants was observed (Kaufman et al., 2003; Southgate, Csibra, Kaufman, & Johnson, 2008). Further, gamma-band activity in adults has been associated with maintaining an object's visible properties in mind (Hoogenboom, Schoffelen, Oostenveld, Parkes, & Fries, 2006; Lachaux et al., 2005). However, current studies have not investigated time-frequency changes in children's brains by using an occlusion paradigm with a moving stimulus, nor have they investigated differences between preterm and full-term children by using this type of study. Successful deceleration discrimination when following a moving car on a screen that was temporarily occluded, has previously been found in adult EEG (Holth, van der Meer, & van der Weel, 2013). When it comes to EEG performed on children, it is unclear whether the brain of the young child also successfully discriminates between different speeds during temporary occlusion of moving objects.

The present study investigated visual motion perception and prospective responses in preterm and full-term children at 6 years of age on a timing task that consisted of stopping a temporarily occluded car moving at three different speeds in a designated target area. The children were instructed to stop the car right after the occlusion period. High-density EEG was used to detect oscillatory brain activity through time-frequency analysis and coherence connectivity analysis of the events *before occlusion*, *during occlusion*, perfectly timed responses (*HITS*) and missed responses (*MISSES*). Based on previous EEG studies mentioned above, one expects to find gamma-band activity when the children followed the moving object. The preterm children were expected to show an altered functional network activation compared to the full-term children, both in the time-frequency analysis and connectivity analysis. Timing errors were also analysed. Compared to the full-term children, preterm children were expected to show less accuracy in predicting the timing of the reappearance of the occluded car. Finally, as a supplementary tool to evaluate and compare motor performance between groups, the Movement Assessment Battery for Children (M-ABC) was applied, which is a widespread motor test used on children of school age (Bos, Van Braeckel, Hitzert, Tanis, & Roze, 2013; Broström et al., 2016; Cserjesi et al., 2012). Previous research has detected atypical performance in preterm children at 3 years of age (De Rose et al., 2013;

Foulder-Hughes & Cooke, 2003). Hence, the preterm children were expected to show less accurate performances than the full-term children on the M-ABC test.

2. Methods

2. 1. Participants

20 healthy children, 10 preterm and 10 full-term, were included in this study and the two groups are matched according to age and gender. The participants are a part of a longitudinal follow-up programme from infancy and beyond, and they were recruited through birth announcements and with help of the paediatrician in charge of the Neonatal Intensive Care Unit at St. Olav's University Hospital in Trondheim, Norway. To ensure valid matching, the preterm children were tested at ages corrected for prematurity. The preterm children (6 girls/ 4 boys) had a mean age of 6 years and 1 month ($SD = 9$ months), and the full-term children (6 girls/ 4 boys) had a mean age of 6 years and 2 months ($SD = 7$ months). The preterm children were born at a mean gestational age of 31 weeks and 3 days ($SD = 2.2$, range: 26 - 32 weeks) and had a mean birth weight of 1608 g ($SD = 515$, range 710 - 2670 g). At birth, the full-term children had a mean gestational age of 39 weeks and 5 days ($SD = 1.2$, range 37 - 41 weeks) and a mean birth weight of 3590 g ($SD = 357$, range 3250 - 4295 g). One of the preterm children had an intraventricular haemorrhage grade 3 in the first week of life but did not experience any major developmental delays. The rest of the preterm children did not have any major neurological deficits requiring serious medical interventions that may lead to abnormal development.

Electroencephalogram (EEG) is a physiological procedure that causes no harm or pain to the participants. Prior to the experiment, the parents gave their informed written consent and were made aware that they were free to withdraw their child from the study at any time. The study was approved by the Norwegian Center for Research Data and the Norwegian Regional Ethics Committee.

2. 2. Occlusion stimulus

The stimulus consisted of an animated red car moving on a straight horizontal path, during which it disappeared twice behind a green tunnel (see Figure 1). The experiment was made as a game where the participants were instructed to stop the car with a touchpad, and they were asked to press the button to stop the car precisely between the two tunnels. The car had a length of 40 pixels (px) (7 cm), while the tunnels had a length of 100 px (18 cm) each. The car travelled 424 px (75 cm) before it reached the first tunnel. In order to vary the spatiotemporal information available in each trial, three different decelerations were included:

fast (15% deceleration), medium (60% deceleration), and slow (95% deceleration). The different decelerations and the stopping mechanism helped increase the children's interest in the task.



FIGURE 1. Stimulus set-up: The car moved along a horizontal path on a large screen and was occluded twice on its way. The car started at high speed, 0.33 px/ms, and after 303 ms moved under three different constant decelerations, i.e., “fast” (15% deceleration), “medium” (60% deceleration), and “slow” (95% deceleration), corresponding to 0.000118 px/ms², 0.000076 px/ms², and 0.00015 px/ms². One trial was counted with the car starting in the left corner and disappearing behind the second tunnel, which took 1692 ms, 2117 ms, and 3214 ms for fast, medium, and slow speed, respectively, or when the child stopped the car. The car was completely occluded behind the first tunnel at 174 ms, 262 ms, and 410 ms during fast, medium, and slow speeds, respectively. The prospective response (pressing the button on the touchpad) was perfectly timed when the car was stopped exactly between the two tunnels, i.e., 1550 ms, 1891 ms, and 2421 ms into the trial for fast, medium, and slow car speed, respectively. Inter-stimulus intervals were set to 2000 ms.

2. 3. Apparatus

The moving car and the two tunnels were presented on a large screen (187 cm wide, 105 cm high) placed 70 cm from the child's face, and they were generated with E-Prime (Psychology Software Tools, Inc.). EEG activity was recorded using a Geodesic Sensor Net (GSN) 200 containing 256 electrodes evenly distributed over the child's head. Triggers about the onset/offset of the trial and the button-press responses were communicated from E-prime onto the EEG recording. All electrode impedances were set to the recommended value of 50 k Ω to ensure an optimal signal-to-noise ratio (Ferree, Luu, & Tucker, 2001). The amplified EEG signals were recorded on Net Station software using a sampling rate of 500 Hz with a low-pass filter of 200 Hz and a 0.1 Hz high-pass filter. To make it possible to observe the child's attention and behaviour during the experiment, digital videos were recorded by two small cameras positioned at different angles in front of the child. The data was then stored on a hard disc for further offline analysis.

2. 4. Procedure

The experiment took place at the Developmental Neuroscience Laboratory (Nu-lab) at the Department of Psychology at the Norwegian University of Science and Technology, Norway. The children arrived with their caregivers some time before the experiment started, and both the children and the caregivers were given information about the purpose of the experiment, its duration, and the experimental procedure. The child's head circumference was then measured to ensure that the correct net size was selected. Before the electrode net was placed on the child's scalp, it was soaked in a solution of distilled water, saline, and a few drops of baby shampoo for at least 10 minutes for optimal contact. After the net was mounted on the head, the child was guided into the experimental room and seated in front of the large screen. The electrode net was connected to the amplifier, and the impedance was checked. The experiment was conducted in a quiet and dimly-lit room, separated by a soundproof window from the control room where the computers for stimulus generation and data acquisition were placed. The occlusion experiment was shown in a series of four experiments that measured other aspects of visual motion perception, where the present experiment was usually presented as the third experiment. Each experiment lasted approximately 7-10 minutes, and the whole session lasted for 30-40 minutes. If needed due to tiredness and lack of attention, the experiments could be paused. Before the experiment started, an assistant gave the child instructions to press a button on the touchpad to stop the car when it was precisely between the two tunnels. An assistant was present in the experimental room during the experiment, together with the child's caregiver. After the session, the child was debriefed about its experience of the experiments and asked for feedback. The preterm children were shown on average 67 trials ($SD = 10$), and the full-term children were shown on average 70 trials ($SD = 11$), equally divided between the three car speeds that were presented in random order. After a brief break in which the child was offered some refreshments, the child and two assistants went on to do the M-ABC test in an adjacent large room. At the same time, the caregivers filled out a questionnaire belonging to the M-ABC about their child's motor abilities in everyday life situations.

2. 5. EEG data analysis: Time-frequency analysis

Time-frequency analysis was carried out to investigate the differences between preterm and full-term children regarding oscillatory activity in the visual areas of interest. The analysis

represented changes in amplitude over time and was carried out in BESA research software version 7.0. To avoid researcher bias, all data analysis was performed blindly. The name of the children was removed from the files by an assistant and replaced with numbers from 1 to 20. Then, the files were placed in either “group 1” or “group 2”, one group including preterm children and the other group including full-term children. By visual inspection on electrode level, artefact-contaminated channels and trials resulting from head and body movements were defined as bad or re-estimated using spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989; Picton et al., 2000). None of the children had more than 10% of the channels defined as bad. To remove mainline noise interference in the EEG data, notch filter was set at 50 Hz. High cut-off filter was set at 80 Hz to remove channels contaminated with high-frequency activities, while low cut-off filter was set at 1.6 Hz to remove slow drift in the data. To remove physiological artefacts such as blinking from the raw EEG, the data were transformed into a reference-free montage showing EEG at 27 standard electrodes. A manual form of artefact correction was employed, designed to separate artefacts and brain activity based on spatial filtering. In scanning for artefacts, threshold values for gradient and low signal were set at 75 μV and 0.1 μV , respectively, while maximum amplitude was set at 200 μV .

Before computing the time-frequency analysis, event-files were prepared for each child separately and added to the raw EEG data. The event-files were made to separate each trial into four different events: *before occlusion*, *during occlusion*, *HITS*, and *MISSES*. The responses were defined as either a HIT or a MISS depending on how much of the car was visible when it was stopped (*HITS* > 50% visible, all other responses were defined as *MISSES*). Hence, twelve different events were compared, i.e., 3 (fast, medium, slow) x 4 (*before occlusion*, *during occlusion*, *HITS*, and *MISSES*). During occlusion, the car was completely occluded behind the first tunnel.

BESA Statistics 2.1 was used to test for significant clusters between events and groups, and the program required the epochs to be the same length. Because the car drove at three different speeds, epoch lengths for the three car speeds were different. Therefore, shortening the epoch *before occlusion* and *during occlusion* for medium and slow car speeds was necessary. Hence, the epoch of fast car speed was used for *before occlusion* (-100 ms to +1262 ms) and *during occlusion* (-100 ms to +174 ms) in the medium and slow car speeds since those were the longest epochs that could be used when performing the statistics. The

epochs of *HITS* and *MISSES* were set to -300 ms to +300 ms, where 0 ms was the child's response. After cleaning the data, the mean number of accepted trials for the brain data was 63 ($SD = 12$) for the preterm children and 65 ($SD = 13$) for the full-term children. Both groups had similar distribution of the responses, where 51% of the responses were *HITS* and 49% of the responses were *MISSES*. The accepted trials formed the basis for the included responses in the timing-error task.

A time-frequency analysis (Temporal Spectral Evolution – TSE) required the data to be transformed from electrode level to source montage dipoles. Pre-defined multiple source dipoles were used. They model activities in the visual area of the parietal and visual cortices and other brain regions. The display is generated from single trials by averaging spectral density amplitudes over trials. Thus, each displayed graph plotted the spectral amplitude density of one montage channel over time and frequency, normalised to baseline for each frequency (Hoechstetter et al., 2004; Pfurtscheller, Neuper, & Mohl, 1994; Pfurtscheller, Stancák, & Neuper, 1996). A complex demodulation transformed time-domain signals into the time-frequency domain (Papp & Ktonas, 1976). In order to have only the displays of oscillatory brain activity, signals from averaged evoked responses were removed from the single trial time series before calculating TSEs. Measuring oscillatory brain activity by surface electrodes is not ideal due to the smearing effect of brain conduction in EEG and the nature of dipole fields. The focal brain activity is widely distributed and contributes with mixed signals to the scalp waveforms. Therefore, a source montage was used to achieve optimal separation of focal brain activities. It was obtained using a multiple source model (Scherg & Berg, 1991), where source waveforms maximally separated activities from different brain regions. The source montage consisted of 17 sources that modelled visual pathway activities. Of these sources, visual cortex ventral midline (VCvM), visual cortex radial right (VCrR), and visual cortex lateral right (VCIR) were further analysed (see Figure 2).

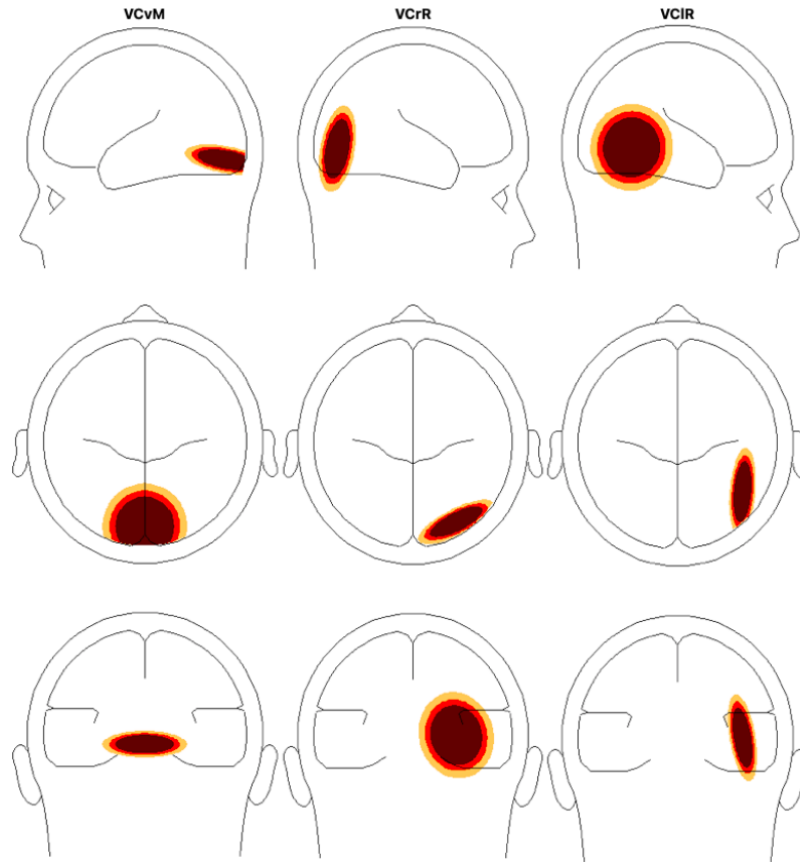


FIGURE 2. Head model of associated brain regions in visual cortical areas VCvM, VCrR, and VCIR. The red area reflects the estimated source activity in the related brain region in an active state.

As recommended, bone thickness and bone conductivity were set to 5 mm and 0.018σ for children (Richards, Sanchez, Phillips-Meek, & Xie, 2016). TSE displays for all events were set from 4 to 80 Hz with a frequency of 1 Hz and a time sample of 50 ms. In addition, individual artefact coordinated files were added for each child. To observe significant oscillatory activity patterns that are not visible in the overall average TSE, individual TSE probability maps were computed (change in amplitude from baseline to a particular time-frequency sampling point) for each child. To correct for multiple testing, Bonferroni procedure and permutation tests were applied to each set of time samples belonging to one frequency bin (Simes, 1986).

2. 6. EEG data analysis: Coherence connectivity analysis

The computed time-frequency data were further used to quantify the functional connectivity between the visual areas of interest in preterm and full-term children. A functional connectivity analysis was performed by applying the coherence method in BESA Connectivity version 1.0. Coherence is a measure of linear covariance between two signals in

a particular time-frequency bin (Rosenberg, Amjad, Breeze, Brillinger, & Halliday, 1989). Hence, the coherence analysis describes the numbers of in-phase components of two brain source signals at a specific frequency. In the coherence analysis, the same sources as in the time-frequency analysis were used, focusing on the following sources: central midline (CM), parietal midline (PM), visual cortex lateral left (VCIL), visual cortex lateral right (VCIR), visual cortex radial left (VCrL), visual cortex radial right (VCrR), visual cortex bilateral left (VCbL), visual cortex bilateral right (VCbR), and visual cortex ventral midline (VCvM). All the sources are illustrated in Figure 3.

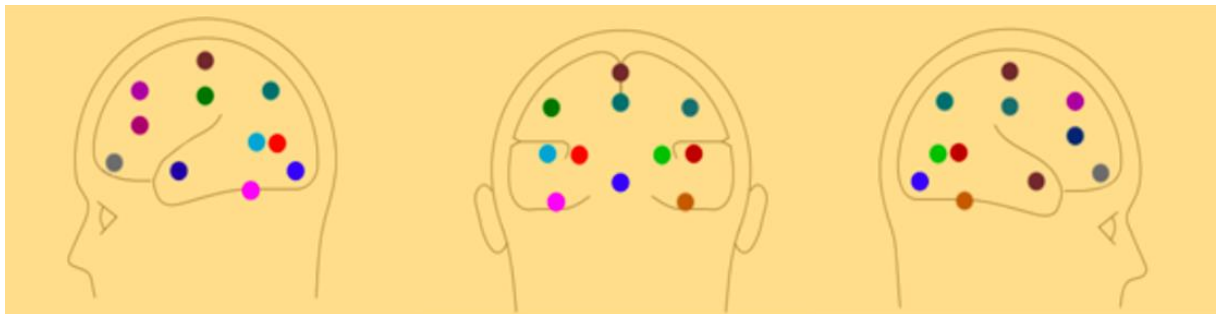


FIGURE 3. Head model with illustration of the sources of interest, with approximate Talairach coordinates: **CM** ($x=0.0, y=24.2, z=60.5$); **PM** ($x=0.0, y=-72.3, z=37.0$); **VCIL** ($x=-45.2, y=-57.2, x=6.5$); **VCIR** ($x=45.2, y=-57.2, z=6.5$); **VCrL** ($x=25.6, y=-73.0, z=4.2$); **VCrR** ($x=25.6, y=73.0, z=4.2$); **VCbL** ($x=-40.0, y=48.6, z=22.7$); **VCbR** ($x=40.0, y=48.6, z=22.7$); **VCvM** ($x=0.0, y=84.9, z=14.3$).

BESA Statistics 2.1 was used to test for significant differences between groups and events. A combination of permutation tests and data clustering was employed in the statistical tests to address the multiple comparison problem. The epochs must be the same to test the significant difference between the events. Therefore, the epoch of *before occlusion* was shortened to the same epoch as of *during occlusion* (-100 to +174 ms). Further, comparisons between *before occlusion* versus *during occlusion* and *HITS* versus *MISSES* were computed within the preterm and full-term groups separately to show the different connectivity patterns within each group, as this is not captured by the cluster comparison in BESA Statistics between groups. In addition, preterm children and full-term children were compared in the four events (*before occlusion*, *during occlusion*, *HITS* and *MISSES*) to show main significant cluster differences between groups.

2. 7. Behavioural analysis: Prospective responses

An analysis of the children's button pressing was conducted to investigate the difference between preterm and full-term children in timing of prospective responses. The children were asked to press the button on the touchpad in order to stop the car precisely between the two tunnels, which is referred to as a perfectly timed response. The timed responses were stored in the raw EEG file for each child as events recorded during the experiments. The events were then downloaded for further analysis. Each car speed was analysed separately, where the time window between a perfectly timed response and the child's response was calculated and combined into a continuous variable of timing errors. The responses where the whole car was visible before the first tunnel and invisible behind the second tunnel were excluded (preterms: $M = 2.3$, $SD = 1.2$, full-terms: $M = 2.3$, $SD = 1.9$) from the analysis to ensure that only reasonable responses were included. The three continuous variables consisted of both positive numbers (early responses) and negative numbers (late responses) and would have been zeroed out when averaged together. Hence, a root means square averaging procedure was used to overcome this problem.

2. 8. Behavioural analysis: M-ABC

The Movement Assessment Battery for Children (M-ABC) was used to assess the children's motor abilities (Henderson & Sugden, 1992). The battery consists of three categories: Manual Dexterity, Ball Skills, and Static and Dynamic Balance. The categories were tested with eight tasks. The tasks were explained by a research assistant to the children, and a second assistant rated the child's performance according to the procedure, where the possible total score ranged from 0 to 40 points. A total score of 13.5 points or higher indicates a possible delay in motor development. The children were tested using tasks according to their age group. The whole session lasted between 20 and 40 minutes and was video recorded in case an extra check of the children's performance was needed.

3. Results

3. 1. EEG data analysis

3. 1. 1. Brain source activity in the time-frequency domain of single subjects

A time-frequency analysis was carried out for the twelve different events, 3 (fast, medium, slow speed) x 4 (*before occlusion, during occlusion, HITS, MISSES*) for all children separately. No significant differences with respect to car speed were found when the TSEs of the events were compared with each other. Thus, fast, medium, and slow car speed were combined into one motion condition and analysed separately for the remaining events (*before occlusion, during occlusion, HITS, and MISSES*).

Figure 5 shows TSE plots of significant ($p < 0.05$) oscillatory activity for a typical preterm child and a typical full-term child. The individual TSEs of the preterm child showed a pattern of desynchronised gamma-band (> 30 Hz) activity *before occlusion, during occlusion,* and after a successful response (*HIT*). In contrast, the full-term child showed a pattern of synchronised gamma-band activity *before occlusion, during occlusion,* and after a *HIT*. In addition, for the full-term child, a pattern of synchronised theta activity (4-8 Hz) was shown *during occlusion* and after a *HIT*. Both children showed desynchronised gamma-band activity after a *MISS* response, and the preterm child showed, in addition, desynchronised theta activity, while the full-term participants showed synchronised theta activity.

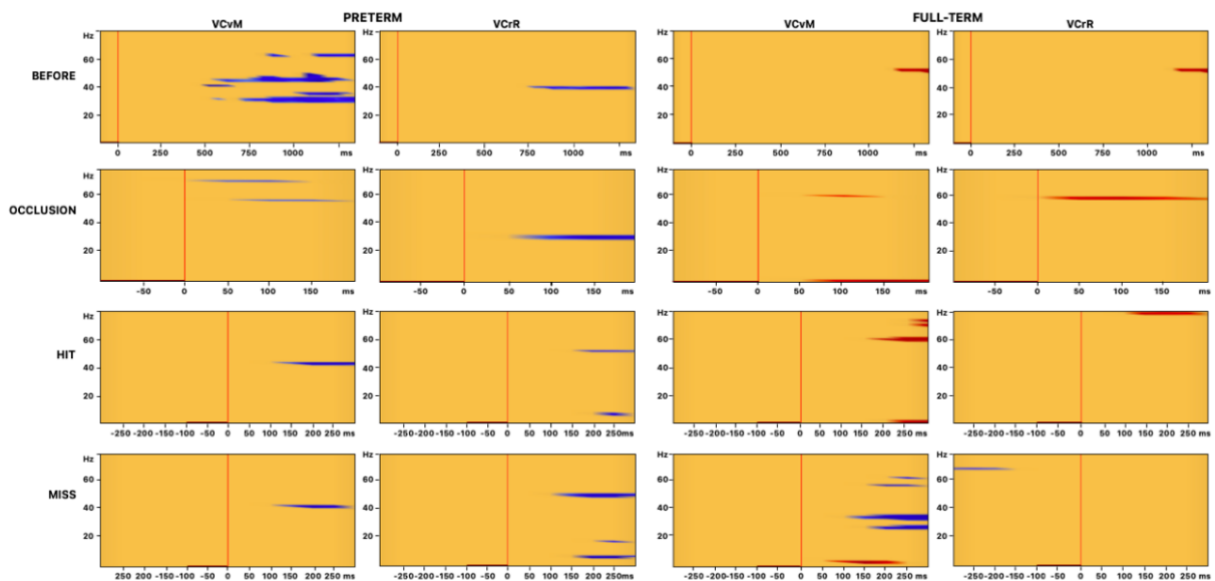


FIGURE 5. Oscillatory activities in the sources of interest (VCvM and VCvR) in TSE probability maps of the combined motion events *before occlusion, during occlusion, HIT,* and *MISS* for a typical full-term and preterm child. In the TSE probability maps, significant increase (red areas) and decrease (blue areas) of amplitudes ($p <$

0.05) in TSEs of combined motion when compared to baseline. The typical full-term child showed gamma-band synchronisation in *before occlusion*, *during occlusion* and *HIT*, and gamma-band desynchronisation for *MISS*. The typical preterm child showed gamma-band desynchronisation in all the events. Epoch was from -100 to +1262 ms (*before occlusion*), where the red vertical line marks the start of the deceleration of the car, -100 to +174 ms (*during occlusion*), where the red vertical line marks the beginning of the tunnel, -300 to +300 ms (*HIT* and *MISS*) where the red vertical line marks the child's response. The baseline was set from -100 ms to 0 ms for all events. Frequency (Hz) on the y-axes ranges from 4 to 80.

3. 1. 2. Brain source activity in the time-frequency domain of average group data

When brain activity *during occlusion* in preterm and full-term children was compared, a significant cluster ($p < 0.05$) was found in the occipital source of interest, i.e., visual cortex lateral right (VCIR) in the gamma frequency band (53 Hz), indicating that preterm children had significantly lower cluster values ($M = -0.052$) than full-term children ($M = 0.043$) (see Figure 6).

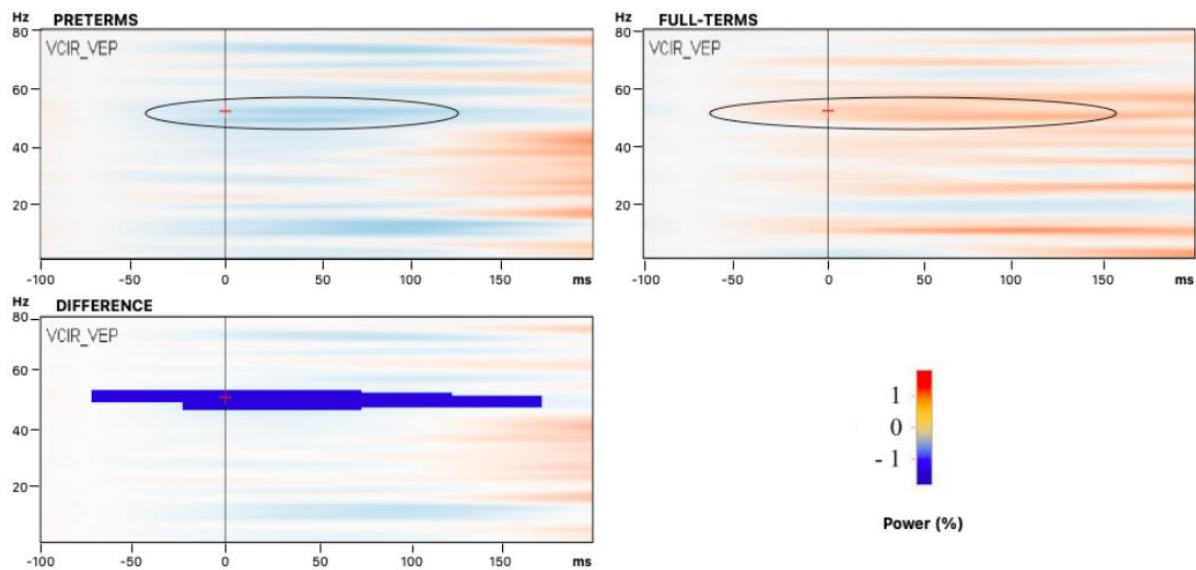


FIGURE 6. Averaged visualisation of the significant data cluster *during occlusion* when comparing preterm and full-term children. Top left represents preterm children, and top right represents full-term children. Bottom left is the area of significant cluster difference ($p < 0.05$) between preterm and full-term children. The dark blue area indicates that the difference was negative, meaning that the cluster values of preterm (black oval in the top left) were significantly lower than the cluster values of full-term (black oval in top right) children.

3. 1. 3 Brain source activity in coherence connectivity analysis: Within group

As in the TSE analysis, no significant connectivity differences between the three car speeds were found, so they were further analysed as four combined motion events (*before occlusion*, *during occlusion*, *HITS*, and *MISSES*). To test for significant connectivity differences between

the events *before occlusion* and *during occlusion* within the groups of preterm and full-term children, paired t-tests of the coherence connectivity pattern were computed. For preterm children, the results showed no significant ($p > 0.05$) cluster between the two events, while the full-term children showed 6 significant cluster differences in band power. The differences were in the gamma (30 – 80 Hz) range in the visual sources of interest (see Figure 7). Further, both groups had significant ($p < 0.05$) cluster differences in the gamma range when comparing the events *HIT* vs *MISS*. Preterm children had 9 significant connectivity differences in the occipital region of the brain. Full-term children had 12 significant connectivity differences in the occipital and parietal regions, including three interactions with the parietal midline (PM) source in the lower dorsal stream. In Figure 7, these differences are visualised in a network with proposed hubs (red dots ≥ 4 departures/arrivals), nodes (black dots, ≤ 3 departures/arrivals), and edges. Hubs have a higher degree of involvement in the network than nodes, as expressed through their functional connectivity values (edges). The findings suggest that full-term children, compared to preterm children, use a more specialised and stronger functional connectivity pattern when they perform a *HIT* as opposed to a *MISS*. The full-term children showed more significant connectivity differences, stronger connectivity, and use of higher visual areas in the connectivity network.

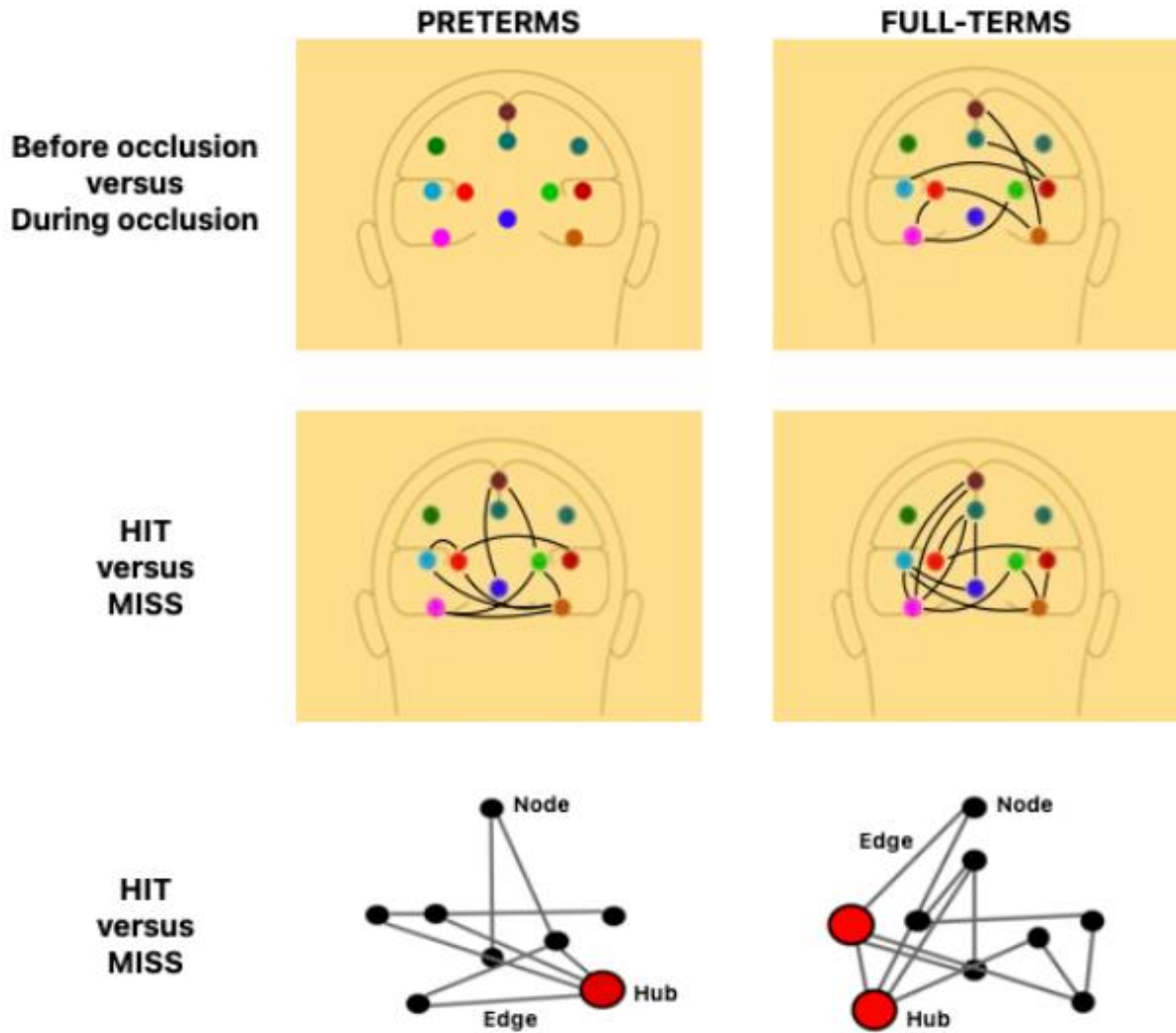


FIGURE 7. Brain maps of coherence connectivity when comparing the combined motion events *before occlusion* versus *during occlusion* and *HIT* versus *MISS* within the groups of preterm (left) and full-term (right) children. A coherence method followed by complex demodulation with time and frequency sampling at 50 ms and 1 Hz, respectively, was applied. The significant connectivity differences ($p < 0.05$) in the gamma frequency range are visualised by the black lines between the colour coded sources of interest: **CM**, **PM**, **VCIL**, **VCIR**, **VCrL**, **VCrR**, **VCbL**, **VCbR**, **VCvM**. At the bottom, the network differences between *HIT* and *MISS* are visualised with hubs (in red, ≥ 4 departures/arrivals) and nodes (in black, ≤ 3 departures/arrivals) through their functional connectivity values, edges (in grey).

3. 1. 4. Brain source activity in coherence connectivity analysis: Between groups

When preterm and full-term children were compared (unpaired t-test) in the four events, a significant ($p < 0.05$) coherence cluster between the source visual cortex radial left (VCrL) and visual cortex radial right (VCrR) was shown at 60 Hz in *before occlusion*, *HIT* and *MISS*. Here, preterm children showed a significantly greater coherence ($Mean = 0.44$) than the full-

term children ($Mean = 0.24$) (see Figure 8). The findings suggest that connectivity is stronger between VCrL and VCrR in the functional connectivity networks for preterms compared to full-terms, which confirms the use of different connectivity networks between the groups. No significant cluster differences were detected *during occlusion*.

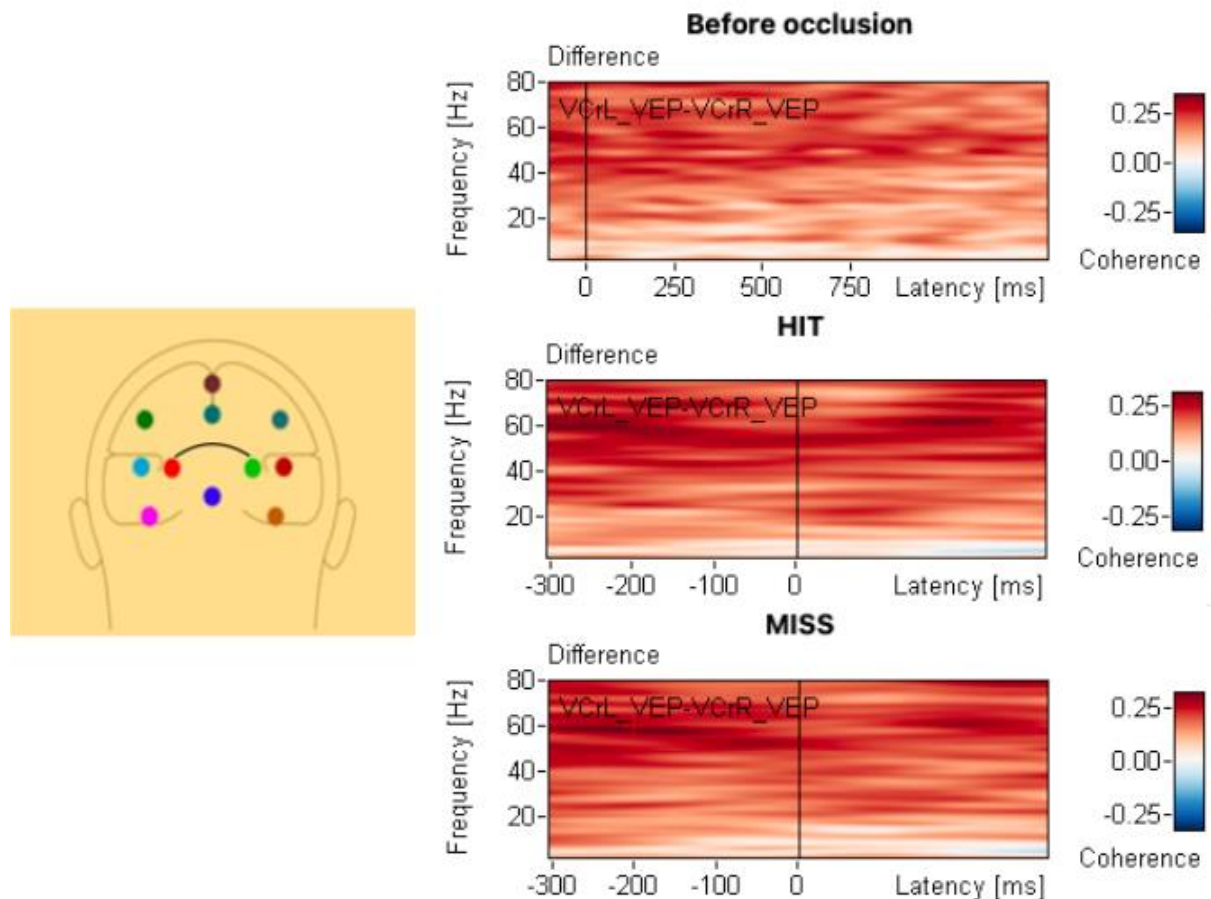


FIGURE 8. Plots of significant cluster coherence ($p < 0.05$) between sources VCrL and VCrR between preterm and full-term children *before occlusion*, *HIT*, and *MISS*. The plot colours represent the strength of the interactions compared to baseline (-100 to 0 ms). The left head model visualises the connectivity between **VCrL** and **VCrR** with a black line.

3. 2. Behavioural data analysis

3. 2. 1. Prospective responses: Timing error analysis

There were no significant differences, $F(1,18) = .003$, $p = .956$, found between the preterm and the full-term children for the timing task of pressing the button to stop the car between the two tunnels. RMS values as an indication of timing error for the three car speeds were calculated. Timing errors for preterm children were $M = 88.9$ ms ($SD = 16.7$), $M = 137.0$ ($SD = 23.7$), and $M = 226.3$ ($SD = 101.0$) and for full-term children they were $M = 85.6$ ($SD = 15.6$), $M = 140.6$ ($SD = 27.5$), and $M = 227.1$ ($SD = 55.0$) for fast, medium, and slow car

speed, respectively. Both groups had the longest timing error for the slow car speed and the shortest timing error for the fast car speed (see Figure 9).

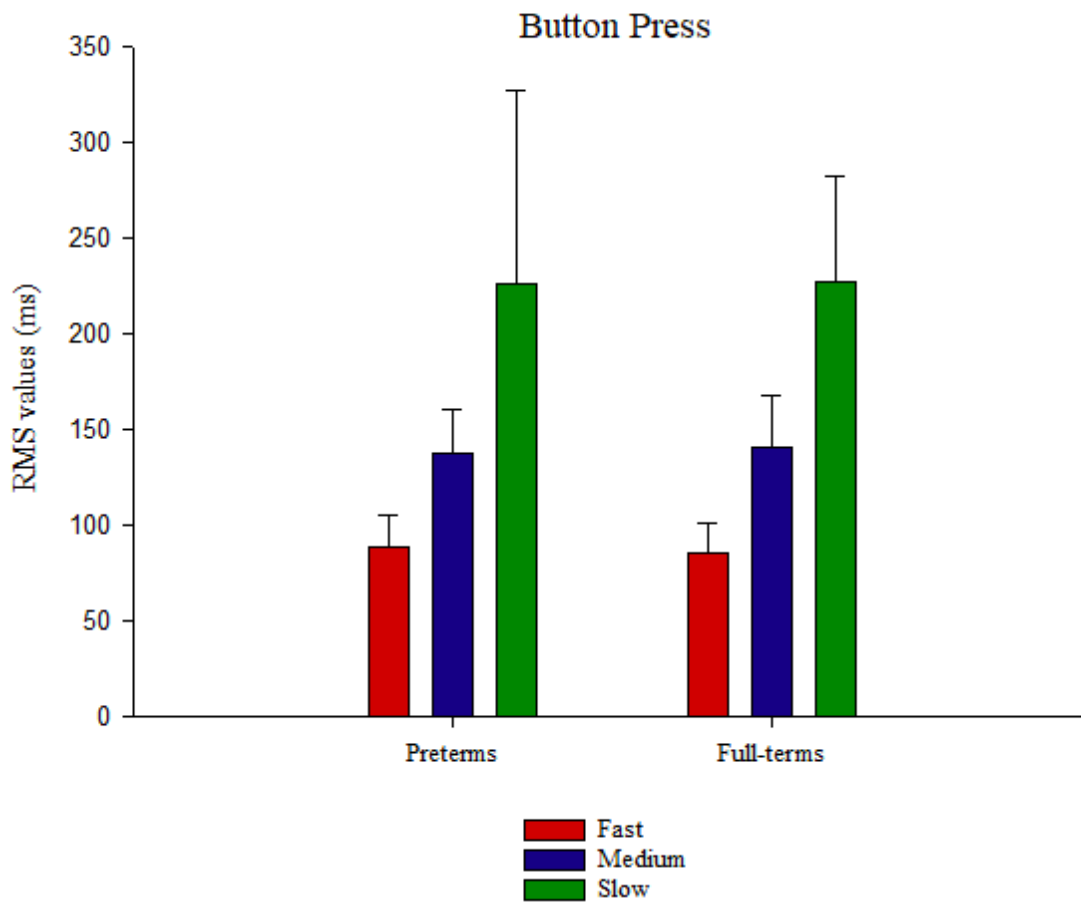


FIGURE 9. Each bar represents the average of the RMS values in fast, medium, and slow car speeds for preterm and full-term children. The two groups preformed similarly on the timing task, with the shortest timing errors for fast car speed.

3. 2. 2. Motor performance: Movement ABC scores

Table 1 shows the performance results for children in both groups on the M-ABC test. A total score equal to or above 13.5 might indicate a delay or impairment in motor skills in relation to the motor capabilities of children at the same stage in life. On average, a two-tailed t-test demonstrated no significant differences ($p = .723$) in scores for motor performance between the preterm group ($M = 8.85$, $SD = 7.57$) and full-term group ($M = 7.8$, $SD = 5.27$). However, a total of 5 children showed surprisingly high scores.

M-ABC scores	
Preterm	Full-term
13	6
21	14
5.5	6
2	14.5
4	1.5
4	14
3.5	11
23	5
7.5	6
5	0

TABLE 1. Individual scores of motor performance in the M-ABC test for 10 preterm and 10 full-term children. Scores above 13.5 are highlighted and indicate a possible motor delay.

4. Discussion

This present study investigated the difference between preterm and full-term children at 6 years of age in visual motion perception, prospective responses, and motor abilities. High-density EEG was used to study brain electrical activity as a perceptual response to a timing task consisting of stopping a temporarily occluded car moving at three different speeds in a designated target area. The findings demonstrated that preterm and full-term children engage neural systems for visual motion perception and timing of responses differently. The basis for this conclusion is a set of key findings, based on observed differences in power within the gamma frequency band, differences in theta-gamma band coupling, and differences in connectivity network in the visual areas. However, no differences between the groups were observed in terms of timing errors and M-ABC scores.

Both the preterm and full-term children showed oscillations in the gamma frequency band in the visual areas distributed along the ventral and dorsal streams, during the whole occlusion experiment. Previous studies have also observed gamma activity in complex object processing in visual regions (Hoogenboom et al., 2006; Kaufman et al., 2003; Lachaux et al., 2005). Gamma-band activity may represent top-down processing (high-speed memory comparison) of the object template maintained over the perceptual gap with the perceived stimulus (Herrmann & Mecklinger, 2001). Further, both the ventral and the dorsal streams showed gamma-band activity, which may indicate that the ventral stream, associated with object representation, and the dorsal stream, associated with motion perception and prediction of a response, are cooperating in the processing of occlusion events.

However, differences in power within the gamma frequency band were observed. Preterm children showed a significant pattern of desynchronised (ERD) gamma-band activity *before occlusion, during occlusion*, and after a successful response (*HIT*), while the full-term children showed a significant pattern of synchronised (ERS) gamma-band activity. These differences in power in the gamma frequency band corroborate previous research on visual motion perception in infants (Agyei et al., 2016a) and children (Doesburg et al., 2011). An MEG study found power differences in the alpha frequency range where preterm children exhibited long-range desynchronisation and full-term controls exhibited long-range synchronisation of alpha oscillations during a visual short-term memory task (Doesburg et al., 2011). ERD is associated with increased task complexity, attention and/or, learning

(Pfurtscheller & Lopes da Silva, 1999). For full-term children in the present study, neuronal assemblies fired in a desynchronised pattern during a *MISS* response, this might be due to need of more effort and attention in order to learn how to correctly predict the stopping of the car, when timing has been learned and the prediction action is performed more automatically, the desynchronised pattern were reduced, as seen in the synchronised activity during a *HIT* response. The preterm children showed desynchronised activity in all the events, which may indicate that they perceived the whole experiment, and not only the *MISS* response, as more complex and needed a higher degree of effort and attention throughout the experiment compared to the full-term children.

The perceived complexity of the task for preterm children may be due to white matter abnormalities. Most neuroimaging studies agree that there is a white matter abnormality characterised by the appearance of diffuse and excessive high signal intensity (DEHSI) throughout the cerebral cortex in children born preterm (Atkinson et al., 2008; Skiöld et al., 2010). It is possible that white matter abnormality affects the structural thalamocortical connectivity (Counsell et al., 2007), which is critical for the functional specialisation of the cortex. Gamma oscillations are critically dependent on thalamocortical interplay, and the different power within the gamma frequency range between the two groups may be explained by a disturbance in this interplay.

During the responses *HIT* and *MISS*, the full-term children showed oscillations in the theta frequency band together with gamma-band activity. The theta-gamma-band coupling is associated with enhanced cognition (Solomon et al., 2017) and attention (Landau et al., 2015). Hanslmayr et al. (2013) suggested that the low-frequency oscillatory signal in the theta range dynamically opens and closes the time window for sensory information transfer between lower-level occipital and higher-level parietal brain regions. Presumably, an ongoing theta phase modulates the likelihood of integrating distributed features, like object recognition and motion perception, into a coherent stimulus representation which can be perceived by the child and acted upon. During a *HIT* response, the information may be transferred in the precise coupling between synchronised local gamma and widespread theta oscillations. *MISSSES* showed desynchronised local gamma activity, which makes the information transformation less efficient. However, preterm children did not show any theta activity during *HITS* response, but they showed desynchronised theta during *MISSSES* instead. The lack of efficient theta-gamma coupling may be due to abnormal structural thalamocortical

connection, which further influence the perceived task complexity so that the task may need a higher degree of attention (Sarnthein, Morel, von Stein, & Jeanmonod, 2005).

The analysis of the localisation of the functional connectivity showed that connectivity would reflect the co-activation of ventral and dorsal processing pathways during the whole experiment of the occluded stimulus observed in preterm and full-term children. Both groups evidenced functional connectivity between visual areas in the occipital lobe, which may indicate that the connection between these regions subserved the recognition and establishment of an object in mind during an occlusion event in both groups. The use of these areas is consistent with studies of occluded objects who have identified activity in these areas during occlusion tasks (Grill-Spector et al., 2001; Hegde et al., 2008). However, clear differences in the network activation were observed. The preterm children showed significant connectivity differences between the processing of *HITS* and *MISSES* that were centred mainly in the lower visual areas in the occipital lobe, with only two connections to the central midline (CM) in the parietal lobe. By comparison, in full-term children, significant connectivity differences between the processing of *HITS* and *MISSES* were divided between the areas in the occipital and parietal lobe, including the parietal midline (PM) at the beginning of the dorsal pathway. Earlier research has found that the dorsal pathway is associated with spatial and temporal object information and is involved in guiding actions (van Polanen & Davare, 2015), and that being born preterm is a risk factor for a vulnerability in these areas (Braddick et al., 2003). The vulnerability may rely on the structural distinction in the cerebral white matter volume. This structural distinction could prevent the formation of the functional networks found in full-term control children and can therefore lead to a developmental delay in maturation of the neural circuits in preterm children. Alternatively, the engagement of mostly the occipital regions in the connectivity circuit in preterm children may represent a compensatory strategy to overcome difficulties in the perception of visual motion. Studies of dyslexic children have described similar findings, and researchers have hypothesised that disruption in normal reading pathways results in the engagement of alternate systems to compensate for conventional circuit failure (Shaywitz et al., 2002).

Interestingly, the quantification of the functional connectivity showed more differences in the network activation between preterm and full-term children. When the events *before occlusion* and *during occlusion* were compared, preterm children showed no significant connectivity differences, while full-term children showed 6 significant connectivity differences. In

addition, the comparison of correct responses (*HITS*) with incorrect responses (*MISSES*) showed a similar pattern: where preterm children showed only 9 significant connectivity differences, full-terms showed 12 significant connectivity differences. Further, in the functional connectivity network of preterm children, only one hub was identified. By comparison, full-term children displayed two hubs. Hubs are a collection of neurons that mediate a larger fraction of signals and are associated with higher-order cognition (Oldham & Fornito, 2019). This finding corroborates a study on performance in a response inhibition task, where adults born preterm activated less specific brain regions to the task than full-term controls (Lawrence et al., 2009). It has been proposed that the recruitment of less specialised brain regions may be an adaptive mechanism employed by the brain to cope with highly demanding tasks (Just & Varma, 2007). Hence, this may indicate that preterm children have a less specialised functional connectivity network and reduced network integration compared to full-term children, and that they also need a functional reorganisation of the visual motion perception pathways to catch up with their full-term peers.

Despite several differences between preterm and full-term children observed with high-density EEG in visual motion perception, no significant differences were observed in the timing of prospective responses at the behavioural level. Interestingly, both groups showed a similar pattern of timing error in relation to the three different car speeds, with the shortest timing error for fast, then medium, and the longest timing error for slow car speed. In the performance of motor responses, people tend to favour either accuracy or speed of the response according to the task's demands, which is entitled the "speed-accuracy-trade-off principle" (Schmidt, 1982). Thus, if speed is favoured, it will affect the accuracy and vice versa. Nonetheless, the principle called "velocity effect" is an exception of this rule, which anticipates that the accuracy of a motor timing response increases when movement time decreases and velocity increases (Newell, Hoshizaki, Carlton, & Halbert, 1979; Schmidt, 1982). Hence, in the present study, the responses to the fast velocity of the car elicited the shortest timing error. The velocity effect may explain this, because the attempt to respond quickly might increase the chances of timing the response more consistently than for responding to the medium and slow speeds of the car. Slower car speeds give the children more time to respond and subsequently longer timing error. Of the 20 children in this study, only one preterm child showed motor responses that were not consistent with the velocity effect. This child had its shortest timing error for fast, then slow, and medium car speeds.

However, fast velocity still showed the shortest timing error, which could be in line with the velocity effect.

In addition to the analysis of prospective responses, the children's motor performance scores on the M-ABC were adequate to what was expected in their developmental stage. This was the case for most children in both groups, with no significant group differences. However, three of the full-term children were slightly above the threshold at 13.5 points (i.e., 14 and 14.5), and two preterm children were quite above the threshold (i.e., 21 and 23). One of the full-term children was tested with another version of M-ABC due to the testing age; the child had just reached 7 years and was tested with the tasks for the age group of 7- to 10-year-olds, including more demanding and complex tasks than the version for 4- to 6-year-olds, which all the other children completed. The two other full-terms above the threshold tested the system during the test session and may not have done their best due to lack of attention. The two preterm children who were quite above the threshold were mainly struggling with the manual dexterity tasks and may have a certain degree of impairment in the fine motor domain. They were born at weeks 31 and 32 with low birth weights, which corroborates with previous findings that such risk factors are associated with complications in motor performance during childhood (Bos et al., 2013; Moreira et al., 2014).

Several studies have shown that preterm children are at risk for the development of less severe motor difficulties (Bracewell & Marlow, 2002; Wocadlo & Rieger, 2008). This has also been confirmed through studies using the M-ABC (Bos et al., 2013). In addition, multiple MRI investigations have documented both volumetric and microstructural changes in the brain of preterm children during school age, and these changes could explain the motor difficulties (Constable et al., 2008; Kesler et al., 2004; Miller & Ferriero, 2009). In contrast, recent studies have revealed a pattern of improvement in motor performance over time in the prematurely born children (Cserjesi et al., 2012), also when using M-ABC (Broström et al., 2016). The improvements are in line with the findings in this study, both timing errors and M-ABC scores. Taken together, these findings may reflect a large variability within the preterm group and their development (Nishiyori et al., 2021). In addition, it may be partially accounted for by neuronal plasticity in the development of functional connectivity systems. As has been reported for prematurely born children with congenital focal brain lesions, neural plasticity may permit the recruitment of alternate pathways of language processing (Chilosi et

al., 2005). Neuroplasticity may facilitate the establishment of compensatory mechanisms, so that preterm children might catch up with their full-term peers in motor performance.

Neuroplasticity is a complex interplay between environmental stimulation and experience, with the establishment of cortical white and grey matter (DeMaster et al., 2019). On the one hand, the high plasticity of rapidly developing neural tissue makes the premature brain more vulnerable to injury, especially in the dorsal stream developed during the third trimester of pregnancy (Braddick et al., 2003). On the other hand, plasticity is the mechanism in which enriching experiences might be leveraged as potential neuroprotective factors. Hence, individuals born preterm are potentially more vulnerable to negative environmental experiences but also benefit more from positive environmental conditions. Therefore, enriching environmental experiences is an essential contributor to the functional reorganisation of the brain network of perceptual information in preterm children so that they develop the same behaviour as their full-term peers.

Environmental stimulation could partly account for the similar performance in the motor domain between preterm and full-term children, as well as the functional reorganisation of the brain network in the preterm children in this study. In Norway, postnatal care for preterm infants includes physiotherapists, occupational therapists and neurologists (St. Olavs University Hospital, 2022), which may facilitate motor stimulations and enhance motor development. Additionally, participating in sports outside school is shown to improve motor development in preterm children (Wocadlo & Rieger, 2008). Sports activities are highly recognised in the Norwegian culture, and 5 out of 10 preterm children in this study were practicing one or more sports outside school during the week at the time of their participation in this study. This fact may be a reason for the lack of significant differences in the motor domain and the altered functional connectivity network found in this study.

Interestingly, the preterm child with a cerebral haemorrhage in the first week after birth had no markedly different results than the other preterm children. The child also had the lowest birth weight and was the only participating child born before week 28. Both low birth weight and early birth are significant risk factors for visuomotor impairments (Moreira et al., 2014). In the timing task, the child had slightly longer timing errors than the mean in the preterm group but did not differ in functional connectivity network from the other preterm children. One possible explanation may be good physiotherapy service during the first year of life,

when the brain is highly pliable (DeMaster et al., 2019). Enriched motor stimulation may have contributed to a functional reorganisation of the cortical areas in the brain. After the first year, the child has been active, with several sports activities after school during the week, which may have enriched motor stimulation and enhance the performance in this study.

The preterm population is not a homogeneous group (Latal, 2009; Nishiyori et al., 2021), and therefore it is reasonable to assume that the functional reorganisation of the brain connectivity systems of perceptual information may affect preterm children differently at the behavioural level. The functional reorganisation of brain connectivity affects the children's perceptive skills, and perceptual information gears the children's movements. For effective therapy and minimise long-term consequences, each individual child's problems need to be assessed. Surface assessment, e.g., assessment that measures general motor abilities, can only describe the symptoms of movement difficulties. To determine the underlying causes and focus the therapy, it is necessary to measure the perceptuo-motor functions that subserve the disordered everyday skills. Van der Weel and his colleagues (1996) conducted a study on hemiparetic cerebral palsy children where they measured the interaction of perception and motor abilities of the children's motor problems. The children were instructed to knock an approaching ball off a track. The results showed that the children started the hitting action earlier with their affected arm than their unaffected arm, thus compensating for the fact that the affected arm moved slower than the unaffected arm. The relationship between the perception of when to start the arm movement and the actual movement (perceptuo-motor coupling) captured the underlying causes of their motor difficulties due to cerebral palsy, which an assessment of only the movement would not have captured. Thus, in-depth assessments are needed to detect the underlying cause of the difficulties preterm children may experience. The current study contributes to a better understanding of the electrical brain activity during visual motion perception of a temporarily occluded object in preterm children compared to full-term children, which is crucial for further development of in-depth assessments.

5. Conclusion

The results of the present study demonstrated an altered functional brain connectivity network of visual motion perception in preterm children at 6 years of age compared to their full-term peers. The altered functional connectivity network may function as a compensatory mechanism for the structural white matter injury in the dorsal visual pathway in order to perform similarly at the behavioural level as full-term children. The preterm children in this study have received enriching postnatal care and actively participated in sports activities, which might have facilitated the establishment of compensatory brain mechanisms that were observed. However, the preterm population is by no means homogenous, and therefore individual differences need to be assessed. This study is a contribution to further the knowledge about the functional reorganisation of brain connectivity, which could be used to assess and further develop therapeutic practices, and hopefully minimise long-term cognitive consequences to prematurely born children.

6. References

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