Neurophysiological mechanisms of cognition in the developing brain: Insights from intracranial EEG studies

Qin Yin [a,b], Elizabeth L. Johnson [c,d], Noa Ofen [a,b,*]

[a] Department of Psychology, Wayne State University, Detroit, MI, USA
[b] Life-span Cognitive Neuroscience Program, Institute of Gerontology and Merrill Palmer Skillman Institute, Wayne State University, Detroit, MI, USA
[c] Departments of Medical Social Sciences and Pediatrics, Northwestern University, Chicago, IL, USA
[d] Department of Psychology, Northwestern University, Evanston, IL, USA

ARTICLE INFO

ABSTRACT

The quest to understand how the development of the brain supports the development of complex cognitive functions is fueled by advances in cognitive neuroscience methods. Intracranial EEG (iEEG) recorded directly from the developing human brain provides unprecedented spatial and temporal resolution for mapping the neurophysiological mechanisms supporting cognitive development. In this paper, we focus on episodic memory, the ability to remember detailed information about past experiences, which improves from childhood into adulthood. We review memory effects based on broadband spectral power and emphasize the importance of isolating narrowband oscillations from broadband activity to determine mechanisms of neural coordination within and between brain regions. We then review evidence of developmental variability in neural oscillations and present emerging evidence linking the development of neural oscillations to the development of memory. We conclude by proposing that the development of oscillations increases the precision of neural coordination and may be an essential factor underlying memory development. More broadly, we demonstrate how recording neural activity directly from the developing brain holds immense potential to advance our understanding of cognitive development.

1. Introduction

The ability to remember detailed information about past experiences is essential to our daily life. Studies have shown continued development of memory performance from childhood into adulthood (Billingsley et al., 2002; Cycowicz et al., 2001; Dirks and Neisser, 1977; Mandler and Robinson, 1978). A wide range of neuroimaging techniques, such as functional MRI (fMRI) (Ofen, 2012; Ofen et al., 2019; Ofen and Shing, 2013) and scalp EEG (Bhavnani et al., 2021; Werkle-Bergner et al., 2006) have been used to investigate brain development and establish links between brain measures and developmental improvements in memory. These techniques provide invaluable insights into the neural correlates underlying memory development but are limited in either temporal or spatial resolution to quantify brain development.

Used in evaluation for the clinical management of epilepsy, intracranial EEG (iEEG) provides spatially localized brain measures with the high temporal precision needed to identify neurophysiological underpinnings of cognitive processes (Johnson et al., 2020; Parvizi and Kastner, 2018). The high spatial and temporal precision of the recorded signals makes iEEG a powerful tool to investigate the neurophysiological mechanisms supporting memory (Johnson et al., 2020; Johnson and Knight, 2015) and is particularly exciting as applied to the study of memory development (Johnson et al., 2018, 2022; Ofen et al., 2019; Yin et al., 2020). iEEG is a promising method for offering novel insights into critical aspects of brain activity that underlie memory and its development: precise timing of localized activity and neural oscillations with high spatial resolution.

First, with its exceptional temporal precision (≤ 1 ms), iEEG enables researchers to pinpoint the exact timing of neural activity in specific brain regions relative to external events, such as stimuli onsets, or observable behavior, such as subjects' task responses. Of note, high-frequency broadband activity between ~70–150 Hz provides a partial proxy for neuronal population firing (Fedele et al., 2020; Leszczyński et al., 2020; Rich and Wallis, 2017; Watson et al., 2018) and correlates with fMRI blood level oxygen-dependent (BOLD) signals (Haufe et al., 2018; Hermes et al., 2012; Jacques et al., 2016; Nir et al., 2007), making

---

it an outstanding tool for adding localized temporal dimension to prior work. The high temporal precision also enables examining the timing of neural activity of one brain region relative to another, making it possible to investigate the temporal dynamics of interactions between brain regions. This unique capability allows measuring brain activity in real-time during the execution of memory tasks and examining the temporal dynamics of neural processes underlying memory.

Second, iEEG enables measures of neural oscillations with high spatial resolution (≤1 cm). Neural oscillations, or rhythms, play important roles in cognitive processes, such as alpha rhythms (~8–13 Hz) in visual perception (Clayton et al., 2018) and theta rhythms (~3–8 Hz) in memory and spatial navigation (Buzsáki and Moser, 2013; Herweg et al., 2020; Herweg and Kahana, 2018). Neural oscillations reflect periodic changes in excitability and thus provide optimal time windows to coordinate activity within and between brain regions to support cognition (Buzsáki et al., 2012, 2013; Buzsaki and Draguhn, 2004; Canolty and Knight, 2010; Fiebelkorn and Kastner, 2019; Fries, 2005, 2015; Helfrich et al., 2018; Lisman and Jensen, 2013). Focusing on neural oscillations in development appears particularly exciting given observed developmental differences in the frequency of neural oscillations from scalp EEG findings (e.g., Cellier et al., 2021; Lindsley, 1939; Miskovic et al., 2015) and recent iEEG discoveries (Johnson et al., 2022; Yin et al., 2020). The observed age differences in the frequency of neural oscillations hold potential implications for memory development, as they may reflect, or even enable, the increased precision of neural coordination via associated oscillatory mechanisms over development.

The ability to measure the precise timing of neural activity and characterize oscillations with high spatial resolution holds significant promise for advancing our understanding of the neurophysiological mechanisms of memory development and cognitive development more broadly. In this paper, we provide a brief review of findings from iEEG studies in adults demonstrating the spatiotemporal dynamics of neural activity during successful memory encoding, and then present such iEEG findings from the developing brain. We further review the functional roles played by neural oscillations in memory processes, and link the development of neural oscillations to the development of memory from the burgeoning field of developmental iEEG. We conclude by proposing that the increased precision of neural coordination and maturation of oscillatory mechanisms may be an essential aspect of brain development that supports memory development. More broadly, we demonstrate how recording neural activity directly from the developing brain holds immense potential to advance our understanding of cognitive development.

2. Moving from spatial activations to spatiotemporal dynamics of memory

Neuroimaging studies of memory utilize laboratory tasks to examine memory-related brain activity. Among these, the subsequent memory paradigm has been widely used to investigate the neural correlates of successful memory formation in adults (Kim, 2011; Paller and Wagner, 2002; Spaniol et al., 2009) and children (Ofen, 2012; Ofen et al., 2019; Ofen and Shing, 2013). In the subsequent memory paradigm, subjects study a series of stimuli, usually visual stimuli, in preparation for a memory test. Subsequent memory effects are analyzed retroactively by contrasting brain activity across studied stimuli that are later remembered to activity across studied stimuli that are later forgotten. With high spatial resolution, fMRI studies have identified subsequent memory brain activation in the prefrontal cortex (PFC), medial temporal lobe (MTL), and occipitotemporal cortices (Kim, 2011; Spaniol et al., 2009). However, the spatiotemporal dynamics of brain activity among key memory brain regions are less understood. Using the subsequent memory paradigm, iEEG studies in adults have examined memory formation-related effects in spectral power across different frequency ranges and revealed how memory encoding is coordinated across these key memory brain regions.

2.1. Spatiotemporal dynamics of memory revealed by broadband spectral power

The power of broadband high-frequency that ranges above ~30 Hz positively correlates with fMRI blood level oxygen-dependent (BOLD) signals in task-related brain regions (Haufe et al., 2018; Hermes et al., 2012; Jacques et al., 2016; Nir et al., 2007). Leveraging broadband high-frequency power above ~30 Hz, iEEG studies of memory in adults have revealed the spatiotemporal dynamics of neural activity across key memory regions (Burke et al., 2014; Greenberg et al., 2015; Kucewicz et al., 2014, 2019) (e.g., Fig. 1A). For example, using a verbal free recall task, Burke et al. (2014) found that successful word encoding was associated with increased high-frequency (64–95 Hz) power compared to unsuccessful encoding. During the 1600-ms word encoding window, high-frequency power increases appeared initially in occipitotemporal cortices at ~ 500 ms after word onset, then in hippocampus at ~800 ms, and last in PFC at ~1000 ms. This study is one of several utilizing broadband high-frequency power to show the spatiotemporal dynamics of activity among different brain regions during successful word encoding (Greenberg et al., 2015; Kucewicz et al., 2014, 2019).

In contrast to increases in broadband high-frequency power, successful memory formation is also associated with decreases in broadband low-frequency power below ~30 Hz (Greenberg et al., 2015; Long et al., 2014; Roux et al., 2021; Serruya et al., 2014; Solomon et al., 2019) (Fig. 1A). When examining subsequent memory effects in broadband low-frequency power along with broadband high-frequency power, a notable pattern emerges: broadband low-frequency power decreases exhibit similar spatiotemporal dynamics during successful memory encoding as broadband high-frequency power (Burke et al., 2014; Greenberg et al., 2015; Long et al., 2014; Serruya et al., 2014; Solomon et al., 2019). For example, using a verbal cued-recall task, Greenberg et al. (2015) examined both high- and low-frequency power during the successful encoding of word pairs. They observed that, similar to spatiotemporal dynamics revealed by broadband high-frequency power, decreases in broadband low-frequency power appeared initially in occipital cortices at ~ 500 ms, then in MTL and ventrolateral temporal cortex at ~ 800 ms, and last in PFC at ~ 1000 ms (Fig. 1A).

The comparable spatiotemporal dynamics in high- and low-frequency broadband power indicate that both increased broadband high-frequency power and decreased broadband low-frequency power likely reflect increased neural activity. Indeed, studies have documented that broadband low-frequency power negatively correlates with fMRI BOLD signal (Harvey et al., 2013; Haufe et al., 2018), suggesting that, similar to increases in broadband high-frequency power, decreases in broadband low-frequency power may also index increased neural activity. The opposite direction of changes in broadband high- compared to broadband low-frequency power has been referred to as a tilt in the power spectrum (e.g., Fig. 1B). Indeed, iEEG studies have shown that successful memory encoding is associated with a flatter power spectrum compared to unsuccessful encoding (Burke et al., 2014; Rubinstein et al., 2021), suggesting that a flatter power spectrum may index increased neural activity associated with successful memory formation (for review see Herweg et al., 2020). Taken together, both increases in broadband high-frequency power and decreases in low-frequency power are indices of increased neural activity.

Although broadband spectral power indicates neural activity and as such can be considered a general neural correlate for cognitive processes (for reviews see Burke et al., 2015; Johnson et al., 2020), in this review we highlighted its relevance to memory, and more specifically memory formation. The general role of broadband spectral power is evident when considering the multiple other cognitive processes supporting memory such as those involved in perception, information representation, and cognitive control. Notably similar patterns of spatiotemporal dynamics in spectral power are evident in various other cognitive tasks, such as language processing (Nakai et al., 2017) and working memory (Kambara et al., 2017). In sum, task modulation of broadband spectral
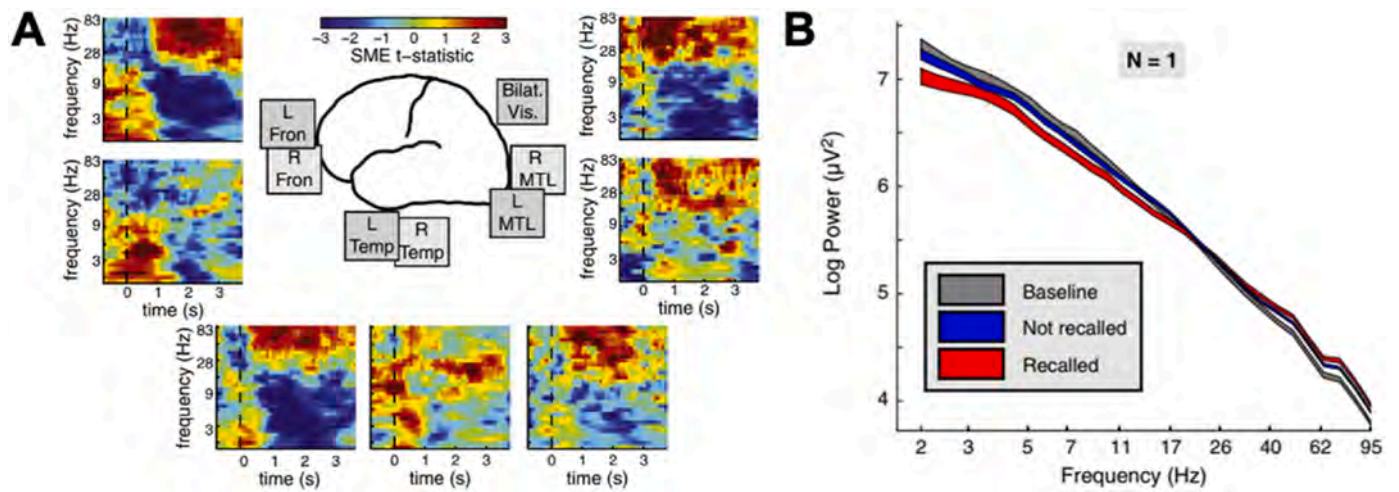
Fig. 1. Spatiotemporal dynamics of memory revealed by broadband spectral power. (**A**) Time-frequency representations of memory formation-related spectral power across key memory regions in a verbal free recall task. (**B**) Average power during the encoding period for subsequently recalled (red), not recalled (blue), and baseline (gray) events from 2 to 95 Hz in one left temporal electrode, showing a flatter power spectrum during successful encoding.
(A) Adapted from Greenberg et al. (2015). (B) Adapted from Burke et al. (2014).

power is likely signature of multiple cognitive processes. The spatio-temporal dynamics observed in key memory brain regions, as revealed by subsequent memory effects, illuminate the coordination of different cognitive processes in support of memory formation.

2.2. More than broadband activity: narrowband neural oscillations in memory

Dissociable from the broadband high- and low-frequency power modulations described above, iEEG studies have reported notable power increases in the theta range (~3–8 Hz) during successful memory encoding (Fell et al., 2011; Kota et al., 2020; Lega et al., 2012; Lin et al., 2017; Sederberg et al., 2003). Theta power increases are mainly observed in the hippocampus (Fell et al., 2011; Kota et al., 2020; Lega et al., 2012, 2016; Lin et al., 2017) (e.g., Fig. 2A) and lateral PFC (Sederberg et al., 2003). Power increases in theta range may be a manifestation of narrowband neural oscillations that play essential roles in facilitating memory encoding (Johnson et al., 2020; Rudoler et al., 2023). The consistently observed power increases in the narrowband theta range during successful memory encoding corroborate the significance of theta oscillations in memory processes.

The widely observed broadband low-frequency power decreases and narrowband theta power increases suggest that spectral power subsequent memory effects consist of both broadband and narrowband effects

(Herweg et al., 2020). As an example, illustrated in Fig. 2B, is a possible scenario in which low-frequency power decreases and narrow band power increases are concomitantly observed in the hippocampus during successful memory encoding. Successful (blue) compared to unsuccessful (grey) encoding may manifest as a flatter power spectrum and thus broadband low-frequency power decreases and high-frequency power increases. Meanwhile, a narrowband neural oscillation in the theta range may manifest as a peak in the power spectrum that is larger for successful compared to unsuccessful encoding and thus the power difference between the peaks results in observed increases in narrowband theta power during successful memory encoding. Indeed, after separating broadband and narrowband activities, Rudoler et al. (2023) observed power increases in narrowband theta (~ 2–5 Hz) and decreases in broadband low-frequency during successful compared to unsuccessful words encoding in the hippocampus.

The above example of hippocampal subsequent memory effects in spectral power demonstrates the involvement of two components of electrophysiological signals in memory: broadband activity and narrowband oscillations. These components are also commonly referred to as aperiodic and periodic components, respectively. Aperiodic activity is arrhythmic and has been termed "background" neural activity; it manifests as a 1/f-like shape in the power spectrum, where power decreases with increasing frequency (B. J. He, 2014). Periodic activity is rhythmic and appears as a peak above the 1/f-like shape in the power
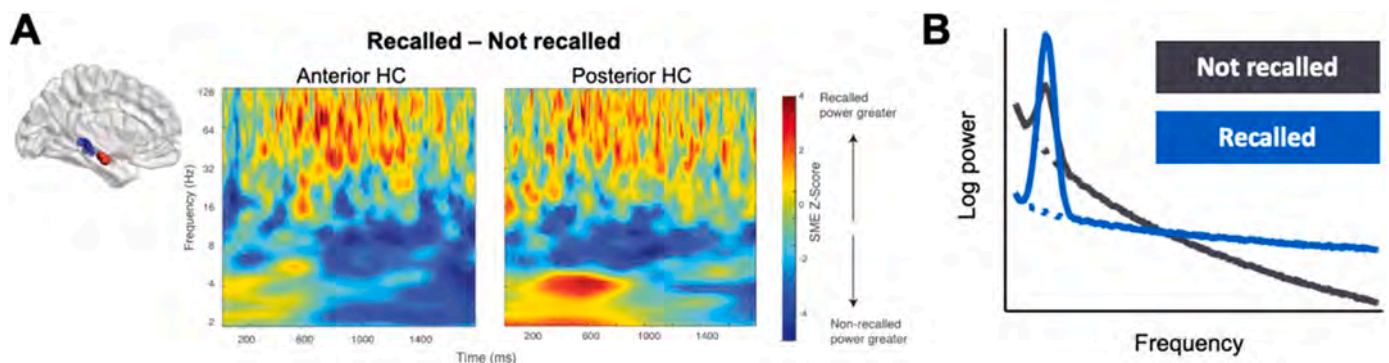

Fig. 2. Narrowband neural oscillations in memory. (**A**) Positive theta subsequent memory effects in the hippocampus during a verbal free recall task. (**B**) Hypothesized hippocampus subsequent memory effects in the power spectrum, demonstrating increased narrowband theta oscillations against a flatter power spectrum during successful memory encoding.
Adapted from Lin et al. (2017).

spectrum (Buzsáki et al., 2013; B. J. He, 2014). Several methods have been developed to disentangle and parameterize aperiodic and periodic activities (Donoghue and Watrous, 2023), aiming to study the distinct functional relevance of these two components in cognition separately (Donoghue et al., 2020; B. J. He, 2014; Herweg et al., 2020).

The aperiodic component can be parameterized with two measures, exponent and offset (Donoghue et al., 2020). The exponent describes the flatness/steepness of the power spectrum and reflects synaptic excitation and inhibition (E:I) balance, with a steeper power spectrum associated with a reduced E:I ratio (Gao et al., 2017; Gerster et al., 2022). Studies have linked the exponent to different cognitive behaviors such as language learning (Cross et al., 2022), working memory capacity (Virtue-Griffiths et al., 2022), processing speed (Ouyang et al., 2020), and cognitive control (Zhang et al., 2023). The offset describes the y-intercept of the power spectrum and changes denote shifts of power across a wide range of frequencies. Studies have linked the offset to neuronal firing rate and cortical activation, with higher offset associated with increased neuronal firing rate and cortical activation (Manning et al., 2009; Miller et al., 2014). The offset has also been shown to correlate with memory performance (Sheehan et al., 2018).

The periodic component can be parameterized with three measures, center frequency, aperiodic-adjusted power, and bandwidth (Donoghue et al., 2020). Peak center frequency has been most widely studied and linked to cognitive task performance. For example, peak alpha frequency, i.e., the center frequency of the largest peak in the scalp EEG, is associated with visual perception precision (Samaha and Postle, 2015), working memory load (Haegens et al., 2014), and general intelligence (Grandy et al., 2013). Aperiodic-adjusted power is the power of the peak relative to the 1/f-like shape. Bandwidth is the width of the peak.

Notably, in developmental studies, age differences have been documented in these parameters (for review see Ostlund et al., 2022). For example, studies that explicitly parameterized the power spectrum have reported age-related decreases in the exponent and offset (Cellier et al., 2021; Hill et al., 2022), indicating that the power spectrum flattens with development. Studies that parameterize neural oscillations have consistently reported age-related increases in peak alpha frequency (for meta-analysis see Freschl et al., 2022), showing that the alpha frequency increases quickly in early childhood and stabilizes at ~10 Hz in adolescence at approximately 13 years. No age differences have been observed in aperiodic-adjusted peak alpha power (Cellier et al., 2021; Hill et al., 2022; Schaworonkow and Voytek, 2021). The relationship between age differences in these parameters and memory and cognitive development, in general, remains largely unknown. Moreover, few studies have explicitly investigated the links between aperiodic-adjusted power or bandwidth and cognitive functions which may hold relevance in developmental studies and are thus a target for future work.

In this section, we reviewed key aspects of the spatiotemporal dynamics of activity across key brain regions during successful memory encoding and highlighted the dissociable involvement of broadband activity and narrowband oscillations in memory. We next review new findings about brain development gained by leveraging broadband high-frequency spectral activity and the temporal information it provides. In later sections, we come back to review neurophysiological mechanisms of memory formation that are tied to neural oscillations and novel findings about brain development gleaned from studying the development of neural oscillations.

3. Broadband high-frequency power indexes spatiotemporally precise activity in the developing brain

In the first iEEG study of memory in children and adolescents, Johnson et al. (2018) sought to build on fMRI memory development research (Ofen et al., 2007; Tang et al., 2018). They measured broadband high-frequency power (30–250 Hz) to examine the spatiotemporal dynamics of frontal regions during memory formation in a sample of 17 patients aged 6–19 years. In this task, subjects studied pictures of scenes

(3 s each) and indicated whether each picture depicted an "indoor" or "outdoor" scene in preparation for a recognition test (Fig. 3A). The authors first showed that broadband high-frequency power tracks indoor/outdoor responses in the developing PFC (i.e., inferior, middle, and superior frontal gyri [IFG, MFG, SFG]) and precentral gyrus (PCG), with peak high-frequency power occurring before the response on the single-trial level (Fig. 3B). Moreover, the timing of IFG, MFG, and PCG activity, as measured by the latency of peak high-frequency power relative to scene onset, predicted task performance, with a shorter latency predicting better memory performance. The timing of IFG activity partially explained age-related gains in performance (Fig. 3C), suggesting increased PFC control during memory formation with development.

Having demonstrated the importance of the timing of PFC activity to memory formation, Johnson et al. (2018) further investigated the timing of activity in frontal subregions relative to each other. To do this, they computed cross-correlations of broadband high-frequency power and found that the spatiotemporal propagation of activity among frontal subregions predicted subsequent memory. For example, successful compared to unsuccessful memory encoding was associated with earlier PCG relative to IFG activity before response onset (Fig. 3D). At response onset, increased IFG-PCG coactivation explained age-related gains in memory performance (Fig. 3D). These discoveries illustrate that behaviorally relevant shifts in the spatiotemporal propagation of frontal activity are refined with age, providing further evidence suggesting increased PFC control during memory formation with development.

Consistent with the protracted development of PFC observed in fMRI studies (Ofen et al., 2007; Tang et al., 2018), these findings add novel insights into how the development of PFC supports the development of episodic memory. Specifically, they highlight increased precision of neural activity and coordination among frontal regions with development, an important aspect of brain and cognitive development that could only be discovered by applying iEEG to study the developing brain.

4. Oscillatory mechanisms underlying successful memory encoding

Neural oscillations underlie memory by coordinating neural activity within and across brain regions. In this section, we present key notions and empirical iEEG findings that highlight a role for oscillations in coordinating the precision of neural activity and its importance for memory formation. We focus on two oscillatory mechanisms, cross-frequency phase-amplitude coupling (PAC) and inter-regional oscillation phase synchrony. These mechanisms are posited to coordinate neural activity within and across brain regions to support information representation and transfer (Buzsáki, 2005; Fries, 2005, 2015; Lisman and Jensen, 2013), as well as inter-regional interactions (Hasselmo and Stern, 2014; Helfrich and Knight, 2016).

4.1. Oscillatory mechanisms underlying intra-regional processing

Cross-frequency PAC underlies intra-regional information and mnemonic representation. PAC is a ubiquitous neurophysiological phenomenon in which higher-frequency amplitude is modulated by lower-frequency phase (Fig. 4A). It is viewed as a critical mechanism of efficient local cortical processing (Canolty and Knight, 2010). Here, we focus on theta oscillations in MTL (including the hippocampus and surrounding structures) and alpha oscillations in occipital cortex to review how neural oscillations underlie memory formation by facilitating local information processing and mnemonic representation.

4.1.1. Theta-gamma coupling and mnemonic representation

As the predominant neural oscillations in MTL, theta has been linked to memory and various MTL-dependent cognitive functions (Herweg et al., 2020; Herweg and Kahana, 2018; Johnson et al., 2020).
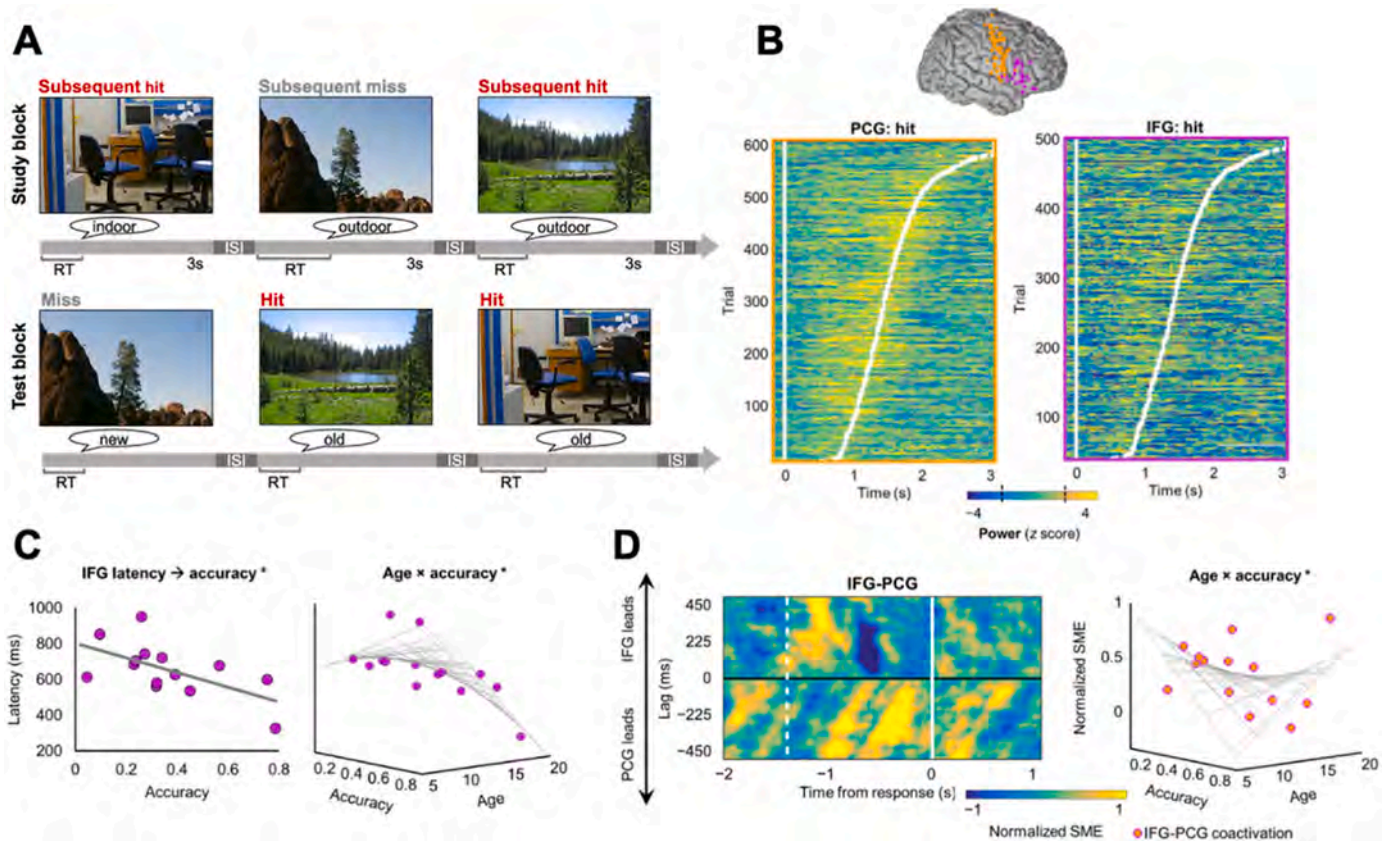
Fig. 3. Broadband high-frequency power indexes the spatiotemporal dynamics of behavioral responses in the developing brain. (A) Subsequent memory paradigm. During the study block, subjects study picture of scenes and indicate whether each scene is "indoor" or "outdoor" in preparation for a memory recognition test. During the test block, subjects indicate whether they recognize each scene by responding "old" or "new". (B) Top: electrode coverage in PCG and IFG. Bottom: broadband high-frequency activity (30–250 Hz) in PCG and IFG during the encoding of subsequently recognized scenes from all subjects, sorted by the onset of the behavioral indoor/outdoor response of each trial (white ticks). The vertical line at 0 s indicates scene onset. (C) Left: earlier IFG peak latency, measured by the latency of peak high-frequency power relative to scene onset, predicted superior memory performance. Right: the negative correlation between peak IFG latency and memory performance explained superior performance in adolescents. (D) Left: Subsequent memory effects in the cross-correlation of broadband high-frequency power between IFG and PCG. Here, cross-correlation was calculated with 500-ms epochs of power shifted with 25-ms temporal lags. The vertical line at 0 s indicates the response onset and the dashed line indicates the average scene onset. Right: The cross-correlation effect at response explained superior memory performance in adolescents. PCG, precentral gyrus. IFG, inferior frontal gyrus.
Adapted from Johnson et al. (2018).

Theta-gamma PAC has been widely studied and is proposed as a mechanism to support information representation and binding in the hippocampus, and thus supports forming associations in memory (Buzsáki, 2005; Lisman and Jensen, 2013).

This proposal is inspired by the observed phase precession in rodents during spatial navigation (O'Keefe and Recce, 1993). Phase precession refers to the temporal relationship between neuronal spiking and ongoing theta oscillations in the hippocampus. In this phenomenon, a place cell fires earlier and earlier relative to the peak of the theta cycle on successive theta cycles as the rodent runs towards a specific location, until it fires at its maximum rate at the trough of the theta cycle on entering the place field (O'Keefe and Recce, 1993). Phase precession observed in rodents provides important insights into theta phase coding of sequential information, such as ordered items or events. Phase precession suggests that one place cell representing the current location fires at the trough of the theta cycle while other place cells representing different locations fire at different theta phases within the same theta cycle, resulting in several cells representing different items firing within the same theta cycle (Buzsáki, 2005; Lisman and Jensen, 2013). It is therefore hypothesized that theta cycles organize a sequence of locations in spatial navigation or items in episodic memory. The nesting of neuronal spiking and by extension of high-frequency broadband or gamma activity within the theta cycle is thought to represent individual

items and the temporal or spatial relationship among these items (Buzsáki, 2005; Buzsáki and Moser, 2013; Lisman and Jensen, 2013). This hypothesis emphasizes the importance of coupling between local neural activity and ongoing theta oscillations in supporting memory.

iEEG studies of memory have reported coupling between hippocampal theta oscillations and neuronal spiking or gamma activity during successful memory formation. For example, Rutishauser et al. (2010) analyzed the coupling of single-unit neuronal activity and theta oscillations in the hippocampus while subjects performed a picture subsequent memory task. They found that neuronal spiking was phase-locked to theta oscillations at ~5 Hz, with stronger spike-field coupling during the encoding of subsequently recognized compared to unrecognized pictures. Likewise, in a verbal free recall task, Lega et al. (2016) observed greater PAC between hippocampal slow theta oscillations (2.5–5 Hz) and gamma (34–140 Hz) activity during successful compared to unsuccessful word encoding (but see Vaz et al., 2017) (Fig. 4A). These findings suggest that hippocampal theta oscillations coordinate local neural activity to facilitate successful memory encoding.

4.1.2. Alpha-gamma coupling and information representation
In line with the suggested functional role of theta oscillations in organizing items in memory (Buzsáki, 2005; Lisman and Jensen, 2013),
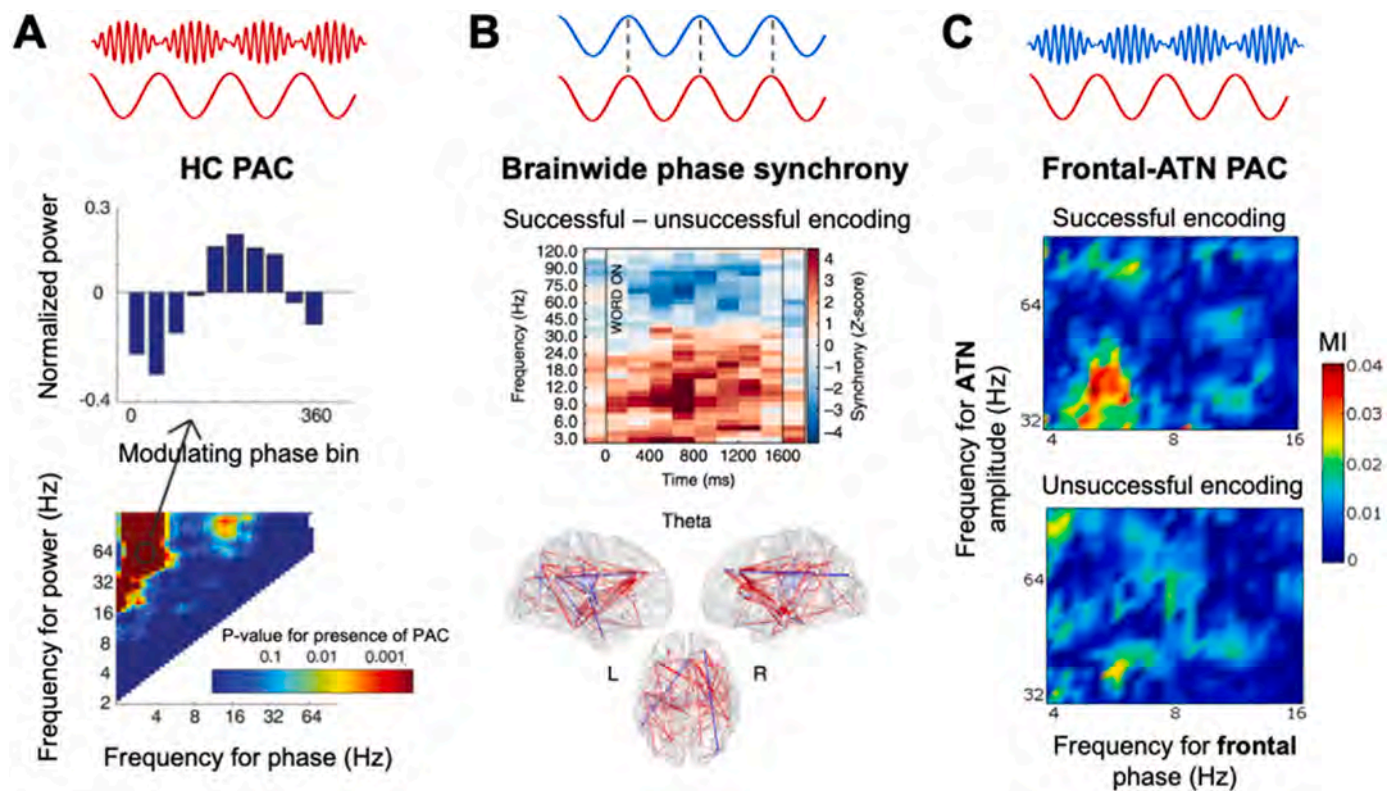
Fig. 4. Oscillatory mechanisms underlying memory encoding. (**A**) Top: schematic illustration of intra-regional cross-frequency PAC. Middle and bottom: HC gamma power was coupled to the phase of slow theta (~4 Hz) in one HC example electrode, indicating cross-frequency PAC during word encoding. (**B**) Top: schematic illustration of inter-regional phase synchrony. Middle: increased brain-wide low-frequency phase synchrony during successful compared to unsuccessful encoding of words. Bottom: whole-brain theta (~3–8 Hz) networks during successful compared to unsuccessful encoding. Red indicates increased synchrony associated with successful encoding, and blue indicates decreased synchrony. (**C**) Top: schematic illustration of inter-regional cross-frequency PAC. Middle and bottom: increased frontal-ATN theta-gamma PAC during successful compared to unsuccessful encoding of visual scenes. PAC, phase-amplitude coupling. HC, hippocampus. ATN, anterior thalamic nucleus.
(A) Adapted from Lega et al. (2016). (B) Adapted from Solomon et al. (2017). (C) Adapted from Sweeney-Reed et al. (2014).

alpha-gamma PAC is also viewed as a mechanism for representing and organizing complex visual information within occipital cortex (Bonnefond et al., 2017; Jensen et al., 2014). For instance, Jensen et al. (2014) proposed that items within a complex visual scene are processed sequentially based on the features of these items, such as contrast and salience. Consequentially, neurons representing different items fire sequentially and at distinct phases of one alpha cycle, and thus the spatial representation of visual scenes is transformed into a temporal code. Similar to theta-gamma PAC, the temporal code is expressed as alpha-gamma PAC at the neuronal population level and is subsequently processed and represented by downstream regions, such as the hippocampus (Jensen et al., 2014).

Indeed, alpha-gamma PAC has been observed in occipital cortex during visual tasks (Bahramisharif et al., 2018; Voytek et al., 2010). For example, Voytek et al. (2010) examined theta-gamma and alpha-gamma PAC in iEEG data sampling several brain regions during the performance of verbal/auditory and visual tasks. They observed greater alpha-gamma PAC during visual tasks in posterior regions including occipital cortex, compared to anterior regions such as PFC. These findings provide further evidence that alpha-gamma PAC supports visual information processing. In another iEEG study, Bahramisharif et al. (2018) investigated the functional role of alpha-gamma PAC in representing multiple items, here, sequentially presented letters being maintained in working memory. They reported increased alpha-gamma PAC in functionally defined letter-selective sites during the maintenance period. Here, the letter-selective sites were mainly located in occipital, fusiform, and lateral temporal cortices. Similar to the functional relevance of theta oscillations, these findings suggest that alpha oscillations coordinate

local neural activity to facilitate visual information processing and mnemonic representations.

4.2. Oscillatory mechanisms underlying inter-regional interactions

Along with their role in facilitating local information representation, evidence points to neural oscillations coordinating inter-regional interactions that support memory formation. Below we focus on two widely studied mechanisms, inter-regional phase synchrony and inter-regional PAC.

4.2.1. Inter-regional phase synchrony supports information transfer

Phase synchrony describes the consistency of oscillatory phases between different neuronal assemblies or brain regions (Fig. 4B). Because neural oscillations reflect periodic neuronal excitability, consistency in excitability between different neuronal assemblies or brain regions provides optimal time windows for communication (Fell and Axmacher, 2011; Fries, 2005, 2015; Fröhlich and McCormick, 2010; X. J. Wang, 2010). Indeed, phase synchrony is hypothesized to enable communication and information transfer between neural assemblies and brain regions (Fries, 2005, 2015).

Human iEEG studies have consistently reported increased interregional phase synchrony in the theta band during successful memory encoding. For example, Solomon et al. (2017) examined phase synchrony between widespread cortical regions in a verbal free recall task. They observed that successful compared to unsuccessful word encoding was associated with increased theta phase synchrony across all sampled regions (Fig. 4B). Burke et al. (2013) further reported that, during the

1600-ms word encoding window, increases in theta phase synchrony appeared initially between occipital and temporal cortices immediately after word onset, and then across widespread regions at ~ 250 ms before concentrating in frontal cortex at ~ 500 ms. These findings suggest that theta phase synchrony coordinates information transfer across brain regions during successful memory formation.

In addition to widespread theta synchrony, iEEG studies have documented theta phase synchrony among MTL subregions (i.e., perirhinal and entorhinal cortices and the hippocampus) during successful memory encoding (Fell et al., 2003; Solomon et al., 2019). Increases in theta synchrony exhibit spatiotemporal dynamics. For example, Solomon et al. (2019) observed that, during the 1600-ms word encoding window, perirhinal-entorhinal theta synchrony occurred ~ − 50–300 ms after word onset, preceding entorhinal-CA1 synchrony at ~ 500–900 ms. This finding suggests neocortical-entorhinal-hippocampal information transfer during successful memory formation and underscore the importance of theta phase synchrony in facilitating memory formation.

4.2.2. Inter-regional cross-frequency coupling supports inter-regional interaction

Inter-regional cross-frequency coupling refers to the modulation of higher-frequency amplitude in one brain region by lower-frequency phase in another region, i.e., inter-regional PAC (Fig. 4C). Inter-regional theta PAC is proposed as an important mechanism underlying memory processes (Hasselmo and Stern, 2014) and, more broadly, PFC control during cognitive tasks including but not limited to memory (Helfrich and Knight, 2016).

Studies in animal models suggest that the phases of theta oscillations influence the direction of synaptic plasticity in the hippocampus. Specifically, rodent studies have shown that stimulating the CA1 region at the peak of the theta cycle induced long-term potentiation (LTP) and stimulating at the trough reduced LTP (Hölscher et al., 1997; Huerta and Lisman, 1995; Hyman et al., 2003). These findings led to the proposal of the Separate Phases of Encoding and Retrieval (SPEAR) model (Hasselmo et al., 2002; Hasselmo and Stern, 2014). The SPEAR model states that hippocampal theta oscillations facilitate both memory encoding and retrieval by operating through distinct theta phases. The theta peak favors LTP and supports memory encoding, while the theta trough favors long-term depression and facilitates memory retrieval (Hasselmo et al., 2002; Hasselmo and Stern, 2014). Therefore, the timing of input to the hippocampus relative to the ongoing theta phase may support memory encoding (Axmacher et al., 2006), as well as retrieval.

Recent iEEG studies provide evidence in humans that is consistent with the SPEAR hypothesis. For instance, ter Wal et al. (2021) observed that phase consistency across encoding and retrieval trials during a cued-recall task peaked at the opposite phases of hippocampal theta (~1–5 Hz), corroborating different theta phases favoring encoding and retrieval. In a recent study, Saint Amour di Chanaz et al. (2023) investigated theta-gamma PAC in the hippocampus in a picture-depictured episodic recall task. They found that gamma activity was coupled to the theta (~4–9 Hz) peak during successful encoding and theta trough during successful retrieval. Yoo et al. (2021) further reported that hippocampal and entorhinal neuron spiking was coupled to different theta (~2–5 Hz) phases during encoding and retrieval in a verbal free recall task, suggesting that the SPEAR hypothesis may have relevance beyond the hippocampus. Lastly, Wang et al. (2021) investigated PAC between hippocampal theta phase and gamma activity in other MTL subregions in a verbal free recall task. They observed increased PAC between hippocampal fast theta (~6–8 Hz) and entorhinal and parahippocampal gamma power during successful word encoding, further indicating the importance of hippocampal theta modulating extra-hippocampal gamma activity. Future iEEG studies are needed to test the SPEAR model between the hippocampus and extra-hippocampal regions, yet the mounting evidence is consistent in supporting the importance of theta-gamma PAC between MTL regions to memory.

Besides PAC between the hippocampus and other MTL subregions, inter-regional PAC subsequent memory effects have been documented between PFC and other brain regions. For example, using scalp EEG, Friese et al. (2013) reported increased PAC between frontal theta (~5–8 Hz) phase and parietal-occipital gamma (~50–80 Hz) power during the successful compared to unsuccessful encoding of visual stimuli. PAC between frontal theta (at individually defined frequencies) phase and posterior gamma (30–70 Hz) power subsequent memory effects have also been reported in a scalp EEG study of working memory (Jones et al., 2020). Finally, in a study using both scalp EEG and iEEG, Sweeney-Reed et al. (2014) found that the successful encoding of scenes was associated with PAC between theta (~5–6 Hz) phase in frontal scalp channels and gamma (~30–50 Hz) power in the anterior thalamic nucleus (Fig. 4C). Taken together, these findings demonstrate the importance of theta phase modulation of inter-regional gamma activity to memory encoding and suggest that PFC theta phase supports top-down control over other brain regions during successful memory formation.

Findings from recording iEEG while subjects are performing memory tasks highlight the importance of neural oscillations in memory. Modulating neural oscillations via oscillatory entrainment can further demonstrate causal relationships between neural oscillations and memory (for review see Hanslmayr et al., 2019) and has been shown to improve cognition (Grover et al., 2023). Similar to frequency modulation through noninvasive stimulation (e.g., transcranial current stimulation tACS), neural oscillations can be modulated by stimulating iEEG electrodes at specific frequencies. Then, by correlating iEEG measures with cognitive performance during or following stimulation, researchers can infer causal relationships between neural oscillations and memory (for reviews see Ezzyat and Rizzuto, 2018; Johnson et al., 2020; Suthana and Fried, 2014). For example, by stimulating the amygdala in the theta range (specifically, 50-Hz pulses at 8 Hz) immediately after object encoding on some trials, Inman et al. (2018) observed improved object recognition the next day for on-stimulation compared to no-stimulation trials. The authors further reported increased theta synchrony and theta-gamma PAC within the amygdala-MTL circuit, thus demonstrating a causal mechanism by which theta oscillations support memory.

In a similar vein, neural oscillations can be modulated through sensory entrainment, achieved by rhythmically changing specific aspects of the stimuli, such as luminance. One iEEG study demonstrated that auditory beats altered neural oscillations not only in auditory regions but also in key memory regions, such as MTL (Becher et al., 2015). Moreover, several scalp EEG studies have shown that sensory entrainment in the theta range (~5 Hz) can facilitate memory performance (Clouter et al., 2017; Köster, Martens et al., 2019; Roberts et al., 2018; Wang et al., 2018) as well as increase theta power (Roberts et al., 2018), theta-gamma PAC (Köster, Martens et al., 2019), and theta synchrony (Clouter et al., 2017; Wang et al., 2018) in sensory regions, corroborating the functional role of theta oscillations in memory. However, due to its limited spatial resolution and inability to record from deep brain regions like the hippocampus, studies using scalp EEG-based sensory entrainment fall short of revealing spatially precise entrainment effects on memory. Future studies integrating sensory entrainment with iEEG may unveil entrainment effects in the hippocampus and other key memory regions to further infer causal links between neural oscillations and memory.

In sum, findings from human iEEG studies not only underscore the importance of precisely timed neural activity and oscillations in memory, but also showcase the immense potential of utilizing iEEG to test theories and bridge findings from animal studies. Converging evidence from animal literature, theoretical frameworks, and iEEG and scalp EEG studies highlights the important roles of neural oscillations in coordinating neural activity to support local processing and inter-regional interactions during memory encoding. In the next section, we turn to review evidence for the development of neural oscillations and present emerging iEEG evidence linking the development of neural oscillations to memory development.

5. Development of neural oscillations and oscillatory mechanisms of memory formation

Building upon evidence from scalp EEG, iEEG studies in children and adolescents reported age differences in oscillation frequencies in key memory regions, including PFC, MTL, and occipital cortex. These intriguing discoveries raise important questions about the links between the development of neural oscillations and the development of memory. Below, we present EEG and iEEG evidence of developmental differences in oscillation frequencies. We then present emerging evidence linking the development of neural oscillations to the development of memory from the burgeoning field of developmental iEEG. We argue that the development of neural oscillations may increase the precision of coordination within and between brain regions, and thus contribute to memory development by refining oscillatory mechanisms of information encoding, representation, and transfer.
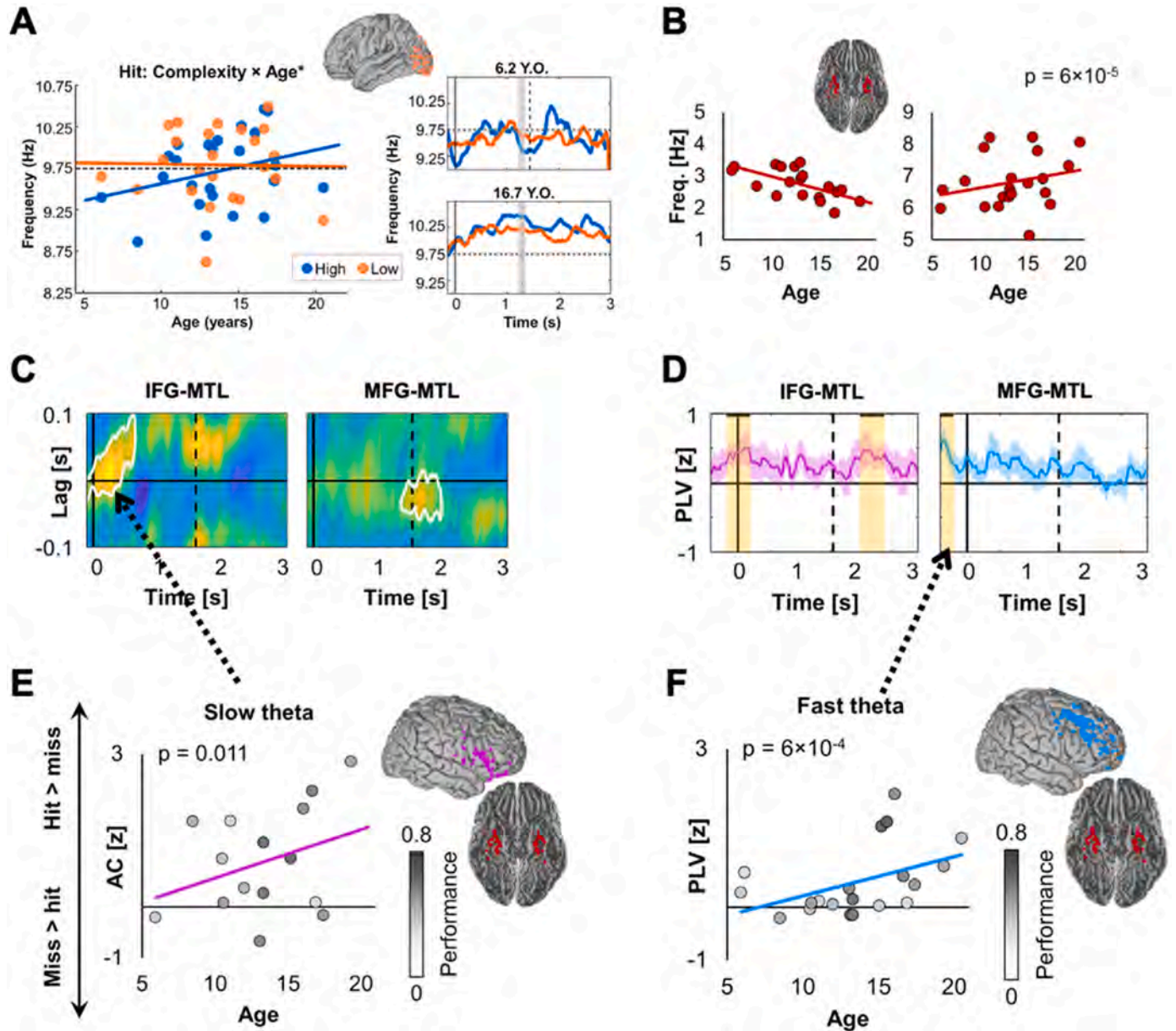

Fig. 5. Development of neural oscillations and oscillatory mechanisms of memory formation. (A) Left: occipital time-resolved peak alpha frequency increased with age during the successful encoding of complex visual scenes (blue). Here, high and low are the two levels of scene complexity defined by the number of unique object categories (high: > 4; low: < 4) depicted in each scene. Right: time-resolved peak alpha frequency of two representative subjects during successful scene encoding. Shaded areas indicate the time window from which the age-related increase in peak alpha frequency was observed in high- but not low-complexity scenes. (B) MTL slow and fast theta differentiated in frequency with age in a double dissociation. The p value indicates a significant interaction of oscillation (slow vs. fast theta) by age. (C) Cluster-corrected subsequent memory effects in IFG-MTL and MFG-MTL slow theta amplitude coupling. Here, amplitude coupling was calculated with cross-correlation across 500-ms epochs of amplitude shifted with 1-ms temporal lag. The vertical line at 0 s indicates the scene onset, and the dashed line indicates the average response onset. (D) Cluster-corrected subsequent memory effects in IFG-MTL and MFG-MTL fast theta phase synchrony. The vertical line at 0 s indicates the scene onset, and the dashed line indicates the average response onset. (E) The IFG-MTL slow theta amplitude coupling subsequent memory effects preceding scene onset explained age-related variability in memory. (F) The MFG-MTL fast theta phase synchrony preceding scene onset explained age-related variability in memory.

(A) Adapted from Yin et al. (2020). (B-F) adapted from Johnson et al. (2022).

5.1. Development of neural oscillations

Alpha activity has long been a topic of interest in developmental EEG studies given its predominance in scalp EEG recordings. By measuring peak alpha frequency during resting-state recordings, scalp EEG studies have consistently reported that posterior peak alpha oscillations speed up during development, from ~4 Hz in infancy to ~8 Hz in early childhood to ~10 Hz in early adolescence (for a meta-analysis see Freschl et al., 2022). For example, in an early EEG study, Lindsley (1939) examined longitudinal changes in alpha frequency in subjects between one month to 16 years old. The author reported that posterior alpha emerged at ~4 Hz at three months and increased to ~6 Hz at one year, showing a quick increase in alpha frequency in the first year. Alpha frequency continued to increase with smaller and smaller annual changes until it stabilized at ~10 Hz at 12 years. Many EEG studies have since reported similar age-related increases in peak alpha frequency during rest (Cellier et al., 2021; Chiang et al., 2011; Cragg et al., 2011; Henry and Greulich, 1944; Hill et al., 2022; Marcuse et al., 2008; Marshall et al., 2002; Miskovic et al., 2015; Perone et al., 2018; Schaworonkow and Voytek, 2021; Stroganova et al., 1999), indicating robust developmental effects on posterior alpha oscillations.

With iEEG recordings of occipital cortex, Yin et al. (2020) examined age differences in time-resolved peak alpha frequency, i.e., instantaneous alpha frequency, during scene encoding in 24 subjects aged 6–21 years (see Section 3 and Fig. 3A for task description). They observed an age-related increase in peak occipital alpha frequency during the successful encoding of complex visual stimuli (Fig. 5A), linking the development of alpha frequency to the development of visual information processing in occipital cortex. In that study, the age-related increase in instantaneous occipital alpha frequency did not explain age-related increases in memory performance, but the authors concluded that it underlies memory development indirectly by speeding up the processing of complex visual information during encoding (Yin et al., 2020). As we explain in our concluding remarks, it is worth noting that the small sample size may limit observing links between neurophysiology and performance. Future research with larger samples is one direction that will help establish such links (Johnson et al., 2022; Johnson and Knight, 2023). More broadly, iEEG findings critically increase what has been documented with resting scalp EEG. Although scalp EEG findings during rest indicate that peak alpha frequency stabilizes at ~10 Hz in early adolescence, the task-related occipital alpha from Yin et al. (2020) shows a continued increase until at least 21 years, suggesting that the development of visual attention impacts the alpha frequency to support cognitive tasks.

In addition to well-established developmental effects on the posterior alpha frequency, findings from a recent iEEG study of 21 subjects aged 5–21 years performing the same scene subsequent memory task extend the developmental effects on neural oscillations to theta frequencies (Johnson et al., 2022). After isolating oscillatory components from aperiodic 1/f-like activity, Johnson et al. (2022) discovered that both MTL and PFC exhibit two distinct oscillations during scene encoding, slow theta at ~3 Hz and fast theta at ~7 Hz. These findings indicate that theta oscillations dominate MTL and PFC during scene encoding in the developing brain. Critically, the authors further discovered distinct age-related differences in these two oscillations, such that slow theta slowed down with age, while fast theta sped up (Fig. 5B). These findings have several important implications for developmental research. First, the age differences observed in theta oscillations in MTL and PFC suggest that developmental effects on neural oscillations are global, and not limited to the alpha band or posterior brain regions. Second, the detected slow and fast theta oscillations suggest that key memory brain regions exhibit multiple oscillations. Third, the distinct developmental effects on slow and fast theta frequencies suggest that brain development manifests not only by speeding up oscillations but also by separating different oscillations within the same brain regions.

Developmental studies have also examined age differences on oscillation power. Of note, most studies examining the age differences on oscillation power used canonical frequency bands (e.g., alpha between ~8–13 Hz). For example, besides time-resolved alpha frequency, Yin et al. (2020) also reported an age-related decrease in the occipital band-limited alpha (~7–14 Hz) power during successful encoding of complex visual stimuli. Moreover, the authors showed that the age-related decrease in alpha power explained age-related increase in memory performance. Specifically, top-performing adolescents had the most decreased alpha power compared to both lower-performing adolescents and children. Recent studies explicitly parameterizing power spectrum in EEG recording during rest have observed no age differences in aperiodic-adjusted alpha power, i.e., the power of the alpha peak above the aperiodic 1/f-like component (Cellier et al., 2021; W. He et al., 2019; Hill et al., 2022; Schaworonkow and Voytek, 2021). Together with observed age-related decreases in the offset and exponent of the aperiodic component (Cellier et al., 2021; W. He et al., 2019; Hill et al., 2022; Schaworonkow and Voytek, 2021), these findings suggest the age differences in band-limited power may reflect differences in the aperiodic component rather than in the oscillation power.

Taken together, these findings suggest that developmental effects on neural oscillations primarily manifest as age-related differences in oscillation frequencies, i.e., oscillations speeding up or slowing down with development, while the oscillation power remains relatively stable over development. In the next subsection, we review emerging iEEG evidence linking the development of neural oscillations to the development of memory.

5.2. Linking the development of neural oscillations to the development of memory

Developmental effects on oscillation frequencies hold significant implications for studying brain development and links between brain development and memory development. As reviewed above in Section 4, neural oscillations provide the functional infrastructure for intra-regional processing and inter-regional interactions during memory formation. The development of neural oscillations may thus underlie the maturation of oscillatory mechanisms underlying memory formation and consequently contribute to developmental gains in memory.

Having identified age differences in slow and fast theta frequencies in MTL and PFC, Johnson et al. (2022) further investigated the link between oscillatory mechanisms and age differences in memory. Using individually detected slow and fast theta oscillations, the authors uncovered two distinct mechanisms underlying MTL and PFC interaction that support successful memory encoding: slow theta amplitude coupling and fast theta phase synchrony. Successful encoding was associated with increased MTL-IFG slow theta amplitude coupling in a time window immediately preceding scene onset, and MTL-MFG slow theta amplitude coupling in a time window around the indoor/outdoor response (Fig. 5C). Successful encoding was also associated with increased MTL-IFG fast theta phase synchrony in a time windows preceding scene onset and following the response, and increased MTL-MFG fast theta phase synchrony in a time window preceding scene onset (Fig. 5D). These effects in slow theta amplitude coupling and fast theta phase synchrony did not overlap in time, further suggesting two distinct yet complementary mechanisms of memory formation.

Critically, the authors found that the strength of both inter-regional interaction mechanisms explained age-related variability in memory performance. Specifically, both MTL-IFG slow theta amplitude coupling subsequent memory effect preceding scene onset (Fig. 5E), and MTL-MFG fast theta phase synchrony subsequent memory effect preceding scene onset explained age-related variability in memory (Fig. 5F). In both effects, top-performing adolescents exhibited stronger inter-regional interactions during successful memory encoding than lower-performing adolescents and children, demonstrating that the maturation of oscillatory interactions between key memory regions contributes to memory development.

Considered together with developmental effects observed in slow and fast theta frequencies, these findings suggest a three-folded maturation of oscillatory mechanisms supporting memory formation: oscillation frequencies, inter-regional interaction strength, and dissociation between different mechanisms within the same brain regions and networks. The three-folded maturation of MTL-PFC interaction mechanisms may underlie memory development by providing increased precision, strength, and number of channels (i.e., increasingly dissociable oscillatory mechanisms) of memory encoding.

These findings provide invaluable yet initial evidence for the link between the development of neural oscillations and the development of memory. The link needs to be further examined. Given the scarcity of iEEG studies in pediatric patients, the above reviewed developmental iEEG studies are based on sample sizes (i.e., n < 25) that may limit the ability to detect small effects or generalize findings to the broader population. Multi-site collaboration and data sharing hold immense promise for increasing sample sizes (Johnson et al., 2022; Johnson and Knight, 2023; Ofen et al., 2019). Additionally, comparing the behavioral performance of patients to that of age-matched, non-clinical samples on the same tasks and obtaining neuropsychological assessments may inform the generalizability of iEEG findings (Johnson and Knight, 2023). Extending investigations beyond MTL-PFC circuits and integrating developmental iEEG with scalp EEG and MEG will further increase the generalizability of developmental iEEG findings.

Here, we propose that the development of neural oscillations may underlie the maturation of intra-regional and inter-regional oscillatory mechanisms and consequently contribute to developmental gains in memory. Alternatively, the relationship between oscillations and such mechanisms might be reversed or bidirectional, indicative of a fundamental aspect of brain development that contributes to memory. Because oscillations and oscillatory mechanisms are inherently intertwined, it is difficult to disentangle their unique contributions. Indeed, studies have shown that both oscillations and oscillatory mechanisms contribute to memory and cognition broadly (see Section 4), posing challenges in determining causal relationships. Nonetheless, future studies utilizing neuromodulation methods such as sensory entrainment may inform causal links between neural oscillations and memory in the developing brain. Due to safety considerations, brain stimulation in children and adolescents has primarily been used to treat neurological disorders (for reviews see Antal et al., 2017; Friel et al., 2016). Brain stimulation for research purposes only is not approved for subjects under the age of 18. However, sensory entrainment is safe and has been used to investigate neurocognitive development (e.g., Kabdebon et al., 2022; Köster, Langeloh et al., 2019; Park, 2018). Developmental iEEG combined with sensory entrainment holds immense potential for inferring causal relationships between oscillations, oscillatory mechanisms, and memory. Furthermore, future studies utilizing longitudinal scalp EEG or MEG data (Ofen et al., 2019), linking neurophysiological and structural measures (Johnson et al., 2022; Johnson and Knight, 2023), and employing computational modeling (Quast et al., 2023) may offer valuable insights into causal relationships between oscillations, oscillatory mechanisms, and cognition.

6. Conclusions and future directions

With its uniquely high spatiotemporal resolution, iEEG studies have begun to provide invaluable insights into brain development and how brain development supports memory development. In this review, we presented novel findings from iEEG studies and how these findings contribute to advancing our understanding of brain development and its link to memory development. First, we reviewed the spatiotemporal dynamics of broadband high-frequency activity during memory formation, underscoring the cascade of neural activities among regions of memory networks during memory formation. We then presented novel insights into brain development provided by leveraging broadband high-frequency activity in the developing brain. These insights

illuminate how neural coordination is refined by age and supports memory development.

Second, we reviewed the functional significance of narrowband neural oscillations in memory, demonstrating how oscillations facilitate local processing and inter-regional interactions during successful memory formation. We then reviewed extensive scalp EEG evidence of developmental differences in the frequency of neural oscillations and presented initial iEEG evidence of the protracted development of oscillations in key memory regions during memory encoding. Taken together with these novel findings, we proposed that the development of neural oscillations contributes to the maturation of oscillatory mechanisms supporting memory formation and, consequently, to memory development. We suggest that increased precision of neural coordination is an important aspect of brain development that contributes to developmental gains in memory ability.

In this review, we highlighted iEEG recordings as a powerful tool for studying brain development and how brain development supports the development of memory and cognition more broadly. Several future research directions can benefit from the advantages of iEEG recordings in the developing brain. First, recent theoretical and methodological advances enable the parameterizing of the broadband activity (Donoghue and Watrous, 2023), or aperiodic activity, in the power spectrum. Several studies have demonstrated that the aperiodic component is modulated by different cognitive tasks (e.g., Cross et al., 2022; Ouyang et al., 2020; Sheehan et al., 2018; Virtue-Griffiths et al., 2022; Zhang et al., 2023) and differs with development (Cellier et al., 2021; W. He et al., 2019; Hill et al., 2022; Schaworonkow and Voytek, 2021) and aging (Thuwal et al., 2021; Voytek et al., 2015). Future iEEG studies may investigate if and how the development of the aperiodic component contributes to developmental gains in cognitive functions. Second, findings of developmental effects in posterior alpha oscillations led us to hypothesize that developmental effects on neural oscillations primarily manifest in oscillation frequencies. However, it remains unclear if this pattern holds true for other oscillations or brain regions, such as theta oscillations in MTL and PFC. Moreover, if and how developmental effects in oscillation power contribute to the development of associated oscillatory mechanisms is largely unknown. Future iEEG studies that carefully parameterize neural oscillations in different brain regions may advance our understanding of developmental effects on neural oscillations.

The development of neural oscillations and associated oscillatory mechanisms may reflect changes in brain structure over development. Neuroimaging evidence shows decreased occipital cortical thickness with development (Ducharme et al., 2016), indicating synaptic pruning (Huttenlocher et al., 1982; Johnston et al., 2009). Moreover, peak alpha frequency has been shown to positively correlate white matter integrity in young adults (Jann et al., 2012; Valdés-Hernández et al., 2010). Furthermore, theta-associated oscillatory mechanisms of memory formation have also been shown to positively correlate with white matter integrity in the developing brain (Johnson et al., 2022). Future iEEG studies together with structural measures, such as cortical thickness and white matter integrity, may elucidate how the structural development gives rise to the development of oscillations and the associated oscillatory mechanisms. Another exciting future direction is the inclusion of brain stimulation in iEEG studies. Brain stimulation with iEEG can not only infer causality but also be used to investigate the development of white matter-related properties, such as transmission speed. For example, using cortico-cortical evoked potentials, a stimulation method employed to map effective networks in the human brain, a recent iEEG study nicely demonstrated earlier cortico-cortical evoked potentials with development, providing evidence for faster interregional communication well into adulthood (van Blooijs et al., 2023).

As we highlight the immense possibilities for profound insights from developmental iEEG studies, we must note limitations such as typical sample sizes. Developmental studies must model single-subject data on the group level to identify developmental variability. To achieve a

relatively large sample size to conduct group-level statistical modeling, the above reviewed developmental iEEG studies have taken a region of interest approach by including subjects with electrode coverage of a large anatomical area (e.g., MTL in Johnson et al., 2022; occipital cortex in Yin et al., 2020). Although this approach is based on anatomy, it fails to capture potential developmental variability within functional sub-regions, such as anterior and posterior MTL. Thus, without increasing sample sizes, developmental iEEG studies face a tradeoff between anatomical precision and statistical power (Johnson and Knight, 2023). To resolve the sample size dilemma in future developmental iEEG studies, it has been recommended to interpret results with caution and increase sample sizes through multi-site collaboration and data sharing (Johnson et al., 2022; Johnson and Knight, 2023; Ofen et al., 2019). Another limitation inherent in developmental iEEG studies is the reliance on cross-sectional analyses when assessing age differences. Future investigations may strive to combine developmental iEEG data with other non-invasive imaging methods from larger samples of individuals that are followed longitudinally (Buzzell et al., 2023; Ofen et al., 2019). Last, future research may strive to integrate iEEG data collected from a wide range of tasks, using diverse stimuli and advanced analyses (Sommer et al., 2022), as well as utilize both rest and task-based investigations of neurophysiological signatures in the developing brain. It is our hope that this review builds excitement for the opportunities for novel insights from using iEEG as a tool to understand brain development and how brain development supports the development of cognition across the lifespan.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

No data was used for the research described in the article.

Acknowledgements

References

Antal, A., Alekseichuk, I., Bikson, M., Brockmöller, J., Brunoni, A.R., Chen, R., Cohen, L. G., Dowthwaite, G., Ellrich, J., Flöel, A., Fregni, F., George, M.S., Hamilton, R., Haueisen, J., Herrmann, C.S., Hummel, F.C., Lefaucheur, J.P., Liebetanz, D., Loo, C. K., Paulus, W., 2017. Low intensity transcranial electric stimulation: safety, ethical, legal regulatory and application guidelines. Clin. Neurophysiol. 128 (9), 1774–1809. https://doi.org/10.1016/j.clinph.2017.06.001.

Axmacher, N., Mormann, F., Fernández, G., Elger, C.E., Fell, J., 2006. Memory formation by neuronal synchronization. Brain Res. Rev. 52 (1), 170–182. https://doi.org/10.1016/j.brainresrev.2006.01.007.

Bahramisharif, A., Jensen, O., Jacobs, J., Lisman, J., 2018. Serial representation of items during working memory maintenance at letter-selective cortical sites. PLOS Biol. 16 (8), e2003805 https://doi.org/10.1371/journal.pbio.2003805.

Becher, A.-K., Höhne, M., Axmacher, N., Chaieb, L., Elger, C.E., Fell, J., 2015. Intracranial electroencephalography power and phase synchronization changes during monaural and binaural beat stimulation. Eur. J. Neurosci. 41 (2), 254–263. https://doi.org/10.1111/ejn.12760.

Bhavnani, S., Estrin, G.L., Haartsen, R., Jensen, S.K.G., Gliga, T., Patel, V., Johnson, M. H., 2021. EEG signatures of cognitive and social development of preschool children–a systematic review. PLoS One 16 (2), e0247223. https://doi.org/10.1371/journal.pone.0247223.

Billingsley, R.L., Lou Smith, M., Pat McAndrews, M., 2002. Developmental patterns in priming and familiarity in explicit recollection. J. Exp. Child Psychol. 82 (3), 251–277. https://doi.org/10.1016/S0022-0965(02)00007-3.

Bonnefond, M., Kastner, S., Jensen, O., 2017. Communication between brain areas based on nested oscillations. eNeuro 4 (2). https://doi.org/10.1523/ENEURO.0153-16.2017.

Burke, J.F., Zaghloul, K.A., Jacobs, J., Williams, R.B., Sperling, M.R., Sharan, A.D., Kahana, M.J., 2013. Synchronous and asynchronous theta and gamma activity during episodic memory formation. J. Neurosci. 33 (1), 292–304. https://doi.org/10.1523/JNEUROSCI.2057-12.2013.

Burke, J.F., Long, N.M., Zaghloul, K.A., Sharan, A.D., Sperling, M.R., Kahana, M.J., 2014. Human intracranial high-frequency activity maps episodic memory formation in space and time. NeuroImage 85, 834–843. https://doi.org/10.1016/j.neuroimage.2013.06.067.

Burke, J.F., Ramayya, A.G., Kahana, M.J., 2015. Human intracranial high-frequency activity during memory processing: Neural oscillations or stochastic volatility? Curr. Opin. Neurobiol. 31, 104–110. https://doi.org/10.1016/j.conb.2014.09.003.

Buzsaki, G., Draguhn, A., 2004. Neuronal oscillations in cortical networks. Science 304 (June), 1926–1929.

Buzsáki, G., 2005. Theta rhythm of navigation: link between path integration and landmark navigation, episodic and semantic memory. Hippocampus 15 (7), 827–840. https://doi.org/10.1002/hipo.20113.

Buzsáki, G., Moser, E.I., 2013. Memory, navigation and theta rhythm in the hippocampal-entorhinal system. Nat. Neurosci. 16 (2), 130–138. https://doi.org/10.1038/nn.3304.

Buzsáki, G., Anastassiou, C.A., Koch, C., 2012. The origin of extracellular fields and currents-EEG, ECoG, LFP and spikes. Nat. Rev. Neurosci. 13 (6), 407–420. https://doi.org/10.1038/nrn3241.

Buzsáki, G., Logothetis, N., Singer, W., 2013. Scaling brain size, keeping timing: evolutionary preservation of brain rhythms. Neuron 80 (3), 751–764. https://doi.org/10.1016/j.neuron.2013.10.002.

Buzzell, G.A., Morales, S., Valadez, E.A., Hunnius, S., Fox, N.A., 2023. Maximizing the potential of EEG as a developmental neuroscience tool. Dev. Cogn. Neurosci. 60, 101201 https://doi.org/10.1016/j.dcn.2023.101201.

Canolty, R.T., Knight, R.T., 2010. The functional role of cross-frequency coupling. Trends Cogn. Sci. 14 (11), 506–515. https://doi.org/10.1016/j.tics.2010.09.001.

Cellier, D., Riddle, J., Petersen, I., Hwang, K., 2021. The development of theta and alpha neural oscillations from ages 3 to 24 years. Dev. Cogn. Neurosci. 50, 100969 https://doi.org/10.1016/j.dcn.2021.100969.

Chiang, A.K.I., Rennie, C.J., Robinson, P.A., van Albada, S.J., Kerr, C.C., 2011. Age trends and sex differences of alpha rhythms including split alpha peaks. Clin. Neurophysiol. 122 (8), 1505–1517. https://doi.org/10.1016/j.clinph.2011.01.040.

Clayton, M.S., Yeung, N., Cohen Kadosh, R., 2018. The many characters of visual alpha oscillations. Eur. J. Neurosci. 48 (7), 2498–2508. https://doi.org/10.1111/ejn.13747.

Clouter, A., Shapiro, K.L., Hanslmayr, S., 2017. Theta phase synchronization is the glue that binds human associative memory. e6 Curr. Biol. 27 (20), 3143–3148. https://doi.org/10.1016/j.cub.2017.09.001.

Cragg, L., Kovacevic, N., McIntosh, A.R., Poulsen, C., Martinu, K., Leonard, G., Paus, T., 2011. Maturation of EEG power spectra in early adolescence: a longitudinal study. Dev. Sci. 14 (5), 935–943. https://doi.org/10.1111/j.1467-7687.2010.01031.x.

Cross, Z.R., Corcoran, A.W., Schlesewsky, M., Kohler, M.J., Bornkessel-Schlesewsky, I., 2022. Oscillatory and aperiodic neural activity jointly predict language learning. J. Cogn. Neurosci. 34 (9), 1630–1649. https://doi.org/10.1162/jocn_a_01878.

Cycowicz, Y.M., Friedman, D., Snodgrass, J.G., Duff, M., 2001. Recognition and source memory for pictures in children and adults. Neuropsychologia 39 (3), 255–267. https://doi.org/10.1016/S0028-3932(00)00108-1.

Dirks, J., Neisser, U., 1977. Memory for objects in real scenes: the development of recognition and recall. J. Exp. Child Psychol. 23 (2), 315–328. https://doi.org/10.1016/0022-0965(77)90108-4.

Donoghue, T., Haller, M., Peterson, E.J., Varma, P., Sebastian, P., Gao, R., Noto, T., Lara, A.H., Wallis, J.D., Knight, R.T., Shestyuk, A., Voytek, B., 2020. Parameterizing neural power spectra into periodic and aperiodic components. Nat. Neurosci. 23 (12), 1655–1665. https://doi.org/10.1038/s41593-020-00744-x.

Ducharme, S., Albaugh, M.D., Nguyen, T.V., Hudziak, J.J., Mateos-Pérez, J.M., Labbe, A., Evans, A.C., Karama, S., Brain Development Cooperative Group, 2016. Trajectories of cortical thickness maturation in normal brain development—The importance of quality control procedures. NeuroImage 125, 267–279. https://doi.org/10.1016/j.neuroimage.2015.10.010.

Ezzyat, Y., Rizzuto, D.S., 2018. Direct brain stimulation during episodic memory. Curr. Opin. Biomed. Eng. 8, 78–83. https://doi.org/10.1016/j.cobme.2018.11.004.

Fedele, T., Tzovara, A., Steiger, B., Hilfiker, P., Grunwald, T., Stieglitz, L., Jokeit, H., Sarnthein, J., 2020. The relation between neuronal firing, local field potentials and hemodynamic activity in the human amygdala in response to aversive dynamic visual stimuli. NeuroImage 213, 116705. https://doi.org/10.1016/j.neuroimage.2020.116705.

Fell, J., Axmacher, N., 2011. The role of phase synchronization in memory processes. Nat. Rev. Neurosci. 12 (2), 105–118. https://doi.org/10.1038/nrn2979.

Fell, J., Klaver, P., Elfadil, H., Schaller, C., Elger, C.E., Fernández, G., 2003. Rhinal-hippocampal theta coherence during declarative memory formation: Interaction with gamma synchronization? Eur. J. Neurosci. 17 (5), 1082–1088. https://doi.org/10.1046/j.1460-9568.2003.02522.x.

Fell, J., Ludowig, E., Staresina, B.P., Wagner, T., Kranz, T., Elger, C.E., Axmacher, N., 2011. Medial temporal theta/alpha power enhancement precedes successful memory encoding: Evidence based on intracranial EEG. J. Neurosci. 31 (14), 5392–5397. https://doi.org/10.1523/JNEUROSCI.3668-10.2011.

Fiebelkorn, I.C., Kastner, S., 2019. A rhythmic theory of attention. Trends Cogn. Sci. 23 (2), 87–101. https://doi.org/10.1016/j.tics.2018.11.009.

Freschl, J., Azizi, L.A., Balboa, L., Kaldy, Z., Blaser, E., 2022. The development of peak alpha frequency from infancy to adolescence and its role in visual temporal processing: a meta-analysis. Dev. Cogn. Neurosci. *57*. https://doi.org/10.1016/J.DCN.2022.101146.

Friel, K.M., Gordon, A.M., Carmel, J.B., Kirton, A., Gillick, B.T., 2016. Chapter 7 - pediatric issues in neuromodulation: safety, tolerability and ethical considerations. In: Kirton, A., Gilbert, D.L. (Eds.), Pediatric Brain Stimulation. Academic Press, pp. 131–149. https://doi.org/10.1016/B978-0-12-802001-2.00007-2.

Fries, P., 2005. A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. Trends Cogn. Sci. 9 (10), 474–480. https://doi.org/10.1016/j.tics.2005.08.011.

Fries, P., 2015. Rhythms for cognition: communication through coherence. Neuron 88 (1), 220–235. https://doi.org/10.1016/j.neuron.2015.09.034.

Friese, U., Köster, M., Hassler, U., Martens, U., Trujillo-Barreto, N., Gruber, T., 2013. Successful memory encoding is associated with increased cross-frequency coupling between frontal theta and posterior gamma oscillations in human scalp-recorded EEG. NeuroImage 66, 642–647. https://doi.org/10.1016/j.neuroimage.2012.11.002.

Fröhlich, F., McCormick, D.A., 2010. Endogenous electric fields may guide neocortical network activity. Neuron 67 (1), 129–143. https://doi.org/10.1016/j.neuron.2010.06.005.

Gao, R., Peterson, E.J., Voytek, B., 2017. Inferring synaptic excitation/inhibition balance from field potentials. NeuroImage 158, 70–78. https://doi.org/10.1016/j.neuroimage.2017.06.078.

Gerster, M., Waterstraat, G., Litvak, V., Lehnertz, K., Schnitzler, A., Florin, E., Curio, G., Nikulin, V., 2022. Separating neural oscillations from aperiodic 1/f activity: challenges and recommendations. Neuroinformatics 20 (4), 991–1012. https://doi.org/10.1007/s12021-022-09581-8.

Grandy, T.H., Werkle-Bergner, M., Chicherio, C., Lövdén, M., Schmiedek, F., Lindenberger, U., 2013. Individual alpha peak frequency is related to latent factors of general cognitive abilities. NeuroImage 79, 10–18. https://doi.org/10.1016/j.neuroimage.2013.04.059.

Greenberg, J.A., Burke, J.F., Kahana, M.J., Zaghloul, K.A., 2015. Decreases in theta and increases in high frequency activity underlie associative memory encoding. NeuroImage 114, 257–263. https://doi.org/10.1016/j.neuroimage.2015.03.077.

Grover, S., Fayzullina, R., Bullard, B.M., Levina, V., Reinhart, R.M.G., 2023. A meta-analysis suggests that tACS improves cognition in healthy, aging, and psychiatric populations. Sci. Transl. Med. 15 (697), eabo2044 https://doi.org/10.1126/scitranslmed.abo2044.

Haegens, S., Cousijn, H., Wallis, G., Harrison, P.J., Nobre, A.C., 2014. Inter- and intra-individual variability in alpha peak frequency. NeuroImage 92, 46–55. https://doi.org/10.1016/j.neuroimage.2014.01.049.

Hanslmayr, S., Axmacher, N., Inman, C.S., 2019. Modulating human memory via entrainment of brain oscillations. Trends Neurosci. 42 (7), 485–499. https://doi.org/10.1016/j.tins.2019.04.004.

Harvey, B.M., Vansteensel, M.J., Ferrier, C.H., Petridou, N., Zuiderbaan, W., Aarnoutse, E.J., Bleichner, M.G., Dijkerman, H.C., van Zandvoort, M.J.E., Leijten, F. S.S., Ramsey, N.F., Dumoulin, S.O., 2013. Frequency specific spatial interactions in human electrocorticography: V1 alpha oscillations reflect surround suppression. NeuroImage 65, 424–432. https://doi.org/10.1016/j.neuroimage.2012.10.020.

Hasselmo, M.E., Stern, C.E., 2014. Theta rhythm and the encoding and retrieval of space and time. NeuroImage 85, 656–666. https://doi.org/10.1016/j.neuroimage.2013.06.022.

Hasselmo, M.E., Bodelón, C., Wyble, B.P., 2002. A proposed function for hippocampal theta rhythm: separate phases of encoding and retrieval enhance reversal of prior learning. Neural Comput. 14 (4), 793–817. https://doi.org/10.1162/089976602317318965.

Haufe, S., DeGuzman, P., Henin, S., Arcaro, M., Honey, C.J., Hasson, U., Parra, L.C., 2018. Elucidating relations between fMRI, ECoG, and EEG through a common natural stimulus. NeuroImage 179 (May), 79–91. https://doi.org/10.1016/j.neuroimage.2018.06.016.

He, B.J., 2014. Scale-free brain activity: past, present, and future. Trends Cogn. Sci. 18 (9), 480–487. https://doi.org/10.1016/j.tics.2014.04.003.

Donoghue, T., & Watrous, A. 2023. How can we differentiate narrow-band oscillations from aperiodic activity? In: Axmacher, N. (Ed.), Intracranial EEG: A Guide for Cognitive Neuroscientists. Springer International Publishing, pp. 351-364. doi.org/10.1007/978-3-031-20910-9_22.

He, W., Donoghue, T., Sowman, P.F., Seymour, R.A., Brock, J., Crain, S., Voytek, B., & Hillebrand, A. (2019). Co-Increasing Neuronal Noise and Beta Power in the Developing Brain (p. 839258). bioRxiv. https://doi.org/10.1101/839258.

Helfrich, R.F., Knight, R.T., 2016. Oscillatory dynamics of prefrontal cognitive control. Trends Cogn. Sci. 20 (12), 916–930. https://doi.org/10.1016/j.tics.2016.09.007.

Helfrich, R.F., Fiebelkorn, I.C., Szczepanski, S.M., Lin, J.J., Parvizi, J., Knight, R.T., Kastner, S., 2018. Neural mechanisms of sustained attention are rhythmic. e5 Neuron 99 (4), 854–865. https://doi.org/10.1016/j.neuron.2018.07.032.

Henry, C.E., Greulich, W.W., 1944. Electroencephalograms of normal children. i–71 Monogr. Soc. Res. Child Dev. 9 (3). https://doi.org/10.2307/1165518.

Hermes, D., Miller, K.J., Vansteensel, M.J., Aarnoutse, E.J., Leijten, F.S.S., Ramsey, N.F., 2012. Neurophysiologic correlates of fMRI in human motor cortex. Hum. Brain Mapp. 33 (7), 1689–1699. https://doi.org/10.1002/hbm.21314.

Herweg, N.A., Kahana, M.J., 2018. Spatial representations in the human brain. Front. Hum. Neurosci. 12 (July), 1–16. https://doi.org/10.3389/fnhum.2018.00297.

Herweg, N.A., Solomon, E.A., Kahana, M.J., 2020. Theta oscillations in human memory. Trends Cogn. Sci. 24 (*3*), 208–227. https://doi.org/10.1016/j.tics.2019.12.006.

Hill, A.T., Clark, G.M., Bigelow, F.J., Lum, J.A.G., Enticott, P.G., 2022. Periodic and aperiodic neural activity displays age-dependent changes across early-to-middle childhood. Dev. Cogn. Neurosci. 54, 101076 https://doi.org/10.1016/j.dcn.2022.101076.

Hölscher, C., Anwyl, R., Rowan, M.J., 1997. Stimulation on the positive phase of hippocampal theta rhythm induces long-term potentiation that can be depotentiated by stimulation on the negative phase in area CA1 in vivo. J. Neurosci. 17 (16), 6470–6477. https://doi.org/10.1523/jneurosci.17-16-06470.1997.

Huerta, P.T., Lisman, J.E., 1995. Bidirectional synaptic plasticity induced by a single burst during cholinergic theta oscillation in CA1 in vitro. Neuron 15 (5), 1053–1063. https://doi.org/10.1016/0896-6273(95)90094-2.

Huttenlocher, P.R., de Courten, C., Garey, L.J., Van der Loos, H., 1982. Synaptogenesis in human visual cortex-evidence for synaptic elimination during normal development. Neurosci. Lett. 33 (3), 247–252.

Hyman, J.M., Wyble, B.P., Goyal, V., Rossi, C.A., Hasselmo, M.E., 2003. Stimulation in hippocampal region CA1 in behaving rats yields long-term potentiation when delivered to the peak of theta and long-term depression when delivered to the trough. J. Neurosci. 23 (37), 11725–11731. https://doi.org/10.1523/jneurosci.23-37-11725.2003.

Inman, C.S., Manns, J.R., Bijanki, K.R., Bass, D.I., Hamann, S., Drane, D.L., Fasano, R.E., Kovach, C.K., Gross, R.E., Willie, J.T., 2018. Direct electrical stimulation of the amygdala enhances declarative memory in humans. Proc. Natl. Acad. Sci. 115 (1), 98–103. https://doi.org/10.1073/pnas.1714058114.

Jacques, C., Witthoft, N., Weiner, K.S., Foster, B.L., Rangarajan, V., Hermes, D., Miller, K. J., Parvizi, J., Grill-Spector, K., 2016. Corresponding ECoG and fMRI category-selective signals in human ventral temporal cortex. Neuropsychologia 83, 14–28. https://doi.org/10.1016/j.neuropsychologia.2015.07.024.

Jann, K., Federspiel, A., Giezendanner, S., Andreotti, J., Kottlow, M., Dierks, T., Koenig, T., 2012. Linking brain connectivity across different time scales with electroencephalogram, functional magnetic resonance imaging, and diffusion tensor imaging. Brain Connect. 2 (1), 11–20. https://doi.org/10.1089/brain.2011.0063.

Jensen, O., Gips, B., Bergmann, T.O., Bonnefond, M., 2014. Temporal coding organized by coupled alpha and gamma oscillations prioritize visual processing. Trends Neurosci. 37 (7), 357–369. https://doi.org/10.1016/j.tins.2014.04.001.

Johnson, E.L., Knight, R.T., 2015. Intracranial recordings and human memory. Curr. Opin. Neurobiol. 31, 18–25. https://doi.org/10.1016/j.conb.2014.07.021.

Johnson, E.L., Knight, R.T., 2023. How can iEEG be used to study inter-individual and developmental differences? In: Axmacher, N. (Ed.), Intracranial EEG: A Guide for Cognitive Neuroscientists. Springer International Publishing, pp. 143–154. https://doi.org/10.1007/978-3-031-20910-9_10.

Johnson, E.L., Tang, L., Yin, Q., Asano, E., Ofen, N., 2018. Direct brain recordings reveal prefrontal cortex dynamics of memory development. Sci. Adv. 4, eaat3702 https://doi.org/10.1126/sciadv.abf1762.

Johnson, E.L., Kam, J., Tzovara, A., Knight, R.T., 2020. Insights into human cognition from intracranial EEG: A review of audition, memory, internal cognition, and causality. J. Neural Eng. https://doi.org/10.1088/1741-2552/abb7a5.

Johnson, E.L., Yin, Q., O'Hara, N.B., Tang, L., Jeong, J.-W., Asano, E., Ofen, N., 2022. Dissociable oscillatory theta signatures of memory formation in the developing brain. Curr. Biol. 1–13. https://doi.org/10.1016/j.cub.2022.01.053.

Johnston, M.V., Ishida, A., Ishida, W.N., Matsushita, H.B., Nishimura, A., Tsuji, M., 2009. Plasticity and injury in the developing brain. Brain Dev. 31 (1), 1–10. https://doi.org/10.1016/j.braindev.2008.03.014.

Jones, K.T., Johnson, E.L., Berryhill, M.E., 2020. Frontoparietal theta-gamma interactions track working memory enhancement with training and tDCS. NeuroImage 211, 116615. https://doi.org/10.1016/j.neuroimage.2020.116615.

Kabdebon, C., Fló, A., de Heering, A., Aslin, R., 2022. The power of rhythms: How steady-state evoked responses reveal early neurocognitive development. NeuroImage 254, 119150. https://doi.org/10.1016/j.neuroimage.2022.119150.

Kambara, T., Brown, E.C., Jeong, J.-W., Ofen, N., Nakai, Y., Asano, E., 2017. Spatio-temporal dynamics of working memory maintenance and scanning of verbal information. Clin. Neurophysiol. 128 (6), 882–891. https://doi.org/10.1016/j.clinph.2017.03.005.

Kim, H., 2011. Neural activity that predicts subsequent memory and forgetting: a meta-analysis of 74 fMRI studies. NeuroImage 54 (3), 2446–2461. https://doi.org/10.1016/j.neuroimage.2010.09.045.

Köster, M., Langeloh, M., Hoehl, S., 2019. Visually entrained theta oscillations increase for unexpected events in the infant brain. Psychol. Sci. 30 (11), 1656–1663. https://doi.org/10.1177/0956797619876260.

Köster, M., Martens, U., Gruber, T., 2019. Memory entrainment by visually evoked theta-gamma coupling. NeuroImage 188, 181–187. https://doi.org/10.1016/j.neuroimage.2018.12.002.

Kota, S., Rugg, M.D., Lega, B.C., 2020. Hippocampal theta oscillations support successful associative memory formation. JN-RM-0767-20 J. Neurosci. 40 (49). https://doi.org/10.1523/jneurosci.0767-20.2020.

Kucewicz, M.T., Cimbalnik, J., Matsumoto, J.Y., Brinkmann, B.H., Bower, M.R., Vasoli, V., Sulc, V., Meyer, F., Marsh, W.R., Stead, S.M., Worrell, G.A., 2014. High frequency oscillations are associated with cognitive processing in human recognition memory. Brain 137 (8), 2231–2244. https://doi.org/10.1093/brain/awu149.

Kucewicz, M.T., Saboo, K., Berry, B.M., Kremen, V., Miller, L.R., Khadjevand, F., Inman, C.S., Wanda, P., Sperling, M.R., Gorniak, R., Davis, K.A., Jobst, B.C., Lega, B., Sheth, S.A., Rizzuto, D.S., Iyer, R.K., Kahana, M.J., Worrell, G.A., 2019. Human verbal memory encoding is hierarchically distributed in a continuous processing stream, 18.2018 eNeuro 6 (1), e0214. https://doi.org/10.1523/ENEURO.0214-18.2018.

Lega, B.C., Jacobs, J., Kahana, M., 2012. Human hippocampal theta oscillations and the formation of episodic memories. Hippocampus 22 (4), 748–761. https://doi.org/10.1002/hipo.20937.

Lega, B.C., Burke, J., Jacobs, J., Kahana, M.J., 2016. Slow-theta-to-gamma phase-amplitude coupling in human hippocampus supports the formation of new episodic memories. Cereb. Cortex 26 (1), 268–278. https://doi.org/10.1093/cercor/bhu232.

Leszczyński, M., Barczak, A., Kajikawa, Y., Ulbert, I., Falchier, A.Y., Tal, I., Haegens, S., Melloni, L., Knight, R.T., Schroeder, C.E., 2020. Dissociation of broadband high-

frequency activity and neuronal firing in the neocortex. Sci. Adv. 6 (33), eabb0977. https://doi.org/10.1126/sciadv.abb0977.

Lin, J.J., Rugg, M.D., Das, S., Stein, J., Rizzuto, D.S., Kahana, M.J., Lega, B.C., 2017. Theta band power increases in the posterior hippocampus predict successful episodic memory encoding in humans. Hippocampus 27 (10), 1040–1053. https://doi.org/10.1002/hipo.22751.

Lindsley, D.B., 1939. A longitudinal study of the occipital alpha rhythm in normal children: frequency and amplitude standards. Pedagog. Semin. J. Genet. Psychol. 55 (1), 197–213. https://doi.org/10.1080/08856559.1939.10533190.

Lisman, J., Jensen, O., 2013. The theta-gamma neural code. Neuron 77 (6), 1002–1016. https://doi.org/10.1016/j.neuron.2013.03.007.

Long, N.M., Burke, J.F., Kahana, M.J., 2014. Subsequent memory effect in intracranial and scalp EEG. NeuroImage 84, 488–494. https://doi.org/10.1016/j.neuroimage.2013.08.052.

Mandler, J.M., Robinson, C.A., 1978. Developmental changes in picture recognition. J. Exp. Child Psychol. 26 (1), 122–136. https://doi.org/10.1016/0022-0965(78)90114-5.

Manning, J.R., Jacobs, J., Fried, I., Kahana, M.J., 2009. Broadband shifts in local field potential power spectra are correlated with single-neuron spiking in humans. J. Neurosci. 29 (43), 13613–13620. https://doi.org/10.1523/JNEUROSCI.2041-09.2009.

Marcuse, L.V., Schneider, M., Mortati, K.A., Donnelly, K.M., Arnedo, V., Grant, A.C., 2008. Quantitative analysis of the EEG posterior-dominant rhythm in healthy adolescents. Clin. Neurophysiol. 119 (8), 1778–1781. https://doi.org/10.1016/j.clinph.2008.02.023.

Marshall, P.J., Bar-Haim, Y., Fox, N.A., 2002. Development of the EEG from 5 months to 4 years of age. Clin. Neurophysiol. 113 (8), 1199–1208. https://doi.org/10.1016/S1388-2457(02)00163-3.

Miller, K.J., Honey, C.J., Hermes, D., Rao, R.P., denNijs, M., Ojemann, J.G., 2014. Broadband changes in the cortical surface potential track activation of functionally diverse neuronal populations. NeuroImage 85, 711–720. https://doi.org/10.1016/j.neuroimage.2013.08.070.

Miskovic, V., Ma, X., Chou, C.A., Fan, M., Owens, M., Sayama, H., Gibb, B.E., 2015. Developmental changes in spontaneous electrocortical activity and network organization from early to late childhood. NeuroImage 118, 237–247. https://doi.org/10.1016/j.neuroimage.2015.06.013.

Nakai, Y., Jeong, J.W., Brown, E.C., Rothermel, R., Kojima, K., Kambara, T., Shah, A., Mittal, S., Sood, S., Asano, E., 2017. Three- and four-dimensional mapping of speech and language in patients with epilepsy. Brain 140 (5), 1351–1370. https://doi.org/10.1093/brain/awx051.

Nir, Y., Fisch, L., Mukamel, R., Gelbard-Sagiv, H., Arieli, A., Fried, I., Malach, R., 2007. Coupling between neuronal firing rate, gamma LFP, and bOLD fMRI is related to interneuronal correlations. Curr. Biol. 17 (15), 1275–1285. https://doi.org/10.1016/j.cub.2007.06.066.

O'Keefe, J., Recce, M.L., 1993. Phase relationship between hippocampal place units and the EEG theta rhythm. Hippocampus 3 (3), 317–330. https://doi.org/10.1002/hipo.450030307.

Ofen, N., 2012. The development of neural correlates for memory formation. Neurosci. Biobehav. Rev. 36 (7), 1708–1717. https://doi.org/10.1016/j.neubiorev.2012.02.016.

Ofen, N., Shing, Y.L., 2013. From perception to memory: changes in memory systems across the lifespan. Neurosci. Biobehav. Rev. 37 (9), 2258–2267. https://doi.org/10.1016/j.neubiorev.2013.04.006.

Ofen, N., Kao, Y.-C., Sokol-Hessner, P., Kim, H., Whitfield-Gabrieli, S., Gabrieli, J.D.E., 2007. Development of the declarative memory system in the human brain. Nat. Neurosci. 10 (9), 1198–1205. https://doi.org/10.1038/nn1950.

Ofen, N., Tang, L., Yu, Q., Johnson, E.L., 2019. Memory and the developing brain: From description to explanation with innovation in methods. Dev. Cogn. Neurosci. 36, 100613 https://doi.org/10.1016/j.dcn.2018.12.011.

Ostlund, B., Donoghue, T., Anaya, B., Gunther, K.E., Karalunas, S.L., Voytek, B., Pérez-Edgar, K.E., 2022. Spectral parameterization for studying neurodevelopment: How and why. Dev. Cogn. Neurosci. 54, 101073 https://doi.org/10.1016/j.dcn.2022.101073.

Ouyang, G., Hildebrandt, A., Schmitz, F., Herrmann, C.S., 2020. Decomposing alpha and 1/f brain activities reveals their differential associations with cognitive processing speed. NeuroImage 205, 116304. https://doi.org/10.1016/j.neuroimage.2019.116304.

Paller, K.A., Wagner, A.D., 2002. Observing the transformation of experience into memory. Trends Cogn. Sci. 6 (2), 93–102. https://doi.org/10.1016/S1364-6613(00)01845-3.

Park, J., 2018. A neural basis for the visual sense of number and its development: a steady-state visual evoked potential study in children and adults. Dev. Cogn. Neurosci. 30, 333–343. https://doi.org/10.1016/j.dcn.2017.02.011.

Parvizi, J., Kastner, S., 2018. Promises and limitations of human intracranial electroencephalography. Nat. Neurosci. 21 (4), 474–483. https://doi.org/10.1038/s41593-018-0108-2.

Perone, S., Palanisamy, J., Carlson, S.M., 2018. Age-related change in brain rhythms from early to middle childhood: Links to executive function. Dev. Sci. 21 (6), e12691 https://doi.org/10.1111/desc.12691.

Quast, K.B., Reh, R.K., Caiati, M.D., Kopell, N., McCarthy, M.M., Hensch, T.K., 2023. Rapid synaptic and gamma rhythm signature of mouse critical period plasticity. Proc. Natl. Acad. Sci. USA 120 (2), e2123182120. https://doi.org/10.1073/pnas.2123182120.

Rich, E.L., Wallis, J.D., 2017. Spatiotemporal dynamics of information encoding revealed in orbitofrontal high-gamma. Nat. Commun. 8 (1), 1139. https://doi.org/10.1038/s41467-017-01253-5.

Roberts, B.M., Clarke, A., Addante, R.J., Ranganath, C., 2018. Entrainment enhances theta oscillations and improves episodic memory. Cogn. Neurosci. 9 (3–4), 181–193. https://doi.org/10.1080/17588928.2018.1521386.

Roux, F., Parish, G., Chelvarajah, R., Rollings, D.T., Sawlani, V., Hamer, H., Gollwitzer, S., Kreiselmeyer, G., Ter Wal, M., Kolibius, L., Wimber, M., Self, M.W., & Hanslmayr, S. (2021). Oscillations support co-firing of neurons in the service of human memory formation. bioRxiv, 2021.01.28.428480.

Rubinstein, D.Y., Camarillo-Rodriguez, L., Serruya, M.D., Herweg, N.A., Waldman, Z.J., Wanda, P.A., Sharan, A.D., Weiss, S.A., Sperling, M.R., 2021. Contribution of left supramarginal and angular gyri to episodic memory encoding: an intracranial EEG study. NeuroImage 225 (September 2020), 117514. https://doi.org/10.1016/j.neuroimage.2020.117514.

Rudoler, J.H., Herweg, N.A., Kahana, M.J., 2023. Hippocampal theta and episodic memory. J. Neurosci. 43 (4), 613–620. https://doi.org/10.1523/JNEUROSCI.1045-22.2022.

Rutishauser, U., Ross, I.B., Mamelak, A.N., Schuman, E.M., 2010. Human memory strength is predicted by theta-frequency phase-locking of single neurons. Nature 464 (7290), 903–907. https://doi.org/10.1038/nature08860.

Saint Amour di Chanaz, L., Pérez-Bellido, A., Wu, X., Lozano-Soldevilla, D., Pacheco-Estefan, D., Lehongre, K., Conde-Blanco, E., Roldan, P., Adam, C., Lambrecq, V., Frazzini, V., Donaire, A., Carreño, M., Navarro, V., Valero-Cabré, A., Fuentemilla, L., 2023. Gamma amplitude is coupled to opposed hippocampal theta-phase states during the encoding and retrieval of episodic memories in humans. e6 Curr. Biol. 33 (9), 1836–1843. https://doi.org/10.1016/j.cub.2023.03.073.

Samaha, J., Postle, B.R., 2015. The speed of alpha-band oscillations predicts the temporal resolution of visual perception. Curr. Biol. 25 (22), 2985–2990. https://doi.org/10.1016/j.cub.2015.10.007.

Schaworonkow, N., Voytek, B., 2021. Longitudinal changes in aperiodic and periodic activity in electrophysiological recordings in the first seven months of life. Dev. Cogn. Neurosci. 47, 100895 https://doi.org/10.1016/j.dcn.2020.100895.

Sederberg, P.B., Kahana, M.J., Howard, M.W., Donner, E.J., Madsen, J.R., 2003. Theta and gamma oscillations during encoding predict subsequent recall. J. Neurosci.: Off. J. Soc. Neurosci. 23 (34), 10809–10814 https://doi.org/23/34/10809 [pii].

Serruya, M.D., Sederberg, P.B., Kahana, M.J., 2014. Power shifts track serial position and modulate encoding in human episodic memory. Cereb. Cortex 24 (2), 403–413. https://doi.org/10.1093/cercor/bhs318.

Sheehan, T.C., Sreekumar, V., Inati, S.K., Zaghloul, K.A., 2018. Signal complexity of human intracranial EEG tracks successful associative-memory formation across individuals. J. Neurosci. 38 (7), 1744–1755. https://doi.org/10.1523/JNEUROSCI.2389-17.2017.

Solomon, E.A., Kragel, J.E., Sperling, M.R., Sharan, A., Worrell, G., Kucewicz, M., Inman, C.S., Lega, B., Davis, K.A., Stein, J.M., Jobst, B.C., Zaghloul, K.A., Sheth, S.A., Rizzuto, D.S., Kahana, M.J., 2017. Widespread theta synchrony and high-frequency desynchronization underlies enhanced cognition. Nat. Commun. 8 (1) https://doi.org/10.1038/s41467-017-01763-2.

Solomon, E.A., Stein, J.M., Das, S., Gorniak, R., Sperling, M.R., Worrell, G., Inman, C.S., Tan, R.J., Jobst, B.C., Rizzuto, D.S., Kahana, M.J., 2019. Dynamic Theta Networks in the Human Medial Temporal Lobe Support Episodic Memory. e4 Curr. Biol. 29 (7), 1100–1111. https://doi.org/10.1016/j.cub.2019.02.020.

Sommer, V.R., Mount, L., Weigelt, S., Werkle-Bergner, M., Sander, M.C., 2022. Spectral pattern similarity analysis: Tutorial and application in developmental cognitive neuroscience. Dev. Cogn. Neurosci. 54, 101071 https://doi.org/10.1016/j.dcn.2022.101071.

Spaniol, J., Davidson, P.S.R., Kim, A.S.N., Han, H., Moscovitch, M., Grady, C.L., 2009. Event-related fMRI studies of episodic encoding and retrieval: Meta-analyses using activation likelihood estimation. Neuropsychologia 47 (8–9), 1765–1779. https://doi.org/10.1016/j.neuropsychologia.2009.02.028.

Stroganova, T.A., Orekhova, E.V., Posikera, I.N., 1999. EEG alpha rhythm in infants. Clin. Neurophysiol. 110 (6), 997–1012. https://doi.org/10.1016/S1388-2457(98)00009-1.

Suthana, N., Fried, I., 2014. Deep brain stimulation for enhancement of learning and memory. NeuroImage 85, 996–1002. https://doi.org/10.1016/j.neuroimage.2013.07.066.

Sweeney-Reed, C.M., Zaehle, T., Voges, J., Schmitt, F.C., Buentjen, L., Kopitzki, K., Esslinger, C., Hinrichs, H., Heinze, H.J., Knight, R.T., Richardson-Klavehn, A., 2014. Corticothalamic phase synchrony and cross-frequency coupling predict human memory formation. eLife 3, e05352. https://doi.org/10.7554/eLife.05352.

Tang, L., Shafer, A.T., Ofen, N., 2018. Prefrontal cortex contributions to the development of memory formation. Cereb. Cortex 28 (9), 3295–3308. https://doi.org/10.1093/cercor/bhx200.

Thuwal, K., Banerjee, A., Roy, D., 2021. Aperiodic and periodic components of ongoing oscillatory brain dynamics link distinct functional aspects of cognition across adult lifespan. ENEURO.0224-21.2021 eNeuro 8 (5). https://doi.org/10.1523/ENEURO.0224-21.2021.

Valdés-Hernández, P.A., Ojeda-González, A., Martínez-Montes, E., Lage-Castellanos, A., Virués-Alba, T., Valdés-Urrutia, L., Valdes-Sosa, P.A., 2010. White matter architecture rather than cortical surface area correlates with the EEG alpha rhythm. NeuroImage 49 (3), 2328–2339. https://doi.org/10.1016/j.neuroimage.2009.10.030.

van Blooijs, D., van den Boom, M.A., van der Aar, J.F., Huiskamp, G.M., Castegnaro, G., Demuru, M., Zweiphenning, W.J.E.M., van Eijsden, P., Miller, K.J., Leijten, F.S.S., Hermes, D., 2023. Developmental trajectory of transmission speed in the human brain (Article). Nat. Neurosci. 26 (4), 4. https://doi.org/10.1038/s41593-023-01272-0.

Vaz, A.P., Yaffe, R.B., Wittig, J.H., Inati, S.K., Zaghloul, K.A., 2017. Dual origins of measured phase-amplitude coupling reveal distinct neural mechanisms underlying

episodic memory in the human cortex. NeuroImage 148 (November 2016), 148–159. https://doi.org/10.1016/j.neuroimage.2017.01.001.

Virtue-Griffiths, S., Fornito, A., Thompson, S., Biabani, M., Tiego, J., Thapa, T., & Rogasch, N.C. (2022). Task-related changes in aperiodic activity are related to visual working memory capacity independent of event-related potentials and alpha oscillations (p. 2022.01.18.476852). bioRxiv. https://doi.org/10.1101/2022.01.18.476852.

Voytek, B., Canolty, R., Shestyuk, A., Crone, N., Parvizi, J., Knight, R., 2010. Shifts in gamma phase–amplitude coupling frequency from theta to alpha over posterior cortex during visual tasks. Front. Hum. Neurosci. 4 https://doi.org/10.3389/fnhum.2010.0019.

Voytek, B., Kramer, M.A., Case, J., Lepage, K.Q., Tempesta, Z.R., Knight, R.T., Gazzaley, A., 2015. Age-related changes in 1 / f neural electrophysiological noise. J. Neurosci. 35 (38), 13257–13265. https://doi.org/10.1523/JNEUROSCI.2332-14.2015.

ter Wal, M., Linde-Domingo, J., Lifanov, J., Roux, F., Kolibius, L.D., Gollwitzer, S., Lang, J., Hamer, H., Rollings, D., Sawlani, V., Chelvarajah, R., Staresina, B., Hanslmayr, S., Wimber, M., 2021. Theta rhythmicity governs human behavior and hippocampal signals during memory-dependent tasks (Article). Nat. Commun. 12 (1), 1. https://doi.org/10.1038/s41467-021-27323-3.

Wang, D., Clouter, A., Chen, Q., Shapiro, K.L., Hanslmayr, S., 2018. Single-Trial Phase Entrainment of Theta Oscillations in Sensory Regions Predicts Human Associative Memory Performance. J. Neurosci. 38 (28), 6299–6309. https://doi.org/10.1523/JNEUROSCI.0349-18.2018.

Wang, D.X., Schmitt, K., Seger, S., Davila, C.E., Lega, B.C., 2021. Cross-regional phase amplitude coupling supports the encoding of episodic memories. *Hippocampus*, *Dec.* 2020, 1–12. https://doi.org/10.1002/hipo.23309.

Wang, X.J., 2010. Neurophysiological and computational principles of cortical rhythms in cognition. Physiol. Rev. 90 (3), 1195–1268. https://doi.org/10.1152/physrev.00035.2008.

Watson, B.O., Ding, M., Buzsáki, G., 2018. Temporal coupling of field potentials and action potentials in the neocortex. Eur. J. Neurosci. 48 (7), 2482–2497. https://doi.org/10.1111/ejn.13807.

Werkle-Bergner, M., Müller, V., Li, S.-C., Lindenberger, U., 2006. Cortical EEG correlates of successful memory encoding: Implications for lifespan comparisons. Neurosci. Biobehav. Rev. 30 (6), 839–854. https://doi.org/10.1016/j.neubiorev.2006.06.009.

Yin, Q., Johnson, E.L., Tang, L., Auguste, K.I., Knight, R.T., Asano, E., Ofen, N., 2020. Direct brain recordings reveal occipital cortex involvement in memory development. Neuropsychologia 148 (September), 107625. https://doi.org/10.1016/j.neuropsychologia.2020.107625.

Yoo, H.B., Umbach, G., Lega, B., 2021. Neurons in the human medial temporal lobe track multiple temporal contexts during episodic memory processing. NeuroImage 245, 118689. https://doi.org/10.1016/j.neuroimage.2021.118689.

Zhang, C., Stock, A.-K., Mückschel, M., Hommel, B., Beste, C., 2023. Aperiodic neural activity reflects metacontrol. Cereb. Cortex 33 (12), 7941–7951. https://doi.org/10.1093/cercor/bhad089.