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Out of Sight, Out of Mind? Neuronal Gamma Oscillations During Occlusion Events in Infants

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ABSTRACT

Object permanence allows infants to interact successfully with objects in the environment. What happens in the human infant brain when objects move in and out of sight? This study used high-density electroencephalography (hdEEG) to record induced oscillatory brain activities in 29 locomotor infants before, during, and after occlusion of a moving object traveling at different speeds. Temporal spectral evolution (TSE) showed that before and after the occlusion event, event-related synchronized (ERS) brain activity was observed, whereas event-related desynchronized (ERD) activity was detected when the car was hidden behind the occluder. Both synchronized and desynchronized brain activities were found in the gamma frequency band (>30 Hz) in visual areas. Coherence connectivity analysis showed significant cluster differences before and during occlusion, during and after occlusion, and before and after occlusion in the gamma (30–150 Hz) and theta range (4–7 Hz) in several brain sources of interest. It was concluded that locomotor infants between 8.5 and 12 months of age show high-frequency brain oscillations while perceiving a moving object going temporarily out of sight. The significant cluster differences indicate the beginning of specialized connectivity networks, where object permanence is processed within dedicated visual, parietal, and central areas along the dorsal processing stream.

1 | Introduction

Visual scenes in our daily lives consist of objects hiding behind and overlapping each other, yet we can perceive single items as enduring entities and meaningful units. For example, when a moving car disappears into a tunnel, we know that it did not disappear into thin air, and we fully expect it to come out of the tunnel at the other side. Knowing that an object exists even though it is out of sight is what Piaget (1954) called object permanence, a skill that develops during the first year of life (Baillargeon and DeVos 1991; Kaufman, Csibra, and Johnson 2003). This skill is one among many other skills that are very

important to develop in order to interact successfully with objects in the environment. The developmental processes that mediate visual perception throughout life are expected to be increasingly efficient after birth (Agyei, van der Weel, and van der Meer 2016a).

Prospective control is the ability to adjust our actions according to the changing environment and our bodily characteristics (van der Meer and van der Weel 2019). The ability to continuously pursue a moving target with head and eye movements is one of the earliest indicators of prospective control behavior in infants (von Hofsten and Rosander 1996). Data on visual tracking and reaching suggest that infants have a neural representation of both

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visible and hidden moving objects during the first half year of life (Rosander and von Hofsten 2004). Already around 2 months of age, infants show prospective control as they continuously track objects using smooth pursuit eye movements (Rosander and von Hofsten 2002). van der Meer, van der Weel, and Lee (1994), (van der Meer et al. 1995) tested how prospective control of reaching develops by investigating reaching abilities in infants catching a moving toy at different speeds. The toy was occluded from view by a screen during the last part of its approach to force the infants to make use of predictive information. All infants showed visual interest in the toy at 16 weeks, but none of them were able to catch it. As soon as it disappeared behind the occluder, the infants lost interest in the toy and seemed surprised when it reappeared at the other end. However, as soon as they started reaching at about 20 weeks of age, infants anticipated the reappearance of the moving toy with their head and eyes, and from about 40 weeks, they showed advanced prospective control ability by shifting their gaze across the occluder and moving their hand forward at certain times, rather than distances, before the toy would reappear. Thus, when infants are about 9 months of age, they make available the same time to catch a toy whether the toy is moving quickly or slowly. Young infants use perceptual information to execute adaptive motor responses (Shirai and Yamaguchi 2010). However, little is known about how the neurons in the infant brain behave during temporary occlusion of objects moving at different speeds.

The visual system of humans starts to develop before birth and continues thereafter. The retina, which is the network of photoreceptors and interneurons at the back of the eye, starts to form around 40 days postconception and may have a relatively complete set of cells by 160 days (Finlay, Clancy, and Kingsbury 2003; Johnson 2013). From the few studies on humans deceased embryos and fetuses, we know that many major structures like neurons, areas, and layers in the brain are in place by the end of the second trimester in utero (e.g., Zilles et al. 1986). A total of 100 billion neurons are found in the brains of human infants at birth, and a few of them are connected. After neurons are formed, have found their place in cortex, and grow, they begin to connect to other neurons (Johnson 2013). Infant neuronal networks consist of a vast number of neurons and dendritic spines (Huttenlocher 1990; Webb, Long, and Nelson 2005). The number of dendrites and synaptic connections in the primary visual cortex is at its peak level at the age of 8 months and 2 years (Klaver et al. 2011). The infant brain takes advantage of the overproduction of neurons in both adaptation and plasticity, where the infant brain doubles in weight during the first year of life, strengthening some connections and pruning others. The strengthening and pruning of neurons affect the processing speed and efficiency in neural pathways due to specializations (Edelman 1993; Johnson 2000). The synapses between neurons are preserved in active cortical circuits and lost in inactive circuits (Johnson 2013). Physical growth of the neurons and pruning of synapses is activity dependent and develops after birth (Greenough, Black, and Wallace 1987; Huttenlocher et al. 1986). Thus, during the first year of life, an interplay between cortical maturation, experience, and learning is forming a complex network of neurons specialized in processing different types of information (Borge Blystad and Van der Meer 2022; Johnson 2013).

One of the key functions of the visual cortex is processing motion to prospectively perceive the environment. At 3 months, infants exhibit a neural response to motion, and from 3 to 5 months, they show higher sensitivity to motion stimuli than to static displays (Atkinson 2017). A study by Biagi et al. (2015) reports that infants show network activation when exposed to motion. Atkinson (2017) points out that the ability to discriminate between simulated directions of heading in optic flow (Gilmore, Baker, and Grobman 2004), to link parts of a partially occluded object by their common motion (Johnson and Aslin 1996), and to predict the trajectory of a moving object that passes behind an occluder (Johnson, Amso, and Slemmer 2003) requires not only global motion processing of directional signals, but also the integration of time and space of the signals to allow the analysis of the global structure of patterns of motion.

Visual perception of information propagates from the lateral geniculate nucleus (LGN), the nucleus within the thalamus that receives input from the optic tracts, to the primary visual cortex (V1). Cortical area V5 is involved in oculomotor smooth pursuit and perception of motion direction (Johnson 1990). Cortical maturation includes the development of form and motion perception caused by maturation of parvo- and magnocellular processing streams (Atkinson 2000; Johnson 2013). Development of visual memory of object features and object locations is caused by maturation of ventral and dorsal processing streams (Mareschal and Johnson 2003). The dorsal visual stream goes from V1 toward the parietal lobe, passing through visual areas V2, V3, and the middle temporal cortex (MT/V5+). However, the ventral stream, important for object recognition and identification, goes from V1 to V2, V3, and V4, until it ends in the inferotemporal cortex. The two visual streams are interconnected and are not strictly independent (van Polanen and Davare 2015).

Electroencephalogram (EEG) is a method of measuring electrical brain activity that is well-suited to study the neural correlates of motion perception and its development. EEG studies in the time-frequency domain have allowed the investigation of perceptual and cognitive functions through the manifestations of the natural frequencies in EEG oscillations (Başar et al. 1999). Induced brain activity, which is only time-locked to an event and not phase-locked, can be detected by frequency analysis. This event-related phenomenon represents frequency-specific changes in the ongoing EEG activity and may consist of either an event-related decrease (desynchronization, ERD) or increase (synchronization, ERS) of power in given frequency bands. ERD and ERS reflect changes in the activity of local interactions between main neurons and interneurons that control the frequency components of the ongoing EEG (Pfurtscheller and Lopes da Silva 1999). ERD is associated with an increase of task complexity or attention and is considered a sign of neuronal networks preparing to process sensory information, whereas ERS is generally associated with neurons in a deactivated state (Pfurtscheller and Lopes da Silva 1999).

Over the years, different classes of oscillations have been distinguished: 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, and van der Meer 2016a). These rhythms

reflect neurophysiological processes that manifest functionally different roles (Buzsaki and Draguhn 2004; Engel and Fries 2010; Ganzetti and Mantini 2013; Saby and Marshall 2012). Delta activity is involved in signal detection and decision-making (Başar et al. 2000), alpha activity is connected to the control of inhibition and cortical processing (Klimesch, Sauseng, and Hanslmayr 2007), and beta activity is involved in multisensory stimulation and shifting of neural systems to a state of attention (Khader et al. 2010), whereas gamma activity is observed in connection with various perceptual and cognitive functions, including feature binding and attentional processes (Müller, Gruber, and Keil 2000).

Several EEG studies using time-frequency analysis have found that infants' visual motion processing at the age of 3–5 months is dominated by ERD of theta oscillations (4–7 Hz) in the visual cortex (Orekhova, Stroganova, and Posikera 1999; van der Weel and Van der Meer 2009). These low-frequency oscillations undergo systematic development from early childhood to adulthood (Stroganova and Orekhova 2007; Stroganova, Orekhova, and Posikera 1999). In infants, these low-frequency rhythms have been attributed to general signs of immaturity (Orekhova et al. 2006; Stroganova and Orekhova 2007). Theta-band oscillations have been reported to play an important role in cognitive processes (Başar et al. 2000; Freunberger et al. 2011; Gruber and Müller 2006; Khader et al. 2010; Klimesch et al. 1996). Agyei et al. (2015) investigated the induced brain responses in infants at 3 to 4 months and 11 to 12 months using an optic flow paradigm. They found a decrease in amplitudes at 5–7 Hz that was observed as theta activity at both 3 to 4 and 11 to 12 months, whereas an increase in amplitudes at 9–13 Hz was observed as synchronized alpha activity only at 11 to 12 months. They concluded that induced brain activities related to visual motion perception are changing from lower to higher frequencies in the human brain during the first year of life (Agyei et al. 2015). ERDs in the theta- and alpha-frequency bands were also found in another study of infants during visual motion perception, whereas ERD beta-band activity was observed in adult frequency data (Vilhelmsen et al. 2018). These results support the fact that brain activities undergo rapid development throughout life, where higher frequencies are more prominent in the brains of older infants and adults. As infants grow older, visual motion processing is characterized by ERS alpha/beta oscillations with fast oscillating cell assemblies that have fewer but more specialized neurons, resulting in improved visual motion perception (Agyei et al. 2015; Agyei, van der Weel, and van der Meer 2016a).

In previous research on occlusion of objects, gamma-band activity at around 40 Hz in human adults has been associated with maintaining an object's visible properties in mind (Tallon-Baudry and Bertrand 1999). More recent studies also report an increase in gamma-band activation during the occlusion period in infants (Southgate et al. 2008). Kaufman, Csibra, and Johnson (2003) carried out an EEG study with infants where a toy train engine entered a tunnel, and as the train engine was leaving the tunnel, a hand lifted the tunnel to reveal either the train engine (appearance) or nothing (disappearance). The appearance or disappearance of the train engine was either expected or not expected. The researchers measured the brain responses of 22 6-

month-old infants, while they watched the different conditions. The infants showed higher activity in the unexpected than in the expected disappearance condition. Gamma power over the right temporal region was found and was consistently higher, whereas the car was occluded. As a sequel, Kaufman, Csibra, and Johnson (2005) did a study with 36 6-month-old infants watching visual stimuli that disappeared either via occlusion (consistent with continued existence) or via disintegration (inconsistent with continued existence). They found that infants' perception of objects relies on the same visual cues as object tracking mechanisms in adults (see Scholl and Pylyshyn 1999). However, current studies have not investigated time-frequency changes in the infant brain using an occlusion paradigm with a moving object. Successful deceleration discrimination following a moving car on a screen that was temporarily occluded has previously been found in adult EEG (Holth, van der Meer, and van der Weel 2013). When it comes to infant EEG, it is unclear whether the infant brain also successfully discriminates among different speeds during temporary occlusion of moving objects.

Functional brain connectivity reflects the brain's abilities to process and integrate information. A functional connectivity organization of the brain would be characterized by a flexible and variable localization of neural activity in response to different motions (van der Weel, Agyei, and van der Meer 2019). The development of visual perceptual and motor abilities may affect functional brain connectivity (DeMaster et al. 2019). Many studies concerning functional brain connectivity in adults have used functional magnetic resonance imaging (fMRI) imaging (e.g., Batalle et al. 2017). Although fMRI provides high spatial resolution, it does not directly measure neuronal activity and has a limited temporal resolution. This prevents the measurement of neurophysiological oscillations and their interregional connections. EEG 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 et al. 1999).

The present study investigated induced oscillatory activities in the human infant brain in relation to temporarily occluded moving objects. High-density EEG was used to detect oscillatory brain activity through time-frequency analysis and coherence connectivity analysis. We analyzed the induced brain responses before, during, and after temporary occlusion of a virtual car driving around a rectangular path on a large screen with three different speeds. On the basis of previous EEG studies using time-frequency analysis mentioned above (e.g., Agyei et al. 2015, Agyei, van der Weel, and van der Meer 2016b; Kaufman, Csibra, and Johnson 2005), we expected to find high-frequency neural oscillations in the 1-year-old infant brain when following the moving car. In addition, we expected to find even higher frequencies during object occlusion. When it comes to speed perception, we did not expect to find any differences as previous time-frequency studies (e.g., Vilhelmsen et al. 2018) had not found any frequency differences related to speed in infant EEG. In the functional coherence connectivity analysis, we investigated network activation between visual sources of interest and expected to find functional connections between them.

2 | Methods

2.1 | Participants

A total of 34 infants were recruited for this study. Five infants had to be excluded from the study because of insufficient data for further analyses. Twenty-nine infants (13 girls, 16 boys) provided sufficient artifact-free data for the analyses. The infants were between 8.5 and 12 months at testing, with a mean age of 10.5 months ($SD = 1.1$). Parental records showed the infants to have on average 10.3 weeks ($SD = 6$) of self-generated locomotor experience at the time of testing, with all infants being able to crawl, whereas three infants were able to walk at least some steps alone.

As a psychological procedure, EEG recordings do not cause any known physical harm to participants. Parents gave their informed consent and could withdraw from the study at any time. The Norwegian Regional Ethics Committee and the Norwegian Data Services for the Social Sciences approved the study. All methods were performed in accordance with relevant guidelines and regulations.

2.2 | Experimental Set-Up

Testing took place in a room with a large projection screen (108 cm wide and 80 cm high) hanging down from the ceiling. Stimuli were generated with E-Prime (Psychology Software Tools Inc.) and mirror-reversed projected onto the screen by means of an ASK M2 projector. EEG activity was recorded with the Geodesic Sensor Net 200 (GSN), which consisted of 128 sensors that were evenly distributed across the infant's scalp. Triggers about the onset and offset of the stimulus were communicated from E-Prime onto the EEG recording. As recommended for the high-input-impedance EGI amplifiers (Ferree, Luu, and Tucker 2001; Picton et al. 2000), all electrode impedances were kept under 50 k Ω to ensure an optimal signal-to-noise ratio. Net Station software recorded the amplified EEG signal on a Macintosh computer, using a sampling rate of 500 Hz with a low-pass filter of 200 and a 0.1 Hz high-pass filter. The visual feed was processed with Clear View software on an HP computer. Digital videos during the experiment were recorded by two cameras positioned at different angles in front of the infant. This made it possible to observe the infant's attention and behavior during the experiment. All data were stored for offline analyses. Trials where the infant was not looking were removed from the raw EEG data.

2.3 | Occlusion Stimuli

The stimulus consisted of an animated red car moving along a rectangular path during which it disappeared twice behind a green occluder (see Figure 1). The start position of the car was set in the lower left corner of the screen. The car's motion from lower left to upper right corner was counted as one trial, whereas its motion from upper right to lower left corner was considered the next trial. The car drove 100 cm horizontally on the screen, which constituted a visual angle of 64°. The vertical movement was 22.5 cm on the screen. The car had a length of 40 pixels (6.7 cm), whereas the occluder had a length of 60 pixels (10 cm).

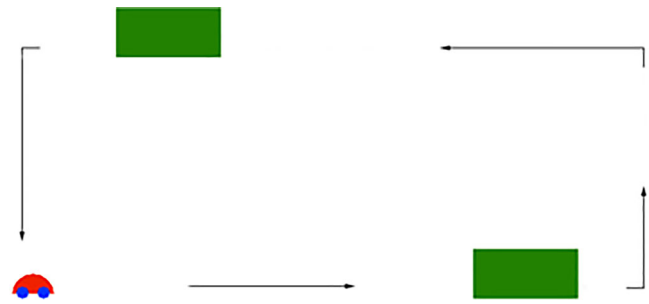


FIGURE 1 | Stimulus set-up: The car moved along a rectangular path on a large screen and was occluded twice on its way. The car started at high speed and moved under three different constant decelerations, that is, “fast” (10% deceleration), “medium” (50% deceleration), and “slow” (90% deceleration). One trial was from lower left to upper right corner, and the next trial from upper right corner to lower left corner. During a trial, the car drove the distance from the start position to the end position in 1486, 1802, and 2352 ms and was occluded for 167, 233, and 334 ms during fast, medium, and slow speed, respectively. Between trials, attention pictures were presented simultaneously with sounds to fixate the infant's attention to the starting position of the car, when necessary. Interstimulus intervals were set to 2000 ms.

The car started at high speed (0.4 px/ms, corresponding to 67 cm/s) and, after traveling 20 cm on the screen, continued its trajectory under three different constant decelerations: fast (10% deceleration), medium (50% deceleration), and slow (90% deceleration); see Figure 1. This way, the spatiotemporal information available in each trial was varied so that the infants could not rely on an automated gaze-shifting response. The different decelerations also helped increase the infants' interest in the task.

2.4 | Procedure

Parents arrived with their infant some time prior to the experiment so that the infant could get comfortable with the laboratory surroundings and the parents could sign the informed consent form. One experimenter informed the parent(s) about the purpose, duration, and experimental procedures and played with the baby so that it became familiar and relaxed before the experiment started. The infant's head circumference was measured to ensure the correct size selection of the GSN 200. The electrode net was then soaked in a solution of distilled water, saline, and baby shampoo to ensure optimal contact with the scalp. The net was placed on the scalp of the infant, whereas it sat on the parent's lap. Small-sounding toys and soap bubbles were used to distract the infant's attention from the net.

Immediately after the net was mounted, the infant was placed in a baby car seat in front of the screen hanging 80 cm away from the infant's face in the experimental room. The electrode net was then plugged into an amplifier, and the impedance of the electrodes was checked. One parent was always sitting next to the infant in the experimental room to avoid any stress an absent parent may cause and was instructed to not interfere unnecessarily. An assistant was also present to help the baby focus on the screen.

The experiment was performed in a quiet and dimly lit experimental room that was divided by a soundproof window from the

control room where the computers for stimulus generation and data acquisition were placed. Each infant was individually tested, and the testing session lasted for about 15–20 min. The occlusion experiment was performed together with an optic flow and a looming experiment, which provided data for other studies. The occlusion experiment was usually conducted last, about 10 min into the testing session, and lasted for about 3–5 min. On average, 69 (SD = 11) trials were presented per infant equally divided over the three car speeds, in a quasi-random order.

2.5 | Data Analysis

EEG data analyses were carried out with the software program BESA (Brain Electrical Source Analysis, GmbH) version 7.0. As an initial preprocessing step, recordings were segmented with Net Station software and exported as raw files to BESA for analysis. By visual inspection, artifact-contaminated channels and trials resulting from head or body movements were discarded or reestimated using spherical spline interpolation (Perrin et al. 1989; Picton et al. 2000). None of the infants had more than 10% of the channels defined as bad, and trials where participants were not looking at the screen were removed by visual inspection using the recorded videos. Notch filter was set at 50 Hz to remove mainline noise interference in the EEG data, whereas low cut-off filter was set at 1.6 Hz to remove slow drift in the data, and high cut-off filter was set at 100 Hz to remove channels contaminated with high-frequency activities. A manual form of artifact correction, designed to separate artifacts and brain activity on the basis of spatial filtering, was employed to remove physiological artifacts such as blinking or pulse from the raw EEG data (Berg and Scherg 1991; Ille, Berg, and Scherg 2002). Horizontal and vertical eye movements that were naturally present in the visual tracking task were also manually removed. A reference-free montage showing EEG at 27 standard electrodes was used. In scanning for artifacts, threshold values for gradient and low signal were set at 75 and 0.1 μV , respectively, whereas maximum amplitude was set at 200–230 μV .

Before computing a TSE, event-files were made for each infant separately and appended to the raw EEG data. The event-files were made to separate each trial into three different conditions: before occlusion, during occlusion, and after occlusion. Thus, nine motion conditions were available for comparison, 3 (fast, medium, slow speed) \times 3 (before, during, and after occlusion). The car was fully visible before and after occlusion, whereas it was completely occluded during occlusion. After the event-files with the new conditions were added to the raw file and the data were cleaned, the mean number of accepted events per infant was 133 (SD = 37), evenly distributed across the nine conditions.

2.5.1 | TSE—Temporal Spectral Evolution

Time-frequency analysis representing changes in amplitude over time (temporal spectral evolution, TSE) was performed in brain space using predefined multiple source dipoles that modeled activities in the visual areas of the parietal and visual cortices and other brain regions. The time-frequency displays were generated from single trials by averaging spectral density amplitudes over trials such that each displayed graph plotted

the spectral amplitude density of one montage channel over time and frequency that were normalized to baseline for each frequency (Hoechstetter et al. 2004; Pfurtscheller, Neuper, and Mohl 1994; Pfurtscheller, Stancák, and Neuper 1996). The time-domain signal was transformed into the time-frequency domain by complex demodulation (Papp and Ktonas 1976). Signals from average evoked responses were removed from the single trial time series before calculating TSEs in order to have only TSE displays of induced oscillatory brain activities. Measuring brain oscillatory activities using surface electrodes may not be ideal as scalp waveforms receive mixed contributions from underlying brain sources. This is due to the wide distribution of focal brain activity because of the smearing effect of brain volume conduction in EEG and the nature of dipole fields. Therefore, to achieve optimal separation of focal brain activities, source montages derived from a multiple source model were used (Scherg and Berg 1991). The source montage consisted of 17 sources that modeled activities in the visual pathway as well as any residual activities in other regions of the brain: Sources visual cortex radial left (VCrL), visual cortex radial right (VCrR), visual cortex ventral midline (VCvM), visual cortex lateral left (VCIL), visual cortex lateral right (VCIR), parietal midline (PM), central left (CL), central midline (CM), central right (CR), visual cortex bilateral left (VCbL), visual cortex bilateral right (VCbR), temporal anterior left (TAL), temporal anterior right (TAR), frontal left (FL), frontal midline (FM), frontal right (FR), and fronto-polar midline (FpM) were further analyzed.

TSE displays were set to frequency cut-off of 2–100 Hz at frequency and time sampling of 1 Hz, 50 ms, respectively. TSE probability maps were also computed to separately test for significant differences in the TSEs (change in amplitude from baseline to time-frequency sampling points) for each infant. This allowed for the observation of significant oscillatory activity patterns across the brain areas of interest for each infant that was not visible in the overall averaged TSEs. To correct for multiple testing, the Bonferroni procedure and permutation tests described by Simes (1986) were applied to each set of time samples belonging to one frequency bin. Frequency cut-offs and time-frequency sampling points were maintained as stated above.

2.5.2 | Coherence Connectivity Analysis

The computed time-frequency data were further used to quantify the functional connectivity between the visual areas of interest. 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 et al. 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 17 sources as in the time-frequency analysis were used, focusing on the following 11 sources: CM, PM, VCIL, VCIR, VCrL, VCrR, VCbL, VCbR, VCvM, CL, and CR. These sources are illustrated in Figure 2.

BESA Statistics 2.1 was used to test significant differences between the events. A combination of permutation tests and data clustering was employed in the statistical tests to address the multiple

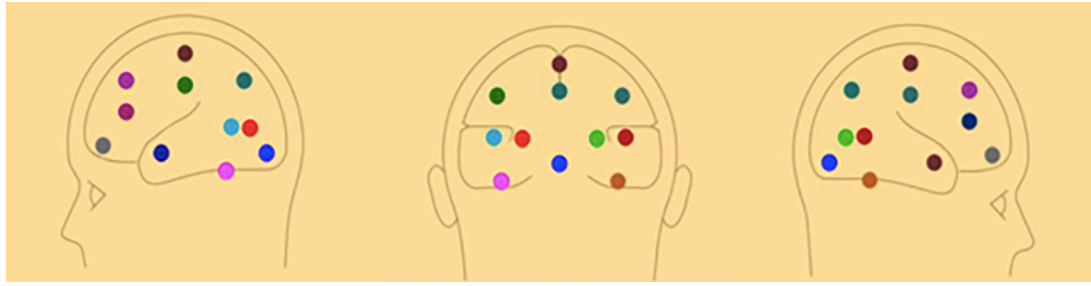


FIGURE 2 | Head model with illustration of the sources of interest, with approximate Talairach coordinates: **CM** ($x = 0.0, y = 24.2, z = 60.5$); **PM** ($x = 0.0, y = -72.3, z = 37.0$); **CL** ($x = -42.9, y = -21.3, z = 38.9$), **CR** ($x = 42.9, y = -21.3, z = 38.9$), **VCIL** ($x = -45.2, y = -57.2, x = 6.5$); **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** ($x = 0.0, y = 84.9, z = 14.3$).

comparison problem. The epochs must be the same length to test for significant differences between events. Therefore, the epochs of *before occlusion* and *after occlusion* were shortened to the same epoch length as that of *during occlusion* (−100 to +162 ms).

3 | RESULTS

3.1 | TSE—Temporal Spectral Evolution

A time-frequency analysis (temporal spectral evolution—TSE) was carried out for the nine different conditions, 3 (speed: fast, medium, slow) \times 3 (occlusion: before, during, after) for all participants separately. No significant differences with respect to speed were found when the TSEs of the conditions were compared with each other. Thus, fast, medium, and slow speeds were combined into one motion condition and analyzed separately for before, during, and after occlusion. TSE plots and their corresponding TSE probability maps for one typical infant are shown in Figure 3, where significant areas in the probability maps correspond to significant oscillatory activities in similar areas in the TSE plots. The individual TSEs of the infants showed a pattern of synchronized gamma-band (>30 Hz) activity in the visual sources before and after occlusion of the car (see Figure 3a,c). Time-frequency analysis revealed a pattern of induced desynchronized oscillatory activity (ERD) within the gamma frequency band during occlusion of the car in the visual sources of interest (see Figure 3b).

3.2 | Brain Source Activity in Coherence Connectivity Analysis

As in the TSE analysis, no significant connectivity differences between the three car speeds were found. Further analyses were conducted for events before occlusion, during occlusion, and after occlusion across motion speeds. To test for significant connectivity differences between the three events, ANOVAs of the coherence connectivity patterns were computed. First, between *before occlusion* and *during occlusion*, three significant cluster differences in band power were observed in the visual sources of interest, and two differences were in the gamma (30–150 Hz) range and one in the theta range (4–7 Hz). Second, between *during occlusion* and *after occlusion*, two significant cluster differences in band power were found, one difference in

the gamma range and one in the theta range. Last, between *before occlusion* and *after occlusion*, the results showed four significant cluster differences in band power, one in the gamma range and three in the theta range (see Figure 4).

4 | Discussion

High-density EEG was used to observe induced electrical brain activity in 8- to 12-month-old infants as a perceptual response to occlusion of moving objects. ERS brain activity in the gamma frequency band was found before and after occlusion of the car in three visual sources of interest. During the temporary occlusion of the car, ERD brain activity, also in the gamma frequency band, was observed in the same visual sources. No significant differences between fast, medium, and slow speed were found. Significant connectivity differences were found between before and during occlusion, between during and after occlusion, and between before and after occlusion in the theta (4–7 Hz) and gamma (30–150 Hz) frequency ranges.

4.1 | Synchronized Gamma Activity When Following the Moving Car When Visible

Oscillations in the gamma frequency band appear appropriate to establish rapid coupling or synchronizing between spatially separated cell assemblies (Pfurtscheller and Lopes da Silva 1999; Singer 1993). The pattern of synchronized gamma activity that was found both before and after occlusion indicates that the neurons in the infant brain are synchronizing between spatially separated cell assemblies when perceiving the car moving in and out of sight. The synchronization suggests different parts of the brain being activated at the same time when communicating with each other. The finding that neurons in the infant brain are synchronizing when perceiving motion is consistent with neurophysiological studies in humans showing that synchronization in cortical structures plays an important role in attentional mechanisms providing the necessary conditions for an effective registration and processing of perceptual information (Borge Blystad and van der Meer 2022; Pfurtscheller and Lopes da Silva 1999; van der Weel and van der Meer 2009). The synchronized gamma frequency found both before and after the occlusion period indicates that fewer, but more specialized, neuronal networks were activated in synchrony when the car was visible

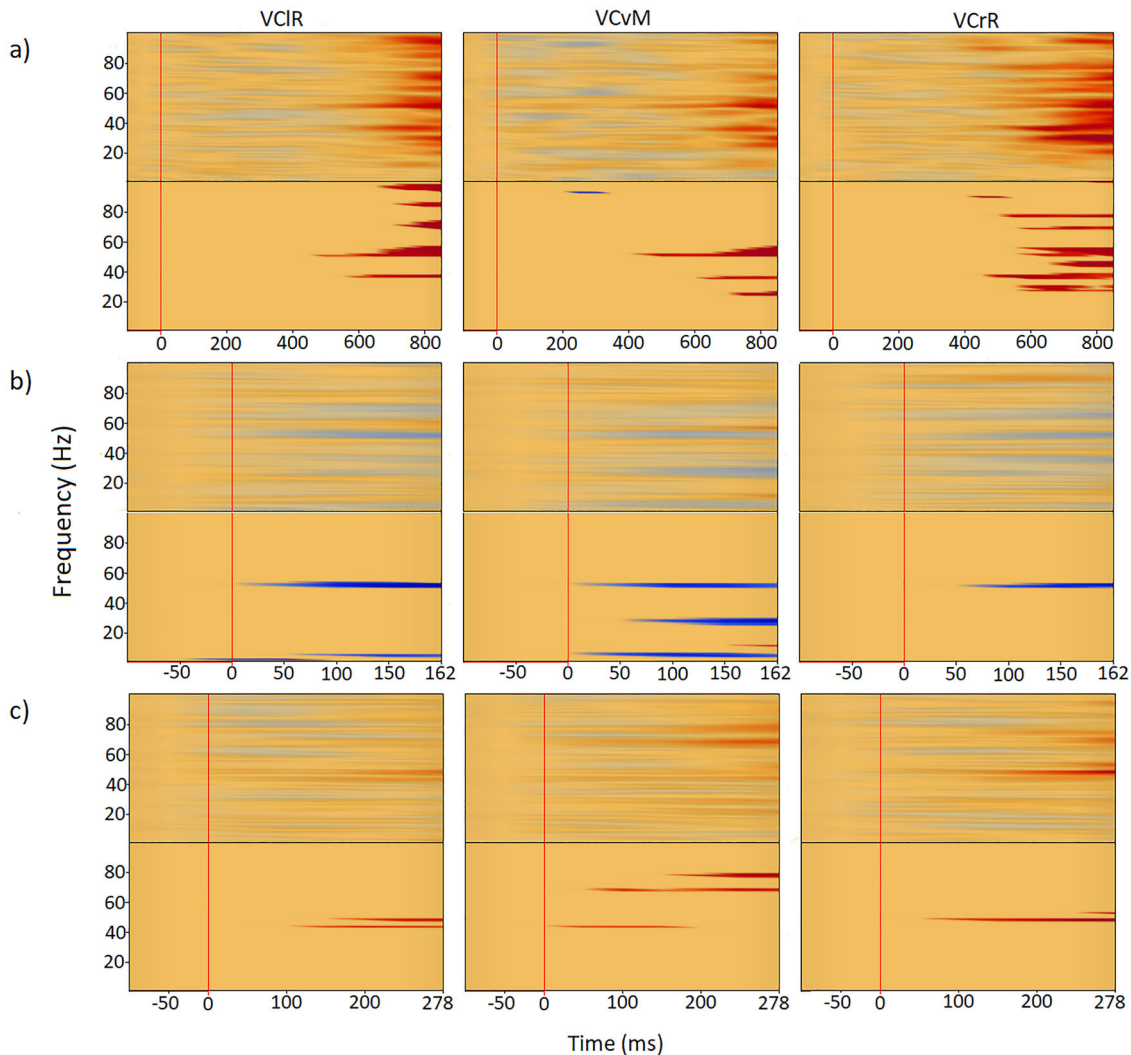


FIGURE 3 | The oscillatory activities in the brain regions of interest (VCrL, VCvM, VCrR) for TSE plots (top row) and the corresponding TSE probability maps (bottom row) before occlusion (a), during occlusion (b), and after occlusion (c) of the car in a typical infant at 11 months. Red colors show synchronized induced oscillatory activities (ERS), whereas blue colors show desynchronized oscillatory activities (ERD) in the TSE plots. TSE probability maps show significant increase (red colors) of amplitudes ($p < 0.05$) in the TSEs before (a) and after (c) occlusion, and a significant decrease (blue colors) of amplitudes ($p < 0.05$) in the TSEs during occlusion (b) when compared to the baseline. Epoch is shown from -100 to 824 ms before occlusion (a), from -100 to 162 ms during occlusion (b), and from -100 to 278 ms after occlusion (c). Baseline was set from -100 to 0 ms. Frequency cut-off was 2 – 100 Hz. Occlusion starts at 899 ms after stimulus onset. VCrL, visual cortex radial left; VCrR, visual cortex radial right; VCvM, visual cortex ventral midline.

than when it was hidden (Pfurtscheller and Lopes da Silva 1999). The infants' locomotor experience may be an explanation for this synchronized gamma activity. Studies have shown that the brain of infants with active locomotion experience (i.e., crawling and walking) shows higher induced frequencies when perceiving motion in contrast to the brain of infants who have only passive locomotor experience (e.g., Agyei et al. 2015, Agyei, van der Weel, and van der Meer 2016b; van der Meer, Fallet, and van der Weel 2008). As the functional detection of visual flow information develops hand in hand with self-produced locomotion in normally developing infants (e.g., James and Swain 2011; van der Meer and van der Weel 2022), we might argue that the gamma oscillations found in this study could be related to the self-produced locomotion experience that the infants had at the time they were tested for this study. Future studies should look at

the longitudinal effects of locomotion on the infant brain when it comes to visual perception of occlusion of moving objects.

4.2 | Desynchronized Gamma Activity When the Moving Car Is Occluded From View

A growing body of evidence indicates that induced gamma activity is more likely to be relevant for high-level cognitive processes, and that it increases during complex or attention-demanding tasks (Tallon-Baudry and Bertrand 1999). Occlusion of the moving object in this study is causing a reduction in synchrony between the neurons' communication (desynchronized activity) that is still mostly at gamma frequencies. The ERD brain activity during car occlusion could suggest that the infants are sustaining the

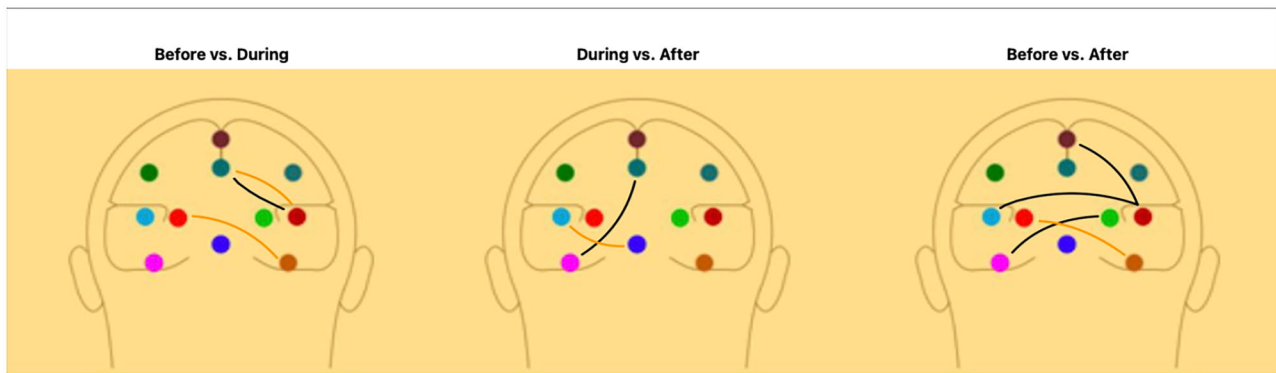


FIGURE 4 | Brain maps of coherence connectivity when comparing the three events before, during, and after occlusion across car speed. A coherence method followed by complex demodulation with time and frequency sampling at 50 ms and 1 Hz, respectively, was applied. The significant connectivity differences ($p < 0.05$) in the gamma (black lines) and theta (orange lines) frequency ranges are visualized between the color-coded sources of interest: CM, PM, CL, CR, VCIL, VCIR, VCrL, VCrR, VCbL, VCbR, VCvM.

image of the object in memory until it re-emerges. The infants are also at an age where the skill of object permanence has developed. For example, studies have shown that infants remember where something is hidden at around 6 months of age (Johnson, Amso, and Slemmer 2003), with recent studies showing the emergence of this ability as early as 4 months of age but with less accuracy compared to infants at 6 months (Tham et al. 2021).

It has been shown that desynchronized activities are associated with an increase in task complexity and attention (Boiten, Sergeant, and Geuze 1992). To keep an object in mind during an occlusion task where the object is moving with different speeds is a complex task that requires the infant to prospectively move their gaze and head, with accurate timing and memory representation of the moving object when occluded from view. The results of the present study reveal that the neurons in the infant brain fire in desynchrony when communicating as the car disappears behind the occluder, which might be explained by the complexity of the task of keeping an object in mind during short disappearances. The desynchronized gamma activity during occlusion suggests that many, but less specialized neurons, are activated. This, in turn, suggests that the infants need more experience with objects being hidden from view to strengthen their cortical connections of keeping an object in mind. The fact that the infant brain also fires with high frequency (gamma) when keeping an object in mind is supported by previous studies (e.g., Kaufman, Csibra, and Johnson 2003; Kaufman, Csibra, and Johnson 2005). They interpreted the bursts of gamma activity that were observed in the temporal lobe as being related to the infants' mental representation of the occluded object. However, the present study also showed gamma activity in the infant brain when the car was visible. In addition, we did not find any distinct pattern of gamma activity in the temporal brain sources.

4.3 | Induced Theta Band Activity

The present study found connectivity differences in both theta and gamma frequency bands in the infants' visual sources of interest. Several studies have found support for lower frequencies to "gate" the occurrence of faster oscillations (Askvik, van der Weel, and van der Meer 2020; van der Weel and van der Meer

2024); for example, theta (4–8 Hz) oscillations in humans often gate gamma (>30 Hz) oscillations (Canolty et al. 2006). Lower frequencies seem to be ideal for enabling communication over longer distances in the brain. Gamma oscillations appear to be underlying mechanisms of neural coding (Singer 1993), and the coupling of theta-gamma band connectivity, which was also found in the present study, seems to be related to studies finding gamma networks to desynchronize and theta networks to synchronize during encoding, retrieval (Solomon et al. 2017), and during memory formation (Burke et al. 2013). Begus and Bonawitz (2020) argue that theta oscillations work as an index for active learning in infancy, where theta activity facilitates information transfer between different structures of the brain (Buzsáki 2006). Thus, the theta activity found in the present study could be a result of the infants' active learning when solving occlusion tasks.

4.4 | Maturation of Visual Pathways

Strengthening of synaptic connections and increasing maturity of visual pathways during the first year of life could explain the synchronized gamma activity found in this study. Infant neuronal networks are characterized by the vast excess of neurons and dendritic spines as part of brain development (Huttenlocher 1990; Webb, Long, and Nelson 2005), and the number of dendrites and synaptic connections in the primary visual cortex reaches a peak level between the ages of 8 months and 2 years (Klaver et al. 2011). This overproduction of neurons is advantageous in adaptation and plasticity of the brain. During the first year of life, the infant brain undergoes rapid changes and doubles in weight, where there is constantly strengthening of some connections and pruning of other connections. This strengthening and pruning of neural pathways might facilitate a developmental change that affects processing speed and efficiency as a more restricted area of the brain gets activated due to specializations of neural pathways (Edelman 1993; Johnson 2000). As 1-year-old infants in this study have some experience with motion through self-produced locomotion and are most likely experienced with the disappearance of objects, this should have strengthened the connections used for motion processing.

In the coherence connectivity analysis, infants showed significant differences in connectivity patterns *before*, *during*, and *after* occlusion. These differences corroborate previous research on functional connectivity in infants. A large-scale study compared global functional connectivity patterns during resting state between neonates, 1-year-old children, and 2-year-old children and found an increasing level of differentiation with age (Shi et al. 2018). Increased differentiation is associated with increasing levels of local specialization (Shi et al. 2018). In the present study with infants who had developed object permanence, the significant connectivity differences may indicate the beginning of specialized connectivity networks within the visual areas.

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 that can be perceived by the infants. The functional coherence analysis showed that connectivity could reflect the co-activation of ventral and dorsal processing pathways during the perception of the moving car. Infants showed functional connectivity between visual areas in the occipital and parietal lobes, but also in the PM at the beginning of the dorsal pathway, which may indicate that the connections between these regions subserved the recognition and establishment of an object in mind during the occlusion event. Activity in the occipital lobe during occlusion tasks has been found in other studies (e.g., Grill-Spector, Kourtzi, and Kanwisher 2001; Hedge et al. 2008), and the dorsal pathway was also earlier found to be associated with spatial and temporal object information and to be involved in guiding actions (van Polanen and Davare 2015).

4.5 | Studies of Induced Gamma Activity

Hoogenboom et al. (2006) found human visual gamma-band activity reliably across subjects and across multiple recording sessions of a given subject using magnetoencephalogram (MEG) and fMRI. They conclude that with optimal stimulation, paradigm, measurement equipment, and data analysis, it is possible to study human visual gamma-band activity with a very high signal-to-noise ratio that can be accurately localized in frequency, time, and space. They argue that the reason they find strong and reliable visually induced gamma-band activity, whereas others find no or less reliable gamma-band activity, is that the paradigms used for investigating stimulus-induced changes in spectral power are often still inspired by paradigms used for investigating event-related potentials (ERPs). In ERP paradigms, trials are often short and dominated by event-related components, which probably reduces the sensitivity for the study of induced brain activity. Previous studies have investigated the stimulus dependence of visual gamma-band activity in animals and humans (e.g., Tallon-Baudry et al. 1996). The general finding is that gamma-band activity is found most strongly and reliably for coherent stimuli or coherently moving stimuli. This might be related to stronger neuronal activation with moving stimuli (Hoogenboom et al.

2006), as can be seen in the present study with the observation of gamma ERS. Fries, Scheeringa, and Oostenveld (2008) showed that neuronal gamma-band synchronization can be investigated with EEG, and researchers should keep their filters wide open (as we had in our study) when looking for induced brain responses.

4.6 | Perception of Speed

The result that the infants did not discriminate between fast, medium, and slow speed could be because they are not that familiar with different speeds yet. The speed differences were most likely too difficult for the infants to detect because of too little self-produced locomotion experience, or the speeds were not distinct enough. It is through crawling or walking that we really get experience with different speeds and how we should respond when, for example, a car comes down the alley and we want to avoid being hit by it. A high-density electroencephalography (hdEEG) study on speed perception found that adults can differentiate among different object speeds during occlusion (Holth, van der Meer, and van der Weel 2013). Moreover, infant studies from our laboratory show that 1-year-old infants have started to differentiate between walking, jogging, and cycling speeds (Rasulo et al. 2021), but not between driving speeds up to 50 km/h (Vilhelmsen et al. 2018).

5 | Conclusions

During the complex task of keeping a moving object in mind while it goes temporarily out of sight, locomotor infants aged 8.5–12 months showed high-frequency brain oscillations in the gamma range, whereas they predictively followed a car traveling under different speeds on a large screen that underwent temporary occlusion along its trajectory. Desynchronized gamma activity may indicate that by the second half of the first year of life, infants use high-frequency brain oscillations to successfully follow a moving object, and that such brain oscillations are used to efficiently perceive and predict the future positions of the moving target during temporary occlusion. Strengthening of synaptic connections and increasing maturity of visual pathways during the first year of life may account for such high-frequency oscillations. Moreover, self-produced locomotor experiences could explain the observed synchronized gamma activity when the moving car was in sight both before and after occlusion. Functional connectivity networks found between the visual sources of interest may indicate that the connections between these regions subserved the recognition and establishment of an object in mind during the occlusion event. It would be interesting to see if younger infants, who have not yet developed object permanence, demonstrate brain oscillations in lower frequencies during occlusion events.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

References

- Ageyi, S. B., M. Holth, F. R. Van der Weel, and A. L. H. van der Meer. 2015. "Longitudinal Study of Perception of Structured Optic Flow and Random Visual Motion in Infants Using High-Density EEG." *Developmental Science* 18, no. 3: 436–451. <https://doi.org/10.1111/desc.12221>.
- Ageyi, S. B., F. R. van der Weel, and A. L. H. van der Meer. 2016a. "Development of Visual Motion Perception for Prospective Control: Brain and Behavioral Studies in Infants." *Frontiers in Psychology* 7: 1–14. <https://doi.org/10.3389/fpsyg.2016.00100>.
- Ageyi, S. B., F. R. van der Weel, and A. L. H. van der Meer. 2016b. "Longitudinal Study of Preterm and Full-Term Infants: High-Density EEG Analyses of Cortical Activity in Response to Visual Motion." *Neuropsychologia* 84: 89–104. <https://doi.org/10.1016/j.neuropsychologia.2016.02.001>.
- Askvik, E. O., F. R. van der Weel, and A. L. H. van der Meer. 2020. "The Importance of Cursive Handwriting Over Typewriting for Learning in the Classroom: A High-Density EEG Study of 12-Year-Old Children and Young Adults." *Frontiers in Psychology* 11: 1–16. <https://doi.org/10.3389/fpsyg.2020.01810>.
- Atkinson, J. 2000. *The Developing Visual Brain*. Oxford: Oxford University Press.
- Atkinson, J. 2017. "Visual Brain Development: A Review of "Dorsal Stream Vulnerability"—Motion, Mathematics, Amblyopia, Actions, and Attention." *Journal of Vision* 17, no. 3: 1–24. <https://doi.org/10.1167/17.3.26>.
- Baillargeon, R., and J. DeVos. 1991. "Object Permanence in Young Infants: Further Evidence." *Child Development* 62, no. 6: 1222–1246. <https://doi.org/10.1111/j.1467-8624.1991.tb01602.x>.
- Başar, E., C. Başar-Eroglu, S. Karakas, and M. Schürmann. 1999. "Oscillatory Brain Theory: A New Trend in Neuroscience." *IEEE Engineering in Medicine and Biology* 18, no. 3: 56–66. <https://doi.org/10.1109/51.765190>.
- Başar, E., C. Başar-Eroglu, S. Karakas, and M. Schürmann. 2000. "Brain Oscillations in Perception and Memory." *International Journal of Psychophysiology* 35: 95–124. [https://doi.org/10.1016/S0167-8760\(99\)00047-1](https://doi.org/10.1016/S0167-8760(99)00047-1).
- Batalle, D., E. J. Hughes, H. Zhang, et al. 2017. "Early Development of Structural Networks and the Impact of Prematurity on Brain Connectivity." *NeuroImage* 149: 379–392. <https://doi.org/10.1016/j.neuroimage.2017.01.065>.
- Begus, K., and E. Bonawitz. 2020. "The Rhythm of Learning: Theta Oscillations as an Index of Active Learning in Infancy." *Developmental Cognitive Neuroscience* 45: 100810. <https://doi.org/10.1016/j.dcn.2020.100810>.
- Berg, P., and M. Scherg. 1991. "Dipole Models of Eye Movements and Blinks." *Electroencephalography and Clinical Neurophysiology* 79, no. 1: 36–44. [https://doi.org/10.1016/0013-4694\(91\)90154-V](https://doi.org/10.1016/0013-4694(91)90154-V).
- Biagi, L., S. A. Crespi, M. Tosetti, and M. C. Morrone. 2015. "BOLD Response Selective to Flow-Motion in Very Young Infants." *PLoS Biology* 13, no. 9: e1002260. <https://doi.org/10.1371/journal.pbio.1002260>.
- Boiten, F., J. Sergeant, and R. Geuze. 1992. "Event-Related Desynchronization: The Effects of Energetic and Computational Demands." *Electroencephalography and Clinical Neurophysiology* 82: 302–309. [https://doi.org/10.1016/0013-4694\(92\)90110-4](https://doi.org/10.1016/0013-4694(92)90110-4).
- Borge Blystad, J., and A. L. H. van der Meer. 2022. "Longitudinal Study of Infants Receiving Extra Motor Stimulation, Full-Term Control Infants, and Infants Born Preterm: High-Density EEG Analyses of Cortical Activity in Response to Visual Motion." *Developmental Psychobiology* 64, no. 5: 1–17. <https://onlinelibrary.wiley.com/doi/10.1002/dev.22276>.
- Burke, J. F., K. A. Zaghoul, J. Jacobs, et al. 2013. "Synchronous and Asynchronous Theta and Gamma Activity During Episodic Memory Formation." *Journal of Neuroscience* 33, no. 1: 292–304. <https://doi.org/10.1523/JNEUROSCI.2057-12.2013>.
- Buzsáki, G. 2006. *Rhythms of the Brain*. Oxford: Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780195301069.001.0001>.
- Buzsaki, G., and A. Draguhn. 2004. "Neuronal Oscillations in Cortical Networks." *Science* 304, no. 80: 1926–1929. <https://doi.org/10.1126/science.1099745>.
- Canolty, R. T., E. Edwards, S. S. Dalal, et al. 2006. "High Gamma Power Is Phase-Locked to Theta Oscillations in Human Neocortex." *Science* 313: 1626–1628. <https://doi.org/10.1126/science.1128115>.
- DeMaster, D., J. Bick, U. Johnson, J. J. Montroy, S. Landry, and A. F. Duncan. 2019. "Nurturing the Preterm Infant Brain: Leveraging Neuroplasticity to Improve Neurobehavioral Outcomes." *Pediatric Research* 85, no. 2: 166–175. <https://doi.org/10.1038/s41390-018-0203-9>.
- Edelman, G. M. 1993. "Neural Darwinism: Selection and Reentrant Signaling in Higher Brain Function." *Neuron* 10, no. 2: 115–125. [https://doi.org/10.1016/0896-6273\(93\)90304-A](https://doi.org/10.1016/0896-6273(93)90304-A).
- Engel, A. K., and P. Fries. 2010. "Beta-Band Oscillations-Signaling the Status Quo?." *Current Opinion in Neurobiology* 20, no. 2: 156–165. <https://doi.org/10.1016/j.conb.2010.02.015>.
- Ferree, T. C., P. Luu, and D. M. Tucker. 2001. "Scalp Electrode Impedance, Infection Risk, and EEG Data Quality." *Clinical Neurophysiology* 112, no. 3: 536–544. [https://doi.org/10.1016/S1388-2457\(00\)00533-2](https://doi.org/10.1016/S1388-2457(00)00533-2).
- Finlay, B. L., B. Clancy, and M. A. Kingsbury. 2003. "The Developmental Neurobiology of Early Vision." In *Neurobiology of Infant Vision*, edited by B. Hopkins and S. P. Johnson, 1–41. Westport, CT: Praeger Publishers.
- Freunberger, R., M. Werkle-Bergner, B. Griesmayr, U. Lindenberger, and W. Klimesch. 2011. "Brain Oscillatory Correlates of Working Memory Constraints." *Brain Research* 1375: 93102. <https://doi.org/10.1016/j.brainres.2010.12.048>.
- Fries, P., R. Scheeringa, and R. Oostenveld. 2008. "Finding Gamma." *Neuron* 58: 303–305. <https://doi.org/10.1016/j.neuron.2008.04.020>.
- Ganzetti, M., and D. Mantini. 2013. "Functional Connectivity and Oscillatory Neuronal Activity in the Resting Human Brain." *Neuroscience* 240: 297–309. <https://dx.doi.org/10.1016/j.neuroscience.2013.02.032>.
- Gilmore, R. O., T. J. Baker, and K. H. Grobman. 2004. "Stability in Young Infants' Discrimination of Optic Flow." *Developmental Psychology* 40, no. 2: 259–270. <https://doi.org/10.1037/0012-1649.40.2.259>.
- Greenough, W. T., J. E. Black, and C. S. Wallace. 1987. "Experience and Brain Development." *Child Development* 58, no. 3: 539–559. <https://doi.org/10.2307/1130197>.
- Grill-Spector, K., Z. Kourtzi, and N. Kanwisher. 2001. "The Lateral Occipital Complex and Its Role in Object Recognition." *Vision Research* 41, no. 10–11: 1409–1422. [https://doi.org/10.1016/S0042-6989\(01\)00073-6](https://doi.org/10.1016/S0042-6989(01)00073-6).
- Grüber, T., and M. M. Müller. 2006. "Oscillatory Brain Activity in the Human EEG During Indirect and Direct Memory Tasks." *Brain Research* 1097: 194–204. <https://doi.org/10.1016/j.brainres.2006.04.069>.
- Hanslmayr, S., G. Volberg, M. Wimber, S. S. Dalal, and M. W. Greenlee. 2013. "Prestimulus Oscillatory Phase at 7 Hz Gates Cortical Information Flow and Visual Perception." *Current Biology* 23, no. 22: 2273–2278. <https://doi.org/10.1016/j.cub.2013.09.020>.
- Hegde, J., F. Fang, S. O. Murray, and D. Kersten. 2008. "Preferential Responses to Occluded Objects in the Human Visual Cortex." *Journal of Vision* 8, no. 4: 1–16. <https://doi.org/10.1167/8.4.16>.
- Hoehstetter, K., H. Bornfleth, D. Weckesser, N. Ille, P. Berg, and M. Scherg. 2004. "BESA Source Coherence: A New Method to Study Cortical Oscillatory Coupling." *Brain Topography* 16, no. 4: 233–238. <https://doi.org/10.1023/B:BRAT.0000032857.55223.5d>.

- Holth, M., A. L. H. Van der Meer, and F. R. Van der Weel. 2013. "Combining Findings From Gaze and Electroencephalography Recordings to Study Timing in a Visual Tracking Task." *NeuroReport* 24, no. 17: 968–972. <https://doi.org/10.1097/WNR.000000000000020>.
- Hoogenboom, N., J.-M. Schoffelen, R. Oostenveld, L. M. Parkes, and P. Fries. 2006. "Localizing Human Visual Gamma-Band Activity in Frequency, Time and Space." *NeuroImage* 29, no. 3: 764–773. <https://doi.org/10.1016/j.neuroimage.2005.08.043>.
- Huttenlocher, P. R. 1990. "Morphometric Study of Human Cerebral Cortex Development." *Neuropsychologia* 28, no. 6: 517–527. [https://doi.org/10.1016/0028-3932\(90\)90031-I](https://doi.org/10.1016/0028-3932(90)90031-I).
- Huttenlocher, P. R., C. de Courten, L. J. Garey, and H. van der Loos. 1986. "Synaptogenesis in Human Visual Cortex—Evidence for Synapse Elimination During Normal Development." *Neuroscience Letters* 33, no. 3: 247–252. [https://doi.org/10.1016/0304-3940\(82\)90379-2](https://doi.org/10.1016/0304-3940(82)90379-2).
- Ille, N., P. Berg, and M. Scherg. 2002. "Artifact Correction of the Ongoing EEG Using Spatial Filters Based on Artifact and Brain Signal Topographies." *Journal of Clinical Neurophysiology* 19, no. 2: 113–124. <https://doi.org/10.1097/00004691-200203000-00002>.
- James, K. H., and S. N. Swain. 2011. "Only Self-Generated Actions Create Sensorimotor Systems in the Developing Brain." *Developmental Science* 14, no. 4: 673–678. <https://doi.org/10.1111/j.14677687.2010.01011.x>.
- Johnson, M. H. 1990. "Cortical Maturation and the Development of Visual Attention in Early Infancy." *Journal of Cognitive Neuroscience* 2, no. 2: 81–95. <https://doi.org/10.1162/jocn.1990.2.2.81>.
- Johnson, M. H. 2000. "Functional Brain Development in Infants: Elements of an Interactive Specialization Framework." *Child Development* 71, no. 1: 75–81. <https://doi.org/10.1111/1467-8624.00120>.
- Johnson, S. P. 2013. "Development of the Visual System." In *Comprehensive Developmental Neuroscience: Neural Circuit Development and Function in the Brain*, edited by J. Rubenstein and P. Rakic, 249–269. Cambridge, MA: Academic Press. <http://doi.org/10.1016/B978-0-12-397267-5.00033-9>.
- Johnson, S. P., D. Amso, and J. A. Slemmer. 2003. "Development of Object Concepts in Infancy: Evidence for Early Learning in an Eye-Tracking Paradigm." *Proceedings of the National Academy Sciences USA* 100, no. 13: 10568–10573. <https://doi.org/10.1073/pnas.1630655100>.
- Johnson, S. P., and R. N. Aslin. 1996. "Perception of Object Unity in Young Infants: The Roles of Motion, Depth, and Orientation." *Cognitive Development* 11, no. 2: 161–180. [https://doi.org/10.1016/S0885-2014\(96\)90001-5](https://doi.org/10.1016/S0885-2014(96)90001-5).
- Kaufman, J., G. Csibra, and M. H. Johnson. 2003. "Representing Occluded Objects in the Human Infant Brain." *Proceedings of the Royal Society, London B* 270, no. S2: S140–S143. <https://doi.org/10.1098/rsbl.2003.0067>.
- Kaufman, J., G. Csibra, and M. H. Johnson. 2005. "Oscillatory Activity in the Infant Brain Reflects Object Maintenance." *Proceedings of the National Academy of Sciences* 102, no. 42: 15271–15274. <https://doi.org/10.1073/pnas.0507626102>.
- Khader, P. H., K. Jost, C. Ranganath, and F. Rosler. 2010. "Theta and Alpha Oscillations During Working-Memory Maintenance Predict Successful Long-Term Memory Encoding." *Neuroscience Letters* 468: 339–343. <https://doi.org/10.1016/j.neulet.2009.11.028>.
- Klaver, P., V. Marcar, and E. Martin. 2011. "Neurodevelopment of the Visual System in Typically Developing Children." *Progress in Brain Research* 189: 113–136. <https://doi.org/10.1016/B978-0-444-53884-0.00021-X>.
- Klimesch, W., M. Doppelmayr, H. Russegger, and T. Pachinger. 1996. "Theta Band Power in the Human Scalp EEG and the Encoding of New Information." *NeuroReport* 7: 1235–1240. <https://doi.org/10.1097/00001756-199605170-00002>.
- Klimesch, W., P. Sauseng, and S. Hanslmayr. 2007. "EEG Alpha Oscillations: The Inhibition-Timing Hypothesis." *Brain Research Review* 53, no. 1: 63–88. <https://doi.org/10.1016/j.brainresrev.2006.06.003>.
- Landau, A. N., H. M. Schreyer, S. Van Pelt, and P. Fries. 2015. "Distributed Attention Is Implemented Through Theta-Rhythmic Gamma Modulation." *Current Biology* 25, no. 17: 2332–2337. <https://doi.org/10.1016/j.cub.2015.07.048>.
- Mareschal, D., and M. H. Johnson. 2003. "The 'What' and 'Where' of Object Representations in Infancy." *Cognition* 88, no. 3: 259–276. [https://doi.org/10.1016/S0010-0277\(03\)00039-8](https://doi.org/10.1016/S0010-0277(03)00039-8).
- Müller, M., T. Gruber, and A. Keil. 2000. "Modulation of Induced Gamma Band Activity in the Human EEG by Attention and Visual Information Processing." *International Journal of Psychophysiology* 38, no. 3: 283–299. [https://doi.org/10.1016/S0167-8760\(00\)00171-9](https://doi.org/10.1016/S0167-8760(00)00171-9).
- Orehkova, E. V., T. A. Stroganova, and I. N. Posikera. 1999. "Theta Synchronization During Sustained Anticipatory Attention in Infants Over the Second Half of the First Year of Life." *International Journal of Psychophysiology* 32, no. 2: 151–172. [https://doi.org/10.1016/S01678760\(99\)00011-2](https://doi.org/10.1016/S01678760(99)00011-2).
- Orehkova, E. V., T. A. Stroganova, I. N. Posikera, and M. Elam. 2006. "EEG Theta Rhythm in Infants and Preschool Children." *Clinical Neurophysiology* 117, no. 5: 1047–1062. <http://doi.org/10.1016/j.clinph.2005.12.027>.
- Papp, N., and P. Ktonas. 1976. "Critical Evaluation of Complex Demodulation Techniques for the Quantification of Bioelectrical Activity." *Biomedical Sciences Instrumentation* 13: 135–145.
- Perrin, F., J. Pernier, O. Bertrand, and J. F. Echallier. 1989. "Spherical Splines for Scalp Potential and Current Density Mapping." *Electroencephalography and Clinical Neurophysiology* 72, no. 2: 184–187. [https://doi.org/10.1016/0013-4694\(89\)90180-6](https://doi.org/10.1016/0013-4694(89)90180-6).
- Pfurtscheller, G., and F. H. Lopes da Silva. 1999. "Event-Related EEG/MEG Synchronization and Desynchronization: Basic Principles." *Clinical Neurophysiology* 110, no. 11: 1842–1857. [https://doi.org/10.1016/S1388-2457\(99\)00141-8](https://doi.org/10.1016/S1388-2457(99)00141-8).
- Pfurtscheller, G., C. Neuper, and W. Mohl. 1994. "Event-Related Desynchronization (ERD) During Visual Processing." *International Journal of Psychophysiology* 16: 147–153. [https://doi.org/10.1016/0167-8760\(89\)90041-X](https://doi.org/10.1016/0167-8760(89)90041-X).
- Pfurtscheller, G., A. Stancák, and C. Neuper. 1996. "Event-Related Synchronization (ERS) in the Alpha Band—An Electrophysiological Correlate of Cortical Idling: A Review." *International Journal of Psychophysiology* 24, no. 1–2: 39–46. [https://doi.org/10.1016/S01678760\(96\)00066-9](https://doi.org/10.1016/S01678760(96)00066-9).
- Piaget, J. 1954. *The Construction of Reality in the Child*. New York, NY: Basic Books.
- Picton, T. W., S. Bentin, P. Berg, et al. 2000. "Guidelines for Using Human Event-Related Potentials to Study Cognition: Recording Standards and Publication Criteria." *Psychophysiology* 37, no. 2: 127–152. <https://doi.org/10.1111/1469-8986.3720127>.
- Rasulo, S., K. Vilhelmsen, F. R. Van der Weel, and A. L. H. van der Meer. 2021. "Development of Motion Speed Perception From Infancy to Early Adulthood: A High-Density EEG Study of Simulated Forward Motion Through Optic Flow." *Experimental Brain Research* 239: 3143–3154. <https://doi.org/10.1007/s00221-021-06195-5>.
- Rosander, K., and C. von Hofsten. 2002. "Development of Gaze Tracking of Small and Large Objects." *Experimental Brain Research* 146, no. 2: 257–264. <https://doi.org/10.1007/s00221002-1161-2>.
- Rosander, K., and C. von Hofsten. 2004. "Infants' Emerging Ability to Represent Occluded Object Motion." *Cognition* 91, no. 1: 1–22. [https://doi.org/10.1016/S0010-0277\(03\)00166-5](https://doi.org/10.1016/S0010-0277(03)00166-5).
- Rosenberg, J. R., A. M. Amjad, P. Breeze, D. R. Brillinger, and D. M. Halliday. 1989. "The Fourier Approach to The Identification of Functional Coupling Between Neuronal Spike Trains." *Progress in Biophysics and Molecular Biology* 53, no. 1: 1–31. [https://doi.org/10.1016/0079-6107\(89\)90004-7](https://doi.org/10.1016/0079-6107(89)90004-7).

- Saby, J. N., and P. J. Marshall. 2012. "The Utility of EEG Band Power Analysis in the Study of Infancy and Early Childhood." *Developmental Neuropsychology* 37, no. 3: 253–273. <https://doi.org/10.1080/87565641.2011.614663>.
- Scherg, M., and P. Berg. 1991. "Use of Prior Knowledge in Brain Electromagnetic Source Analysis." *Brain Topography* 4, no. 2: 143–150. <https://doi.org/10.1007/BF01132771>.
- Scholl, B. J., and Z. W. Pylyshyn. 1999. "Tracking Multiple Items Through Occlusion: Clues to Visual Objecthood." *Cognitive Psychology* 38: 259–290. <https://doi.org/10.1006/cogp.1998.0698>.
- Shi, F., A. P. Salzwedel, W. Lin, J. H. Gilmore, and W. Gao. 2018. "Functional Brain Parcellations of the Infant Brain and the Associated Developmental Trends." *Cerebral Cortex* 28, no. 4: 1358–1368. <https://doi.org/10.1093/cercor/bhx062>.
- Shirai, N., and M. K. Yamaguchi. 2010. "How Do Infants Utilize Radial Optic Flow for Their Motor Actions? A Review of Behavioral and Neural Studies." *Japanese Psychological Research* 52, no. 2: 78–90. <https://doi.org/10.1111/j.1468-5884.2010.00426.x>.
- Simes, R. J. 1986. "An Improved Bonferroni Procedure for Multiple Tests of Significance." *Biometrika* 73, no. 3: 751–754. <https://doi.org/10.1093/biomet/73.3.751>.
- Singer, W. 1993. "Synchronization of Cortical Activity and Its Putative Role in Information Processing and Learning." *Annual Review of Physiology* 55: 349–374. <https://doi.org/10.1146/annurev.ph.55.030193.002025>.
- Solomon, E. A., J. E. Kragel, M. R. Sperling, et al. 2017. "Widespread Theta Synchrony and High-Frequency Desynchronization Underlies Enhanced Cognition." *Nature Communications* 8, no. 1704: 1–14. <https://doi.org/10.1038/s41467-017-01763-2>.
- Southgate, V., G. Csibra, J. Kaufman, and M. H. Johnson. 2008. "Distinct Processing of Objects and Faces in the Infant Brain." *Journal of Cognitive Neuroscience* 20, no. 4: 741–749. <https://doi.org/10.1162/jocn.2008.20052>.
- Stroganova, T. A., and E. V. Orekhova. 2007. "EEG and Infant States." In *Infant EEG and Event-Related Potentials*, edited by M. de Haan, 251–297. New York, NY: Psychology Press.
- Stroganova, T. A., E. V. Orekhova, and I. N. Posikera. 1999. "EEG Alpha Rhythm in Infants." *Clinical Neurophysiology* 110, no. 6: 997–1012. [https://doi.org/10.1016/S1388-2457\(98\)00009-1](https://doi.org/10.1016/S1388-2457(98)00009-1).
- Tallon-Baudry, C., and O. Bertrand. 1999. "Oscillatory Gamma Activity in Humans and Its Role in Object Representation." *Trends in Cognitive Sciences* 3, no. 4: 151–162. [https://doi.org/10.1016/S1364-6613\(99\)01299-1](https://doi.org/10.1016/S1364-6613(99)01299-1).
- Tallon-Baudry, C., O. Bertrand, C. Delpuech, and J. Pernier. 1996. "Stimulus Specificity of Phase-Locked and Non-Phase-Locked 40 Hz Visual Responses in Human." *Journal of Neuroscience* 16, no. 13: 4240–4249. <https://doi.org/10.1523/JNEUROSCI.16-13-04240.1996>.
- Tham, D. S., A. Rees, J. G. Bremner, A. Slater, and S. P. Johnson. 2021. "Orientation Effects in the Development of Linear Object Tracking in Early Infancy." *Child Development* 92, no. 1: 324–334. <https://doi.org/10.1111/cdev.13419>.
- van der Meer, A. L. H., G. Fallet, and F. R. van der Weel. 2008. "Perception of Structured Optic Flow and Random Visual Motion in Infants and Adults: A High-Density EEG Study." *Experimental Brain Research* 186: 493–502. <https://doi.org/10.1007/s00221-007-12512>.
- van der Meer, A. L. H., and F. R. van der Weel. 2019. "The Optical Information for Self-Perception in Development." In *Perception as Information Detection: Reflections on Gibson's Ecological Approach to Visual Perception*, edited by J. B. Wagman and J. C. Blau, 131–151. Abingdon: Routledge.
- van der Meer, A. L. H., and F. R. van der Weel. 2022. *Motor Development: Biological Aspects of Brain and Behavior*. Oxford, UK: Oxford University Press. <https://doi.org/10.1093/acrefore/9780190236557.013.903>.
- van der Meer, A. L. H., F. R. van der Weel, and D. N. Lee. 1994. "Prospective Control in Catching by Infants." *Perception* 23: 287–302. <https://doi.org/10.1068/p230287>.
- van der Meer, A. L. H., F. R. van der Weel, D. N. Lee, I. A. Laing, and J. P. Lin. 1995. "Development of Prospective Control of Catching Moving Objects in Preterm at-Risk Infants." *Developmental Medicine and Child Neurology* 37: 145–158. <https://doi.org/10.1111/j.1469-8749.1995.tb11984.x>.
- van der Weel, F. R., S. B. Agyei, and A. L. H. van der Meer. 2019. "Infants' Brain Responses to Looming Danger: Degeneracy of Neural Connectivity Patterns." *Ecological Psychology* 31, no. 3: 182–197. <https://doi.org/10.1080/10407413.2019.1615210>.
- van der Weel, F. R., and A. L. H. van der Meer. 2009. "Seeing It Coming: Infants' Brain Responses to Looming Danger." *Die Naturwissenschaften* 96: 1385–1391. <https://doi.org/10.1007/s00114-009-0585-y>.
- van der Weel, F. R., and A. L. H. van der Meer. 2024. "Handwriting but Not Typewriting Leads to Widespread Brain Connectivity: A High-Density EEG Study With Implications for the Classroom." *Frontiers in Psychology* 14: 1–9. <https://doi.org/10.3389/fpsyg.2023.1219945>.
- van Polanen, V., and M. Davare. 2015. "Interactions Between Dorsal and Ventral Streams for Controlling Skilled Grasp." *Neuropsychologia* 79: 186–191. <https://doi.org/10.1016/j.neuropsychologia.2015.07.010>.
- Vilhelmsen, K., S. B. Agyei, F. R. van der Weel, and A. L. H. van der Meer. 2018. "A High-Density EEG Study of Differentiation Between Two Speeds and Directions of Simulated Optic Flow in Adults and Infants." *Psychophysiology* 56, no. 1: 1–15. <https://doi.org/10.1111/psyp.13281>.
- von Hofsten, C., and K. Rosander. 1996. "The Development of Gaze Control and Predictive Tracking in Infants." *Vision Research* 36: 81–96. [https://doi.org/10.1016/00426989\(95\)00054-4](https://doi.org/10.1016/00426989(95)00054-4).
- Webb, S. J., J. D. Long, and C. A. Nelson. 2005. "A Longitudinal Investigation of Visual Event Related Potentials in the First Year of Life." *Developmental Science* 8, no. 6: 605–616. <https://doi.org/10.1111/j.1467-7687.2005.00452.x>.
- Zilles, K., R. Werners, U. Busching, and A. Schleicher. 1986. "Ontogenesis of the Laminar Structure in Areas 17 and 18 of the Human Visual Cortex: A Quantitative Study." *Anatomy and Embryology* 174: 339–353. <https://doi.org/10.1007/BF00698784>.