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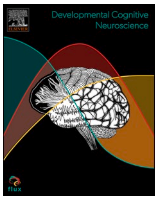

Theta activity and cognitive functioning: Integrating evidence from resting-state and task-related developmental electroencephalography (EEG) research

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ABSTRACT

The theta band is one of the most prominent frequency bands in the electroencephalography (EEG) power spectrum and presents an interesting paradox: while elevated theta power during resting state is linked to lower cognitive abilities in children and adolescents, increased theta power during cognitive tasks is associated with higher cognitive performance. Why does theta power, measured during resting state versus cognitive tasks, show differential correlations with cognitive functioning? This review provides an integrated account of the functional correlates of theta across different contexts. We first present evidence that higher theta power during resting state is correlated with lower executive functioning, attentional abilities, language skills, and IQ. Next, we review research showing that theta power increases during memory, attention, and cognitive control, and that higher theta power during these processes is correlated with better performance. Finally, we discuss potential explanations for the differential correlations between resting/task-related theta and cognitive functioning, and offer suggestions for future research in this area.

1. Introduction

Electroencephalography (EEG) has emerged as a widely used tool for measuring brain activity in developmental research. Compared with other neuroimaging techniques such as functional magnetic resonance imaging (fMRI), EEG represents a more accessible measure of the electrical activity of the brain, providing unique insights into the temporal dynamics of neurocognitive processes (Davidson et al., 2000). In recent years, developmental EEG research has made significant progress by adopting more sophisticated analysis methods (Buzzell et al., 2023). A particularly fruitful area of research has focused on the analysis of oscillatory EEG activity (Cuevas and Bell, 2022; Saby and Marshall, 2012). Oscillatory EEG activity reflects rhythmic changes in local field potentials (LFPs), which are influenced by fluctuations in neuronal excitability (Nunez and Srinivasan, 2006; Thut et al., 2012). These neural oscillations are thought to play a crucial role in shaping cortical networks and coordinating neural activity across brain regions (Buzsaki, 2006; Uhlhaas et al., 2010).

In developmental research, oscillatory EEG activity is typically examined either during resting state (i.e., when participants are sitting “at rest” and perform no assigned tasks; see Section 5.2 for more discussion about this definition) or during cognitive tasks. To characterize oscillatory neural activity, continuous EEG signals are converted from the time domain to the frequency domain and divided into frequency bands bearing the names of Greek letters (delta, theta, alpha, beta, gamma). These bands are defined based on frequency characteristics, functional properties, and spatial distribution (Kuhlman, 1980). The energy within each frequency band is quantified by spectral power (the square of signal amplitude; Thatcher, 1998). Among various frequency bands, the theta band stands out for its prominence in the power spectrum and for its unique position as a transition point traditionally used to differentiate low-frequency (e.g., delta, theta) and high-frequency (e.g.,

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alpha, beta, gamma) bands (Klimesch, 1999; Saad et al., 2018).

Growing evidence suggests that theta activity exhibits distinct functional correlates during resting state versus cognitive tasks. Greater theta power during resting-state recordings has been linked to lower cognitive abilities in children and adolescents (e.g., Maguire and Schneider, 2019; Perone et al., 2018), suggestive of a negative relation between resting theta power and cognitive functioning. By contrast, task-related EEG research has consistently found positive associations between theta power during cognitive tasks and behavioral performance (e.g., Begus et al., 2015; Brandes-Aitken, Metser, et al., 2023). Why does theta power, measured during resting state versus tasks, show distinct correlations with cognitive performance? This article integrates evidence on the functional correlates of theta activity from both resting-state and task-related EEG literatures. We begin with a brief overview of the development of oscillatory EEG activity. Next, we review evidence on how resting theta and task-related theta are linked to different aspects of cognitive functioning, highlighting their divergent patterns of associations. Finally, we synthesize evidence from both literatures and explore potential explanations for the divergent associations observed across contexts.

2. The development of oscillatory EEG activity

Developmental EEG research has demonstrated that frequency bands with similar functional and topographical characteristics tend to be slower in younger (vs. older) individuals (Isler et al., 2022; Marshall et al., 2002; Orekhova et al., 2006; Stroganova et al., 1999). To account for this age-related shift, the boundaries of different frequency bands are usually set at lower values for younger children (Saby and Marshall, 2012). As children grow older, the boundaries of different frequency bands shift upward. For example, although there is some debate about the exact boundaries, theta frequency ranges are typically around 3–5 Hz in infants and 4–8 Hz in adults (Orekhova et al., 1999). An alternative strategy for setting frequency boundaries across age groups involves the use of individual alpha peak frequency (IAF; Doppelmayr et al., 1998; Lansbergen et al., 2011). Because individuals exhibit greater alpha power when their eyes are closed versus open (Gale et al., 1971; Jasper, 1936), IAF can be determined by identifying the specific frequency within the alpha range that shows the greatest power differences between eyes-closed and eyes-open conditions (see also Donoghue, Haller, et al., 2020 for an alternative method of identifying IAF). Subsequently, the boundaries of different frequency bands can be established using proportions of the IAF, with steps of 20 % IAF between bands (e.g., delta:.2×IAF-.4×IAF, theta:.4×IAF-.6×IAF, lower-1-alpha:.6×IAF-.8×IAF, lower-2-alpha:.8×IAF-1×IAF, upper-alpha: 1×IAF-1.2×IAF, beta:1.2×IAF-25 Hz; Doppelmayr et al., 1998; Lansbergen et al., 2011).

As the brain develops, the composition of the EEG power spectrum as a whole also undergoes changes. EEG power is typically calculated either as absolute power (representing the total energy within a frequency band; conversion to dB or other log scales is sometimes employed) or as relative power (i.e., the absolute power of a specific frequency band divided by total absolute power across all frequencies). While there is always some energy within each frequency band across age groups, the relative power of frequency bands changes with age (Fig. 1). During early childhood, the resting EEG power spectrum is dominated by slower oscillations such as delta and theta (Cellier et al., 2021; Schaworonkow and Voytek, 2021). During this period, the peak of oscillatory activity typically falls within the theta range (e.g., 3–4 Hz; Lodder and van Putten, 2011; Rodríguez-Martínez et al., 2017), although some individuals may exhibit two distinct peaks – one in the theta range and one in the alpha range (Klimesch, 1999). From infancy through adolescence, relative power in lower-frequency bands decreases while relative power in higher-frequency bands (e.g., alpha, beta, and gamma) increases (Benninger et al., 1984; Clarke et al., 2001; Marshall et al., 2002; Miskovic et al., 2015; Perone et al., 2018). In adulthood, the peak of oscillatory activity shifts to the alpha range (8–12 Hz; Chiang et al., 2011; Klimesch, 1999).

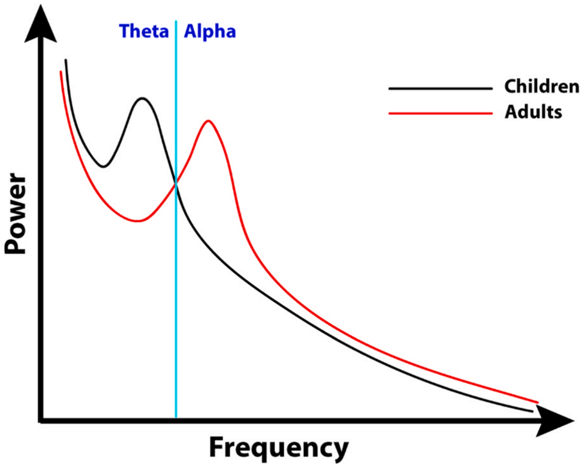

Fig. 1. Schematic illustration showing the age-related shift of resting EEG peak oscillatory activity from the theta range to the alpha range. Adapted from Cellier et al. (2021).

The age-related changes in relative EEG power are linked to synaptic pruning, grey matter reduction, and the maturation of the gamma-aminobutyric acid (GABA) neurotransmitter system (Feinberg and Campbell, 2010; Hashimoto et al., 2009; Smit et al., 2012; Whitford et al., 2007). Animal research has shown that higher-frequency (e.g., gamma) oscillations in mature brains rely on rapid interaction between excitatory pyramidal cells and inhibitory interneurons (Atallah and Scanziani, 2009; Cardin et al., 2009), with GABA playing a crucial role in inhibitory effects (Buzsáki and Wang, 2012; Kubota et al., 2016). In less mature brains, however, GABA functions as an excitatory (vs. inhibitory) neurotransmitter due to a high intracellular concentration of chloride (Cl−). During this developmental stage (e.g., the first two postnatal weeks in rats and until a few days before birth in primates), neural oscillations primarily rely on recurrent, long-lasting potentials known as giant depolarizing potentials (GDPs), which are too slow for generating high-frequency oscillations. Consequently, lower-frequency rhythms dominate the power spectrum in less mature brains. As the brain grows, the intracellular concentration of chloride decreases, allowing GABA to exert its canonical inhibitory effects and giving rise to higher-frequency oscillations (Ben-Ari, 2002; Le Van Quyen et al., 2006). Because lower-frequency oscillations are associated with long-distance neural communication, the age-related decline in lower-frequency EEG power is thought to reflect a relative decrease in long-range connections between individual neurons, more efficiently integrated local networks, and improved white matter integrity across brain regions (Von Stein and Sarnthein, 2000).

3. Resting theta and cognitive functioning

The age-related shift of relative EEG power from lower to higher frequency bands has led to the hypothesis that an excess of power in lower-frequency (i.e., delta, theta) bands during resting state in older children indicates a maturational lag in brain development (Corning et al., 1982, 1986; Matsuura et al., 1993). This hypothesis is supported by research showing that children exposed to environmental adversities often exhibit elevated EEG power in lower-frequency bands and decreased EEG power in higher-frequency bands. For instance, compared with typically-developing children, children who experienced severe psychosocial deprivation due to institutional rearing showed higher relative EEG power in the theta band and lower relative power in the alpha band during resting-state paradigms (e.g., passively viewing a bingo wheel, alternating between having eyes open and closed; Debnath et al., 2020; Marshall et al., 2004; Vanderwert et al., 2016). Such brain activity pattern mediated the associations between institutional rearing and symptoms of hyperactivity and impulsivity at age 54 months (McLaughlin et al., 2010). Magnetic resonance imaging (MRI) research revealed that the effect of institutional rearing on resting EEG power was partially explained by a decrease in cortical white matter volume (Sheridan et al., 2012). Similar patterns of resting EEG activity have been observed in children from low-income (vs. higher-income) families (Harmony et al., 1988; Maguire and Schneider, 2019; Otero, 1994; Otero et al., 2003; Tomalski et al., 2013) and in those exposed to higher caregiver stress (Brandes-Aitken, Pini, et al., 2023; Jensen et al., 2021; Pierce et al., 2019; Troller-Renfree et al., 2020, 2023). Critically, these brain activity patterns appear to be modifiable through randomized control interventions targeting environmental factors (Debnath et al., 2020; Troller-Renfree et al., 2022; Vanderwert et al., 2010, 2016). Together, these studies demonstrate that resting-state brain activity is sensitive to environmental influences, supporting the idea that individual differences in resting brain activity reflect functional brain development.

If individual differences in resting brain activity reflect functional brain development, then patterns of resting EEG observed in more mature brains (e.g., lower resting theta power) should correlate with higher cognitive functioning. In the following sections, we review evidence that individual differences in resting EEG power are associated with different aspects of cognitive functioning, with a particular focus on theta activity (see Table A.1 for a summary of key studies). For recent reviews on EEG activity in other frequency bands, see Anderson and Perone (2018) and Cuevas and Bell (2022).

3.1. Executive functioning

Executive functioning refers to a set of cognitive abilities responsible for regulating thought and behavior (Anderson, 2002; Carlson, 2005; Diamond, 2013). These include working memory (holding and manipulating information), inhibitory control (suppressing prepotent responses), and cognitive flexibility (shifting between tasks or mental sets). While research to date has found no associations between resting theta power and executive functioning in infants (Brito et al., 2016; Troller-Renfree et al., 2020), growing evidence suggests that higher resting theta is associated with lower executive functioning in older children and adolescents.

In a study using the eyes-open/eyes-closed paradigm, Maguire and Schneider (2019) found that 8–15-year-old children from lower- (vs. higher-) income families displayed higher absolute resting theta (4–8 Hz) power over the right parietal brain region and lower absolute resting alpha power over the left frontal and central regions. These findings align with past research linking environmental challenges to resting EEG patterns. Crucially, higher resting theta power was correlated with lower working memory across all participants, whereas higher resting alpha power was correlated with greater vocabulary in participants from low-income families. These results provide evidence for the negative associations between resting theta power and working memory in children and adolescents.

Similar associations between resting theta and executive functioning have been reported in studies using power ratio measures. Using the eyes-open/eyes-closed paradigm, Perone and colleagues (2018) examined resting brain activity in typically developing children and found that relative resting theta (frequency range:.4×IAF-.8×IAF) power over frontal and posterior regions declined from 3 to 9 years of age. Importantly, children with higher theta/beta power ratios during resting state showed lower performance on working memory, inhibitory control, and cognitive flexibility tasks; the effects held even after accounting for age and verbal ability differences. Similarly, Cai and colleagues (2021) examined resting EEG power over the frontal brain region in 7–9-year-old children using the eyes-open/eyes-closed paradigm. They found that, after controlling for age and verbal ability, greater resting alpha/theta and beta/theta ratios (theta frequency range: 4 Hz - IAF-2 Hz) predicted higher inhibition skills, and that greater resting beta/theta ratios predicted higher planning skills. Together, these findings demonstrate the links between resting theta power ratios and various components of executive functioning in children. It is important to note that changes in theta ratio scores can be driven by EEG power changes in the theta band and/or changes in other frequency bands. Hence, theta ratio scores do not necessarily reflect theta activity per se, and care should be taken when interpreting findings based on these ratios.

3.2. Attention

Attention refers to the ability to selectively focus on certain aspects of the environment while ignoring others (Johnston and Dark, 1986). This ability facilitates the allocation of limited mental resources to important tasks and promotes adaptive behaviors. An increasing body of research suggests that higher resting theta power is associated with reduced attentional abilities. In infancy, Perone and Gartstein (2019) recorded EEG in 6–12-month-olds during passive viewing of videos depicting colorful objects, and found that higher relative resting theta (3–6 Hz) power and lower relative resting beta and gamma power over the frontal region were associated with lower parent-reported attentional abilities. In childhood and adolescence, increased lower-frequency power (including theta power) and decreased higher-frequency power during resting state have been linked to attentional deficits (Clarke et al., 2002; Lazzaro et al., 1999; Satterfield et al., 1974). Indeed, increased resting theta power and theta/beta ratio are frequently observed in individuals diagnosed with Attention Deficit Hyperactivity Disorder (ADHD; for a review, see Barry et al., 2003), and the United States Food and Drug Administration (FDA) has approved the use of resting theta/beta ratio as a diagnostic marker for ADHD (Food and Drug Administration, 2013). However, the associations between resting theta/beta ratio and ADHD have not consistently replicated across studies (for reviews, see Arns et al., 2013; Lenartowicz and Loo, 2014; Loo and Makeig, 2012), and increased resting theta/beta ratio has been linked to other mental health conditions such as schizophrenia, obsessive-compulsive disorder (OCD), and internet addiction (Newson and Thiagarajan, 2019). Therefore, the use of resting theta/beta ratio in ADHD assessment remains a subject of debate (Gloss et al., 2016; Saad et al., 2018), and further research is needed to elucidate the relations between resting theta/beta ratio, ADHD, and other mental health conditions. This issue will be revisited in Section 5.1.

3.3. Language

In addition to executive functioning and attentional abilities, higher resting theta power has also been linked to lower language skills in children and adolescents. While no associations were found between absolute resting theta (4–6 Hz) power at birth and language skills at 15 months in infants (Brito et al., 2016), a negative association was found in older children (9–11-year-olds) between absolute theta (4–8 Hz) power over the left central-prefrontal regions during a resting eyes-open condition and performance on a sentence repetition task (Lum et al., 2022); the association was specific to the theta band. Using a similar resting-state paradigm, Meng and colleagues (2022) found that greater reductions in relative resting theta (4–8 Hz) power across the scalp from 7 to 9 years and from 7 to 11 years predicted higher expressive vocabulary at 9 and 11 years, respectively. These associations remained significant after controlling for individual differences in general cognitive abilities, age, home literacy environment, and phonological skills. Conversely, greater increases in beta power across the scalp from 7 to 9 years predicted higher receptive vocabulary at 11 years. These findings provide evidence that higher resting theta power is associated with lower language skills in childhood and early adolescence.

In clinical research, higher resting theta power has been linked to reading difficulties. For instance, Papagiannopoulou and Lagopoulos

(2016) demonstrated that, compared with typically developing children, 8-year-old children diagnosed with dyslexia exhibited increased resting relative theta (3.6–7.4 Hz) power over the left frontal brain region during an eyes-closed condition. Similarly, Arns and colleagues (2007) found that 10–16-year-old children diagnosed with dyslexia displayed increased absolute resting delta and theta (4–7.5 Hz) power over the frontal and right temporal brain regions during an eyes-open condition. These studies provide further evidence for the negative associations between resting theta power and language abilities in children and adolescents.

3.4. *Intelligence quotient (IQ)*

IQ tests are designed to offer a comprehensive assessment of intellectual ability across different cognitive domains, including perceptual reasoning, verbal comprehension, working memory, and processing speed (Wechsler, 2004). Widely used in educational and clinical settings, IQ scores have been shown to predict real-life outcomes such as academic achievement (Deary et al., 2007), job performance (Schmidt and Hunter, 2004), socioeconomic status (Strenze, 2007), and health outcomes (Calvin et al., 2017).

A recent study demonstrates that early individual differences in resting theta power are associated with IQ in adulthood (Tan et al., 2023). This study leveraged data from the Bucharest Early Intervention Project (BEIP), a randomized controlled trial of foster care as an alternative to institutional care (Zeanah et al., 2003), to examine the effects of early institutional rearing and foster care intervention on neurocognitive development. Results showed that higher relative theta (3–5 Hz) power, measured across the scalp during passive viewing of a spinning bingo wheel across three assessments from 22 to 42 months, predicted lower full-scale IQ at 18 years. In addition, institutional rearing and later (vs. earlier) foster care placement predicted higher relative resting theta power in early childhood, which in turn predicted lower IQ at 18 years. These findings suggest that early experiential factors influence long-term cognitive development through changes in early brain activity. Notably, the effects were specific to the theta band, and post-hoc analyses on different domains of the IQ test replicated the overall effects in the perceptual reasoning, working memory, and processing speed domains. These findings suggest that early individual differences in resting theta power hold meaningful implications for predicting global measures of cognitive abilities into adulthood.

3.5. *Interim discussion*

The studies reviewed above provide evidence that early environmental adversity is associated with heightened resting theta power, and that children and adolescents with elevated resting theta power tend to exhibit lower executive functioning, attentional abilities, language skills, and IQ. These findings underscore a negative association between resting theta power and cognitive functioning during childhood and adolescence. It is important to note that most of the relations reported in this section are based on correlational studies, leaving the causal relation between resting brain activity and cognitive functioning unclear. In addition, there are considerable methodological variations among the reviewed studies, including differences in paradigms used to assess resting EEG (e.g., eyes-open/eyes-closed conditions, passive viewing of videos or spinning bingo wheels), brain regions examined (e.g., across the scalp, frontal/parietal/temporal regions), the use of absolute versus relative power, and the use of power versus power ratio scores. These discrepancies make direct comparisons between studies challenging. Nonetheless, the emergence of negative associations despite methodological differences suggests that the overall inverse relation between resting theta power and cognitive functioning is robust.

It is worth noting that the associations between resting theta power and cognitive functioning appear to be less consistent in adults than in children and adolescents (Finnigan and Robertson, 2011; Kavcic et al., 2016; Sargent et al., 2021; cf. Jelic et al., 1996; Roca-Stappung et al., 2012), and recent evidence suggests that the direction and strength of these relations may change with age in late adulthood (Lithfous et al., 2015; Trammell et al., 2017; Vlahou et al., 2014). Thus, the relations between resting theta and cognitive functioning may be nonlinear across development, highlighting the importance of considering age when using resting EEG power as an index of brain development.

Are individual differences in cognitive functioning uniquely associated with theta? While some studies have found specific links between cognitive functioning and resting theta power (e.g., Lum et al., 2022; Tan et al., 2023), similar links have been shown in other frequency bands. For example, greater resting alpha power has been associated with higher executive functioning in infants (Bell and Fox, 1992, 1997; but see Kraybill and Bell, 2013), and greater resting gamma power has been linked to higher executive functioning and language abilities in infants and children (Benasich et al., 2008; Brito et al., 2016; Gou et al., 2011; Tarullo et al., 2017; Williams et al., 2012; see also Barry et al., 2010; Tomalski et al., 2013; for recent reviews, see Anderson and Perone, 2018; Cuevas and Bell, 2022). These findings are in line with the theta/alpha and theta/beta effects reported earlier, and support the hypothesis that decreased lower-frequency power and increased higher-frequency power during resting state are associated with higher cognitive functioning. Indeed, it is possible that the associations between resting theta power and cognitive functioning are driven by effects across the entire power spectrum, rather than theta effects per se. This issue will be revisited in Section 5.1.

4. Task-related theta and cognitive functioning

Task-related EEG studies examine changes in brain activity during specific cognitive processes. These studies often use time-frequency analysis to characterize the temporal dynamics of brain activity in response to events of interest (Morales and Bowers, 2022). In contrast to resting EEG research, which has predominantly found negative correlations between theta power and cognitive functioning, task-related EEG research consistently found positive associations between theta power and cognitive performance. In the following sections, we review evidence that the engagement of cognitive processes (including memory, attention, and cognitive control) is associated with increased theta power, and that greater theta power during cognitive tasks predicts enhanced behavioral performance (see Table A.2 for a summary of key studies).

4.1. *Memory*

The links between theta activity and memory processes have been well-documented in rodent research (Colgin, 2013). At the cellular level, stimulating hippocampal cells during the peak of theta oscillations triggers long-term potentiation (LTP; a long-term enhancement of synaptic efficiency), which is considered a key cellular mechanism for memory formation (Hölscher et al., 1997; Pavlides et al., 1988). By contrast, stimulation during the trough of theta oscillations or at other frequencies is less likely to induce LTP (Greenstein et al., 1988). Behaviorally, increased hippocampal theta power during olfactory and spatial memory tasks predicted better memory performance in rodents (Olvera-Cortés et al., 2002; Wiebe and Stäubli, 2001), and increased hippocampal theta activity before classical conditioning predicted accelerated learning rates (Berry and Thompson, 1978). Moreover, enhancing hippocampal theta through pharmacological manipulation and electrical stimulation improved performance on olfactory/spatial memory and avoidance memory tasks (Landfield, 1977; Staubli and Xu, 1995), whereas disrupting hippocampal theta through lesion or pharmacological manipulation resulted in spatial memory impairments (Chrobak et al., 1989; Winson, 1978). Hippocampal theta is also thought to be involved in information transmission across brain regions. Supporting this idea, increased theta coupling has been observed between the hippocampus and the amygdala during fear memory retrieval (Seidenbecher et al., 2003), and between the hippocampus and the olfactory bulb during olfactory memory processing (Kay, 2005). In addition, increased theta coupling between the hippocampus and medial prefrontal cortex (mPFC) during spatial memory tasks predicted better behavioral performance (Hyman et al., 2010; Jones and Wilson, 2005). Together, these rodent studies suggest that hippocampal theta plays a crucial role in memory processes.

It is important to note that rodent research on hippocampal theta has focused on neural activity directly measured via implanted electrodes. By contrast, human EEG research has focused on electrical activity recorded from the scalp, which does not represent a direct measure of hippocampal activity. Therefore, the links between hippocampal theta and memory processes in rodent research cannot be directly aligned with or generalized to human EEG research. However, given past research demonstrating that hippocampal theta synchronizes with cortical theta (for a review, see Karakaş, 2020), it is possible that scalp EEG provides a readout of cortical theta dynamics that could interact with hippocampal theta.

Indeed, mounting evidence suggests that scalp-recorded theta EEG activity in humans is also related to memory processes. Theta EEG power increases during memory encoding and retrieval across different age groups, including adults (Klimesch et al., 1997; Köster et al., 2017), children (Cuevas et al., 2012; Köster et al., 2017; Rajan and Bell, 2015), and adolescents (Krause et al., 2001, 2007). Moreover, theta EEG power during memory tasks predicts task performance. In adults, greater absolute theta power over the frontal and parietal regions, measured either during or before item encoding, predicted better recall and recognition of these items (for a review, see Herweg et al., 2020). Similar links have been shown in infants and older children. In one study, Begus and colleagues (2015) recorded 11-month-olds' EEG activity while they were exploring novel objects and tested their recognition of these objects in a preferential-looking task. They found that larger differences in absolute theta (3–5 Hz) power over the frontal region between two objects during exploration predicted greater differences in infants' subsequent recognition of these two objects. The effect was specific to the theta band. Similarly, using a mother-infant interaction and object exploration/recognition paradigm, Michel and colleagues (2023) found that greater absolute theta (3.5–5 Hz) power over the fronto-central brain region during object encoding predicted better object recognition in 9–10-month-old infants. The effect was specific to the theta band. In 6–7-year-olds, auditory and visual items that were subsequently remembered (vs. forgotten) elicited greater theta (4–7 Hz) inter-trial phase-synchrony (i.e., greater consistency of phase angle across trials) during memory encoding, although no such effect was observed for theta power (Güntekin et al., 2020). Together, these findings provide evidence that variations in theta EEG activity during item encoding predict subsequent memory performance.

The links between task-related theta and memory processes also involve more complex interactions with gamma oscillations. Theta-gamma coupling describes the modulation of gamma oscillation power by the phase of theta oscillations (Fig. 2). This dynamic interplay is thought to contribute to memory processes by providing temporal references for organizing items within memory and facilitating information transmission across brain regions (for reviews, see Colgin, 2015; Köster, 2024; Lisman and Jensen, 2013). Supporting this idea, rodent studies have shown increased hippocampal theta-gamma coupling during memory tasks involving odor-place and item-context associations. Moreover, the strength of theta-gamma coupling has been found to predict the accuracy of learning performance (Igarashi et al., 2014; Tort et al., 2009). Similarly, studies using scalp-recorded EEG and magnetoencephalography (MEG) in human adults have reported increased theta-gamma coupling during working memory and long-term memory tasks. Importantly, stronger theta-gamma coupling during the tasks predicted better memory performance (Friese et al., 2013; Fuentemilla et al., 2010; Heusser et al., 2016; Köster et al., 2014, 2018). In addition, experimental manipulation of gamma oscillations in specific brain regions has been shown to influence memory processes. For instance, applying bursts of gamma oscillations over the peaks (vs. troughs) of theta oscillations in the prefrontal cortex enhanced spatial working memory in human adults (Alekseichuk et al., 2016). By contrast, applying gamma bursts over the troughs of theta oscillations in the left temporal cortex disrupted verbal long-term memory (Lara et al., 2018). In children, a recent study with 11-year-olds receiving outpatient mental health services found that higher frontal theta-gamma (theta frequency range: 4–7 Hz) coupling during a working memory task predicted better working memory performance (Kavanaugh et al., 2021), although theta power was not associated with task performance. These findings collectively provide evidence for the links between theta-gamma coupling and memory processes across different age groups.

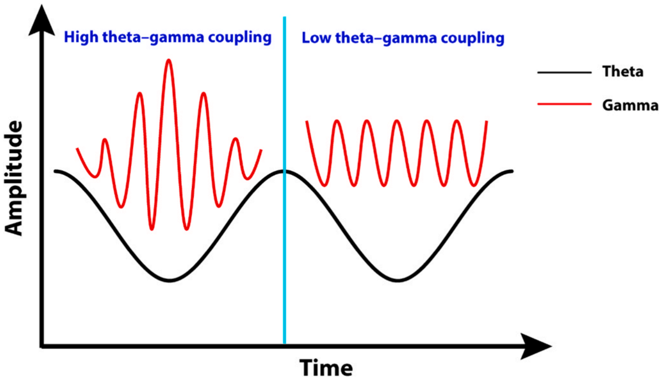

Fig. 2. Theta-gamma coupling. Left: high theta-gamma coupling. Right: low theta-gamma coupling. Adapted from Brooks et al. (2020).

In summary, rodent research demonstrates that hippocampal theta plays a crucial role in memory formation. In human scalp-recorded EEG research, increased theta power and theta-gamma coupling have been observed during memory processes, and higher theta power, theta inter-trial phase-synchrony, and theta-gamma coupling predicted better memory performance. We note that different theta EEG measures may reflect distinct underlying processes. Indeed, dissociations between theta power and theta-gamma coupling have been reported in the literature (e.g., Friese et al., 2013; Köster et al., 2014, 2018). Therefore, findings about one measure of theta (e.g., power) cannot be directly applied to another measure (e.g., theta-gamma coupling). We also note that the associations between theta EEG power and memory performance appear to be more robust in adults (for a review, see Herweg et al., 2020) and infants (Begus et al., 2015; Michel et al., 2023) than in older children (Güntekin et al., 2020; Kavanaugh et al., 2021). Given that developmental evidence on the relations between theta EEG activity and memory is quite limited, more research is needed to clarify these associations in infants and children.

4.2. Attention

Attention and memory are closely related mental processes. Memory research has indicated that successful retrieval of memory items is predicted by theta power not only during, but also before, stimulus presentation (Addante et al., 2011; Guderian et al., 2009; Juergen Fell et al., 2011; Sweeney-Reed et al., 2016). One explanation for these effects is that pre-stimulus theta reflects attention fluctuations that can influence memory encoding (Kim, 2011). However, a detailed examination of the data from these studies (e.g., trial-by-trial analysis) has revealed that attentional fluctuations alone could not entirely explain the pre-stimulus theta effects in memory research (for detailed discussion, see Addante et al., 2011; Sweeney-Reed et al., 2016), suggesting that there are specific links between task-related theta and memory encoding.

Despite this dissociation, the connection between theta brain activity and attentional processes has been well-documented in the literature. Past research suggests that spatial attention samples the environment in theta cycles, with alternating periods of enhanced or attenuated perceptual sensitivity (Dugué et al., 2015; Fiebelkorn et al., 2013; Landau and Fries, 2012; for a review, see Fiebelkorn and Kastner, 2019). These rhythmic fluctuations have been linked to the phase of intrinsic theta brain activity. For example, Busch and VanRullen (2010) demonstrated that visual detection performance for attended stimuli in human adults fluctuated over time. Notably, changes in task performance over time were predicted by the phase of spontaneous theta (~ 7 Hz) EEG activity over the fronto-central brain region before stimulus presentation. Similarly, Helfrich et al., (2018) analyzed brain activity during two attention tasks in adults using intracranial EEG (electrocorticography; ECoG) and found that participants' perceptual performance varied depending on the phase of theta (~ 4 Hz) activity across different cortical regions. Thus, fluctuations in perceptual sensitivity are linked to rhythmic changes in theta activity in the brain.

In addition to oscillatory phase, attentional processes have also been linked to the power of task-related theta EEG activity. In adults, increased theta power over the frontal region is commonly observed during tasks that require heightened attention (Barwick et al., 2012; Gevins et al., 1997; Kamzanova et al., 2011; Wascher et al., 2014). For example, frontal theta power increased during engagement of auditory attention (Ahveninen et al., 2013) and following the presentation of infrequent (vs. frequent) oddball stimuli (Başar-Eroglu et al., 1992; see below for more details about the oddball paradigm). Links between task-related theta power and attentional processes have also been documented in infants. Utilizing a live interaction paradigm, Orekhova and colleagues (1999) demonstrated that 8–11-month-old infants exhibited a sharp increase in absolute theta (3.6–6 Hz) power over the frontal region during anticipatory attention (e.g., when expecting the reappearance of a person in the peek-a-boo game). Moreover, individual differences in frontal theta power during the task predicted infants' ability to maintain internally controlled attention (see also Stroganova et al., 1998). Similarly, using an object exploration task, Wass and colleagues (2018) demonstrated that, during solo play with toys, 12-month-old infants who exhibited higher relative theta (3–7 Hz) power over the central region prior to visual fixations showed longer visual attention. These live interaction studies provide evidence for the links between task-related theta power and attentional processes in infants.

The associations between task-related theta and attention-related processes have also been shown in studies examining infants' responses to dynamic videos. For instance, Begus and colleagues (2016) found that 11-month-old infants exhibited increased absolute theta (3–5 Hz) power over the frontal and temporal regions when they could expect to receive information from others. Crucially, greater theta power was observed when infants could expect information from a native speaker than from a nonnative speaker, suggesting that theta activity is sensitive to the source of information. Relatedly, Jones and colleagues (2020) showed that 12-month-old infants exhibited increased absolute theta (3–6 Hz) power over the frontal region when viewing dynamic videos of people and objects. This type of viewing has been linked to attention, learning, and memory processes (Stroganova and Orekhova, 2007). Increases in frontal theta during the first presentation of a video predicted subsequent responses to the same video, confirming that changes in theta activity were related to learning. Additionally, greater increases in theta power over the course of viewing at 12 months predicted higher cognitive skills measured concurrently and prospectively at 2, 3, and 7 years of age. In a similar vein, Braithwaite and colleagues (2020) found that 6-month-old infants showed increased absolute theta (3–6 Hz) power over the frontal region when viewing dynamic non-social videos, and that greater theta power increases over the course of viewing at 6 months predicted higher non-verbal cognitive abilities at 9 months. Together, these findings demonstrate that task-related theta is associated with attentional processes early in life, and that individual differences in theta activity during tasks predict cognitive abilities.

In infancy, sustained attention is characterized by a reduction in heart rate (Richards, 2008; Richards and Casey, 1991), and the links between theta and attentional processes have also been shown in studies using heart-rate deceleration as an index of sustained attention. For instance, Xie and colleagues (2017) found that 10- and 12-month-old infants exhibited increased theta (2–6 Hz) and decreased alpha power spectral density (PSD) during periods of heart rate-defined sustained attention; no effects were found for beta power. The theta effects were localized to the orbital frontal, temporal pole, and ventral temporal brain regions. Using the same paradigm, Brandes-Aitken and colleagues (2023) found higher absolute theta (4–6 Hz) power over the frontal region in 3-month-old infants during heart rate-defined sustained attention; no significant effects were found for alpha power. Moreover, greater theta power increases during sustained attention were associated with a greater proportion of time spent in sustained attention, and individual differences in theta power increases during sustained attention at 3 months predicted recognition memory at 9 months. These findings further demonstrate the links between task-related theta and attentional processes in infancy, and support the hypothesis that early individual differences in task-related theta predict cognitive abilities.

In attention research, theta activity has also been examined using the oddball paradigm, where brain responses elicited by frequently repeated (standard) and infrequent (deviant) sounds are compared. Neural responses during this paradigm are thought to reflect change/novelty detection and attention orienting (Escera et al., 1998; Näätänen et al., 2007; Polich, 2007). Studies using a two-stimulus oddball task (involving standard and deviant sounds) have found increased absolute theta power and theta inter-trial phase synchrony in response to deviant (vs. standard) sounds over the frontal region in adults (Fuentemilla et al., 2008) and children (Müller et al., 2009). Similarly, in a three-stimulus auditory oddball task (which includes complex novel sounds in addition to standard and deviant sounds), a recent study found that children ages 4–11 years showed increased absolute delta and theta (4–8 Hz) power in response to novel (vs. standard) sounds over the frontocentral region. These effects increased with age, and greater theta inter-trial phase synchrony in response to novel sounds predicted better inhibitory control (Morales et al., 2023). These findings demonstrate that task-related theta activity is implicated in attention-related processes across age groups, with developmental changes occurring throughout childhood and adolescence.

In summary, past research has shown that fluctuations in perceptual sensitivity are linked to the phase of theta activity, and that theta EEG power increases during attentional processes in adults, infants, and children (see also Michelini et al., 2022 for a review showing that individuals with ADHD exhibit weaker theta increases during cognitive tasks, although the effect size was small). These effects have been demonstrated across multiple paradigms, including live interactions, dynamic videos, heart rate-defined sustained attention, and auditory oddball tasks. Importantly, heightened theta activity during attention tasks predicted higher task performance, providing further evidence for the associations between task-related theta activity and cognitive functioning.

4.3. *Cognitive control*

Cognitive control refers to the ability to monitor one's own behaviors for conflicts, errors, and feedback, and to adjust behavior accordingly to achieve desired goals (Ridderinkhof et al., 2004). This ability has been shown to be a strong predictor of real-life outcomes such as academic performance and mental health (Hirsh and Inzlicht, 2010; Tajik-Parvinchi et al., 2021). Past research suggests that cognitive control is closely linked to theta activity in the medial-frontal brain region (for reviews, see Cavanagh and Frank, 2014; Cohen, 2014). Theta activity is thought to be involved in the interplay between task-related brain regions during cognitive control (Cavanagh and Frank, 2014; Fries, 2005; Varela et al., 2001). Supporting this idea, studies have found increased theta phase consistency between the medial-frontal region and task-related brain regions (e.g., lateral prefrontal cortex, motor/-sensory cortices) in response to events signaling a need for control (Bowers et al., 2021; Buzzell et al., 2019; Cavanagh et al., 2009; Hanslmayr et al., 2008; Morales et al., 2022; Nigbur et al., 2012; Van de Vijver et al., 2011; van Driel et al., 2012). Theta phase resetting is also believed to be related to event-related potential (ERP) components commonly observed during engagement of cognitive control, including the error-related negativity (ERN; evoked by one's own errors), the N2 (evoked by signals indicating the need for control), and the feedback-related negativity (FRN; evoked by negative feedback; for a review, see McLoughlin et al., 2021). These ERP components have been source localized to brain areas associated with cognitive control processes, including the anterior cingulate cortex (ACC; Luu et al., 2003; Veen and Carter, 2002) and the posterior cingulate cortex (PCC; Buzzell et al., 2017; for reviews, see Botvinick et al., 2004; Taylor et al., 2007).

In addition to phase synchrony and ERP components, the association between theta activity and cognitive control has also been shown in EEG power. In adults, increased theta power has been observed when individuals detect errors in the environment, including arithmetic errors (Tzur et al., 2010; Tzur and Berger, 2007, 2009) and semantic errors (Hald et al., 2006). Similar effects have been shown in infants (for reviews, see Begus and Bonawitz, 2020; Berger and Posner, 2022). For instance, Berger and colleagues (2006) found that 6–9-month-old infants exhibited greater absolute power in the theta and alpha ranges over the medial-frontal region when presented with incorrect (e.g., 1+1=1) versus correct (e.g., 1+1=2) arithmetic solutions. Similarly, Conejero and colleagues (2018) found greater theta (6–7 Hz) power over the medial-frontal region in adults and 16–18-month-old children when they viewed incorrect (vs. correct) puzzle configurations, particularly in children from more educated families. Köster and colleagues (2021) further showed that 9-month-old infants exhibited increased absolute theta (4–5 Hz) power across the scalp when presented with unexpected (vs. expected) outcomes in physical and social events (see also Köster et al., 2019; Reid et al., 2009). This pattern extends to older children and adolescents. For example, Schneider and Maguire (2019) found that 8–9-year-olds, 12–13-year-olds, and adults showed increased absolute theta (4–8 Hz) power over the right frontal and parietal regions to semantically incorrect (vs. correct) sentences. These findings collectively demonstrate that task-related theta power increases when individuals across different age groups process errors in their environment.

Increased midfrontal theta power has also been observed in adults during control processes related to their own behaviors, including response conflicts (Cohen and Cavanagh, 2011; Cohen and Donner, 2013; Nigbur et al., 2011), error monitoring (Cavanagh et al., 2009; Luu et al., 2004; Trujillo and Allen, 2007), task switching (Cunillera et al., 2012), and feedback processing (Cavanagh et al., 2010). Similarly, in infants and children, heightened theta power has been observed during tasks with increased cognitive and emotional demands. For instance, Orekhova and colleagues (2006) found that 7–12-month-old infants and 4–6-year-old preschool children showed increased absolute theta (3.6–5.6 Hz in infants and 4–8 Hz in preschool children) power over frontal and posterior brain regions during situations requiring higher emotional and cognitive load (i.e., actively exploring an attractive toy, attending to child-directed speech) than during baseline (i.e., passively observing an adult blowing soap bubbles; the situation was terminated if infants showed overt emotional responses). In a similar vein, Meyer and colleagues (2019) found elevated absolute theta (3–6 Hz) power over the midfrontal region in 4-year-old children during tasks with higher cognitive demands (e.g., imitating actions in movie clips vs. passively viewing movie clips). This effect was specific to the theta band. Likewise, Adam and colleagues (2020) reported increased absolute theta (4–8 Hz) power over the midfrontal region in 4–6-year-old and 6–8-year-old children when resisting distracting information (e.g., a change in stimulus-response mapping between the previous and current trials) that could interfere with their ongoing action. In adolescence, a recent study showed that theta (4–8 Hz) power over the medial-frontal region before and after motor responses was associated with conflict monitoring and error monitoring, respectively. In addition, theta measures indexing post-response error monitoring and proactive control were affected by social observation, suggesting that theta-related monitoring and control processes are sensitive to social influences (Buzzell et al., 2019). These findings highlight the consistent involvement of midfrontal theta power during cognitive control tasks.

Recent studies suggest that there are age-related changes in theta activity associated with cognitive control. These effects have been shown in two paradigms. In the go/no-go paradigm, participants are instructed to either respond (i.e., pressing a designated key) or withhold a response based on whether a go or no-go signal is presented (Verbruggen and Logan, 2008). In the flanker paradigm, participants make responses (e.g., pressing the left or right arrow key) based on the direction of a target arrow presented in the center of the screen. Crucially, the target is flanked by nontarget arrows that are either facing in the same (congruent) direction or in the opposite (incongruent) direction as the target (Eriksen and Eriksen, 1974). These paradigms have been widely used to assess inhibitory control and error processing. Using the go/no-go paradigm, Xu and colleagues (in press) found increased theta frontocentral power for trials requiring inhibitory control (no-go), compared with go trials, in a sample of 4–11-year-old children. In the same sample, Morales and colleagues (2022) found that 4–9-year-old children showed increased absolute delta and theta (4–8 Hz) power over the frontocentral region following an incorrect (vs. correct) response, and that the magnitude of these effects increased with age. Using the same task, Liu and colleagues (2014) found that task-related theta (4–8 Hz) power over the medial prefrontal region during no-go trials increased with age from 8 to 18 years, and that these age-related changes partially mediated improvements in response control ability over time. In studies using the flanker paradigm, age-related increases in theta-related ERPs and source activity have been documented across late childhood and adolescence (Buzzell et al., 2017; Davies et al., 2004; for a review, see Tamnes et al., 2013). These findings collectively demonstrate ongoing developmental changes in theta-related control processes throughout childhood and adolescence.

In summary, past research demonstrates that cognitive control is linked to theta activity over the medial-frontal brain region. Theta activity is associated with ERP components indexing control processes (e.g., the ERN, N2, FRN), and increased theta phase consistency has been observed across brain regions during cognitive control. Theta EEG power increases when adults, infants, and children detect errors in the environment and when they engage in control processes related to their own behaviors. In addition, developmental studies have shown that the magnitude of theta power during control processes increases with age, and that these age-related changes predict improvements in cognitive control over time.

4.4. Interim discussion

The studies reviewed above provide evidence that theta EEG power increases during engagement in memory, attention, and cognitive control tasks. In contrast to the negative correlation typically observed between resting theta power and cognitive abilities, task-related theta power is positively linked to cognitive functioning. It is worth noting that, compared with resting theta, task-related theta effects tend to be more specific to the frontal region (although many task-related studies only analyzed theta activity in frontal areas). We also note that there are considerable variations across task-related EEG studies in analysis time window and the time course of observed theta effects (see Table A.2). While some studies have shown theta power increases over 30-second videos (e.g., Braithwaite et al., 2020), others have reported theta power changes at the millisecond-level timescale (e.g., Morales et al., 2023).

Similar to resting theta, many of the links between task-related theta power and cognitive performance are correlational (e.g., theta power increases during heart rate-defined sustained attention). However, experimental manipulation studies have shown that changes in attentional state (e.g., Begus et al., 2016; Morales et al., 2023), error detection (Berger et al., 2006; Conejero et al., 2018; Köster et al., 2021; Schneider and Maguire, 2019), and cognitive/emotional demands (Meyer et al., 2019; Orekhova et al., 2006) can lead to changes in theta power. In addition, research utilizing transcranial alternating current stimulation (tACS) has shown that applying electrical currents at theta frequency to synchronize neural firing over the frontal and parietal regions improves performance on executive functioning and memory tasks in adults (for recent reviews, see Lee et al., 2023; Nissim et al., 2023), suggesting that alterations in theta activity can have a causal influence on cognitive performance.

As noted earlier, the cognitive processes discussed in this section are interconnected. For instance, cognitive control guides attention, and attention is essential for effective memory encoding. Conversely, memory can affect attention, and attention influences our ability to detect errors, resolve conflict, or process feedback within the internal or external environment. While there is overlap between these cognitive processes, a careful examination of the spatial-temporal-spectral characteristics of theta activity during different tasks reveals that theta activity may represent distinct mechanisms across domains. For a detailed discussion of this topic, see Cohen (2014) and Saby and Marshall (2012).

While the links between task-related theta and cognitive functioning have been most commonly reported in the domains discussed above, changes in theta power have also been associated with other processes, such as language (Fernández et al., 2012; Maguire et al., 2022; Schneider et al., 2023; Schneider and Maguire, 2019; Spironelli and Angrilli, 2010; Zhang et al., 2011) and social processing (Angelini et al., 2023; Haartsen et al., 2022; Jones et al., 2015; Michel et al., 2015; van der Velde et al., 2021). Considering that language and social processing involve higher-level cognitive functions supported by memory, attention, and cognitive control, it is essential for future research to investigate whether and how theta activity is uniquely linked to these higher-level processes beyond its role in the domains discussed above.

Future research should also examine the extent to which the associations between theta power and cognitive functioning are driven by eye movements. Although preprocessing techniques (e.g., independent component analysis; ICA) have been commonly employed to reduce EEG artifacts, it is difficult to entirely remove eye-movement effects from the data. Because eye movements occur at intervals consistent with the theta rhythm (Fries, 2023), the positive associations between cognitive performance and theta power could stem from increased eye movements during cognitive tasks. For example, more frequent eye movements may generate theta-rhythmic artifacts, resulting in increased theta power. Alternatively, neural processing of new visual information following saccades can reset the phase of ongoing rhythms, resulting in theta-rhythmic brain activity (Barczak et al., 2019; Hoffman et al., 2013). To address this question, future research should conduct EEG and eye movement co-recordings to determine the extent to which theta EEG effects are attributable to eye movements. It is also important to note that eye movements may be less likely to account for theta effects observed in studies using auditory (vs. visual) stimuli. For instance, increased theta power has been observed in response to novel versus standard sounds in children (Morales et al., 2023). Here, visual inputs (and presumably eye movements) were not linked to the auditory events eliciting the theta response. However, because participants were not instructed to maintain steady eye positions in this study, it remains difficult to fully rule out the potential effects of eye movements. Nonetheless, research with adults has shown increased theta activity in response to deviant versus standard sounds after excluding EEG epochs containing ocular artifacts (Fuentemilla et al., 2008), suggesting that the effect was not driven by eye movements.

5. Why do resting theta and task-related theta show different correlations with cognitive functioning?

We have presented evidence that resting theta and task-related theta have different relations to cognitive functioning. Specifically, early exposure to environmental adversity is associated with higher resting theta power, and children who exhibit higher resting theta power tend to show lower executive functioning, attentional abilities, language skills, and IQ scores. By contrast, theta power exhibits event-related increases during memory encoding, attention, and cognitive control, and higher theta power during these processes predicts better behavioral performance. Why does theta activity exhibit distinct functional properties across contexts? In the following sections, we explore potential reasons for this disparity and suggest future directions for research addressing this question.

5.1. Narrowband versus broadband EEG activity

One explanation for resting theta and task-related theta's distinct functional properties is that they represent different brain processes. Past research has demonstrated that resting theta and task-related theta show distinct developmental trajectories. While resting theta power decreases with age (Benninger et al., 1984; Clarke et al., 2001; Perone et al., 2018), task-related theta power has been shown to increase with age, at least up until the adolescent period (Liu et al., 2014; Morales et al., 2022; Papenberg et al., 2013; Schneider and Maguire, 2019; see also Crowley et al., 2014; Uhlhaas et al., 2009; van Noordt et al., 2022; Xu et al., in press). These distinct developmental paths support the idea that resting theta and task-related theta may represent distinct neurocognitive processes.

In line with this view, Klimesch (1999) proposed that the increased theta power observed during memory tasks may reflect a narrowband increase in theta synchronization in cortico-hippocampal feedback loops, which is crucial for information encoding (Kota et al., 2020). By contrast, elevated theta power during resting state may reflect irregular slow activity (ISA), which leads to a broadband increase in lower-frequency power but could disrupt information processing. Indeed, the presence of EEG power in a frequency band does not necessarily indicate the presence of physiological oscillations in that specific frequency band (Bullock et al., 2003; Jasper, 1948). An increase in theta power can stem from either an increase in narrowband theta activity or a change in broadband power distribution across the entire spectrum. To understand the differential correlations between resting/task-related theta and cognitive functioning, it is important to dissociate narrowband theta activity from broadband power changes in neural activity.

Recently, there has been a growing interest in parameterizing EEG signals into aperiodic and periodic components (Donoghue, Haller, et al., 2020; Ostlund et al., 2022). Aperiodic activity refers to the irregular, arrhythmic component of neural signals, which is influenced by the average rate of neuronal population spiking (Manning et al., 2009) and the balance between excitatory (glutamatergic) and inhibitory (GABAergic) inputs (Gao et al., 2017). This broadband component contributes to the '1/f' slope of the power spectrum (Fig. 3). Periodic activity refers to the rhythmic component of neural activity that rises above the '1/f' slope of the power spectrum. It represents recurring patterns of neural activity at a specific frequency and is thought to reflect putative oscillations in the brain. These two EEG components have been shown to exhibit distinct properties and dynamics across tasks (He, 2014).

The separation of the aperiodic and periodic EEG components allows for a more precise characterization of brain activity. Recent research suggests that changes in aperiodic activity may explain some effects previously attributed to power changes in specific frequency bands. For

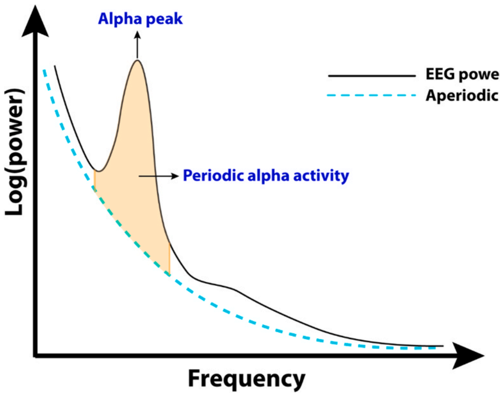

Fig. 3. Aperiodic and periodic EEG activity. Adapted from Donoghue, Haller, et al. (2020).

example, the age-related shift in resting EEG power from lower to higher frequency bands has been shown to be better explained by changes in aperiodic activity rather than power changes in individual frequency bands (Donoghue, Haller, et al., 2020; Finley et al., 2022; Hill et al., 2022; Tran et al., 2020). This is because the aperiodic slope (1/f) gets smaller/flatter with age across development starting from infancy (McSweeney et al., 2021, 2023; Schaworonkow and Voytek, 2021). Moreover, aperiodic activity has been shown to better explain individual differences in theta/beta ratio (Donoghue, Dominguez, et al., 2020) and predict ADHD status in children (Robertson et al., 2019; see also Karalunas et al., 2022; Ostlund et al., 2021) than does power within individual frequency bands. Consistent with this idea, a recent study found that the association between resting alpha power and cognitive processing speed in adults was better accounted for by aperiodic activity than by aperiodic-adjusted alpha power (Ouyang et al., 2020). These findings highlight the importance of disentangling periodic and aperiodic activity in understanding how specific aspects of neural activity relate to cognitive functioning (Herweg et al., 2020).

We reason that resting theta may primarily reflect individual differences in aperiodic activity, whereas changes in theta power during cognitive tasks may be more attributable to periodic theta activity. Indeed, resting EEG studies have shown that early adversity and lower cognitive functioning are associated not only with an increase in theta power but also with a decrease in higher-frequency (e.g., alpha) power (Debnath et al., 2020; Marshall et al., 2004; Vanderwert et al., 2016), suggesting that these effects are explained by changes in aperiodic activity across the entire spectrum. By contrast, task-related theta studies typically focus on specific time windows during which cognitive processes occur, where EEG power in the theta band increases relative to other frequency bands. Moreover, these studies typically examine condition differences and utilize baseline correction methods, which likely reduce the confounding effects of aperiodic components (Morales and Bowers, 2022). Thus, the positive correlations between task-related theta and cognitive functioning may be more specifically driven by periodic theta activity. This idea is further supported by research showing significant associations between task-related theta power and memory encoding even with the 1/f background signal subtracted from the power spectrum (Caplan and Glaholt, 2007; Fellner et al., 2019; Lega et al., 2012), suggesting that memory encoding is specifically associated with periodic theta activity.

In addition to the spectral parameterization approach described above, theta activity can also be studied using a cycle-by-cycle approach (Cole and Voytek, 2019). Unlike methods that decompose EEG signals across time into constituent sinusoids, this analysis approach segments continuous signals into cycles (by identifying zero-crossings, peaks, and troughs) and computes oscillatory features (e.g., amplitude, period/-frequency) for each cycle. This allows researchers to confirm the presence of theta oscillations at any given moment, without the interference of aperiodic activity. By applying this approach to resting/task-related EEG data, future research can investigate whether participants are more likely to exhibit theta oscillations in EEG signals during cognitive tasks (vs. resting state), how the features of theta oscillations change over time during the tasks, and whether the features of theta oscillations predict individual differences in cognitive abilities.

5.2. *The engagement of cognitive effort during resting state and lower relative increase in theta power during tasks*

If we consider the possibility that resting theta and task-related theta may reflect the same underlying mechanism, then an alternative explanation for the negative correlations between resting theta power and cognitive functioning emerges. It is possible that increased theta power during resting state signifies the engagement of cognitive effort in the absence of specific tasks. We note that developmental EEG studies have used a wide range of paradigms to assess children's "resting" brain activity, including eyes-open/eyes-closed conditions, lights on/off, and passive viewing of stimuli such as videos (e.g., bubbles, moving shapes) or spinning bingo wheels (Anderson and Perone, 2018; Norton et al., 2021). Although children are not tasked with anything specific during these procedures, these paradigms may require increased cognitive control for children to remain still and inhibit physical movement (Camacho et al., 2020). As noted above, theta power tends to increase during sustained attention (Brandes-Aitken et al., 2023; Xie et al., 2017) and elevated task demands (Meyer et al., 2019; Orekhova et al., 2006). Hence, children exhibiting increased theta power during these "resting" periods might be those requiring more mental effort to regulate their behavior, and this behavioral/EEG pattern could be associated with lower cognitive abilities. Indeed, past research suggests that the negative associations between resting theta and cognitive functioning are more robust in children than in adults (Finnigan and Robertson, 2011; Kavcic et al., 2016; Sargent et al., 2021; cf. Jelic et al., 1996; Roca-Stappung et al., 2012). This aligns with the hypothesis that children need more mental effort to remain still and inhibit movement during "resting" periods, rendering resting theta power early (vs. later) in life more predictive of cognitive functioning.

Relatedly, individuals with higher overall levels of theta activity across contexts may also exhibit lower relative increases in theta during cognitive processes. If differences in cognitive functioning are linked to task-related *changes* in theta power from the resting state, then higher resting theta and diminished task-related theta increments could be associated with lower cognitive performance. As previously discussed, task-related theta studies typically focus on changes in theta activity across experimental conditions. Hence, the positive associations between task-related theta and cognitive functioning may primarily stem from task-related increments in theta power rather than the overall levels of theta. Future research should test this hypothesis by examining how cognitive functioning is associated with resting theta power, overall theta power during tasks, and task-related changes in theta power. Such investigations will shed light on whether cognitive performance is better predicted by the relative changes in theta activity during cognitive engagement.

5.3. *Future directions*

To better understand the relations between resting/task-related theta power and cognitive functioning, future research should examine whether these associations stem from periodic theta activity or the aperiodic component of EEG signals (Donoghue, Haller, et al., 2020; Ostlund et al., 2022). While previous studies examining relative power have provided insights into how changes in theta power, relative to other frequency bands, are related to cognitive functioning, these effects could still be influenced by broadband effects (e.g., changes in aperiodic slope), leaving it unclear whether periodic theta activity plays a role. We call for future research to parameterize EEG signals into periodic and aperiodic components and systematically examine how these two components are associated with different aspects of cognitive functioning during resting state versus tasks. Additionally, applying cycle-by-cycle analysis (Cole and Voytek, 2019) to resting and task-related EEG data could shed light on whether real-time fluctuations in theta power are driven by putative theta oscillations. Such investigations will provide a more nuanced understanding of theta activity and its relations with cognitive processes.

To explore whether the negative associations between resting theta power and cognitive abilities are driven by cognitive engagement during resting-state procedures, future research should investigate whether these associations are stronger when measured over the medial-frontal region, where theta power increases associated with cognitive control are typically observed (Cavanagh and Frank, 2014). Moreover, it would be valuable to assess whether these associations are influenced by children's physical activity levels. Children with higher physical activity levels may require more cognitive resources to restrain physical movement during resting-state procedures. If resting theta power indeed reflects cognitive control engagement, it should correlate positively with children's physical activity levels. Future research should also examine how the connections between resting/task-related theta and cognitive functioning change across development. If the negative associations between resting theta power and cognitive functioning arise from cognitive effort during resting-state procedures, these associations should decrease as children grow older. This is because older (vs. younger) children likely require less mental effort to inhibit movements and remain still during resting-state procedures. Consequently, resting theta power in older (vs. younger) children is less likely to reflect meaningful individual differences in cognitive capacity.

The nature of resting theta and task-related theta can also be clarified by examining their intercorrelations. We note that existing studies on theta EEG activity tend to focus solely on either resting theta or task-related theta within separate groups/individuals, leaving a gap in understanding the relations between the two and their changes within individuals across time. In a recent study, Pscherer et al. (2021) examined both resting theta and task-related theta during the go/no-go task in individuals ages 8–30 years. They found positive associations between resting theta power and baseline-corrected theta power during correctly rejected no-go trials in individuals over the age of 10.7 years, but not in younger individuals (see also Pscherer et al., 2019, 2020). These findings suggest that resting theta and task-related theta might represent mechanisms that are relatively independent in younger children, and that these mechanisms may become more intertwined with age. Future research should test these relations across different cognitive domains and within individuals over time.

Future studies should also investigate the neural origins of resting and task-related theta activity. Techniques such as cortical source analysis of EEG signals (Beese et al., 2017; Xie et al., 2017) and simultaneous EEG and fMRI recording (Mantini et al., 2007) have provided insights into the brain regions generating oscillatory EEG activity. These methods can help distinguish between different theta-related mechanisms across contexts (Cellier et al., 2021; Cohen, 2014). We call for future research to systematically examine the neural generators of theta during both resting state and tasks. Moreover, a deeper understanding of the differences between resting theta and task-related theta can be attained by carefully examining the spectral characteristics of theta activity across contexts. For instance, consistent peak frequencies in theta activity during resting state, contrasted with varying peak frequencies between resting state and tasks, would support the hypothesis that resting theta and task-related theta represent distinct brain processes.

CRediT authorship contribution statement

Enda Tan: Writing – review & editing, Writing – original draft, Visualization, Investigation, Conceptualization. **Sonya Troller-Renfree:** Writing – review & editing, Conceptualization. **Santiago Morales:** Writing – review & editing, Conceptualization. **George Buzzell:** Writing – review & editing, Conceptualization. **Marco McSweeney:** Writing – review & editing. **Martín Antúnez:** Writing – review & editing. **Nathan Fox:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization.

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.

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Data statement

This review paper did not involve any data collection.

Appendices

Table A.1

Key developmental studies on the relations between resting theta EEG power and cognitive functioning

Resting EEG				
Construct	**Study**	**Participants (Age Groups)**	**Resting EEG Paradigm**	**Main Findings**
Executive functioning	Maguire and Schneider (2019)	8–15-year-olds from high- and low-income families	Eyes-open/eyes-closed	Higher resting theta (4–8 Hz) power over the right parietal brain region was associated with lower working memory.
Executive functioning	Perone et al. (2018)	3–9-year-olds	Eyes-open/eyes-closed	Higher resting theta/beta power ratios (theta frequency range:.4×IAF-.8×IAF) over frontal and posterior regions predicted lower performance on working memory, inhibitory

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Table A.1 (*continued*)

Resting EEG				
Construct	**Study**	**Participants (Age Groups)**	**Resting EEG Paradigm**	**Main Findings**
				control, and cognitive flexibility tasks after controlling for age and verbal abilities.
Executive functioning	Cai et al. (2021)	7–9-year-olds	Eyes-open/eyes-closed	After controlling for age and verbal ability, greater resting alpha/theta and beta/theta ratios (theta frequency range: 4 Hz - IAF-2 Hz) over the frontal brain region predicted higher inhibition skills, and greater resting beta/theta ratios predicted higher planning skills.
Attention	Perone and Gartstein (2019)	6–12-month-olds	Passive viewing of videos depicting colorful objects	Higher relative resting theta (3–6 Hz) power and lower relative resting beta and gamma power over the frontal region were associated with lower parent-reported attentional abilities.
Attention	Clarke et al. (2002)	8–13-year-old males diagnosed with ADHD	Eyes-closed	Participants diagnosed with ADHD exhibited higher absolute and relative theta (3.5–7.5 Hz) power, lower relative alpha, and higher theta/alpha and theta/beta ratios across brain regions.
Attention	Lazzaro et al. (1999)	11–17-year-old males diagnosed with ADHD	Eyes-open (looking at a small circular dot on a screen)	Participants diagnosed with ADHD exhibited higher absolute and relative theta (4.0–7.0 Hz) and alpha power and lower relative beta power across brain regions.
Language	Lum et al. (2022)	9–11-year-olds	Eyes-open (looking at a cross on a screen)	Absolute resting theta (4–8 Hz) power over the left central-prefrontal regions was negatively associated with performance on a sentence repetition task. The association was specific to the theta band.
Language	Meng et al. (2022)	7–11-year-olds	Eyes-open (looking at a cross on a screen)	Greater reductions in relative resting theta (4–8 Hz) power across the scalp from 7 to 9 years and from 7 to 11 years predicted higher expressive vocabulary at 9 and 11 years, respectively. Greater increases in beta power across the scalp from 7 to 9 years predicted higher receptive vocabulary at 11 years.
Language	Papagiannopoulou and Lagopoulos (2016)	8-year-olds diagnosed with dyslexia	Eyes-closed	Participants diagnosed with dyslexia showed increased resting relative theta (3.6–7.4 Hz) power over the left frontal brain region.
Language	Arns et al. (2007)	10–16-year-olds diagnosed with dyslexia	Eyes-open (looking at a red dot on a screen)	Participants diagnosed with dyslexia showed increased absolute resting delta and theta (4–7.5 Hz) power over the frontal and right temporal brain regions.
IQ	Tan et al. (2023)	EEG assessment points: 22–42 months	Passive viewing of a spinning bingo wheel	Higher relative resting theta (3–5 Hz) power measured across the scalp across three assessments from 22 to 42 months predicted lower full-scale IQ at 18 years. The effect was specific to the theta band.

Table A.2
Key developmental studies on the relations between task-related theta EEG power and cognitive functioning

Construct	Study	Participants	Paradigm	Analysis Time Window	Main Findings
Memory	Begus et al. (2015)	11-month-olds	Object exploration and recognition	0–40 s (while the infant was looking at the object)	Larger differences in absolute theta (3–5 Hz) power over the frontal region between two objects during exploration predicted greater differences in infants' subsequent recognition of these two objects. The effect was specific to the theta band.
Memory	Michel et al. (2023)	9–10-month-olds	Object exploration and recognition (with mother)	0–20 s (while the infant was looking at the object)	Greater absolute theta (3.5–5 Hz) power over the fronto-central brain region during object encoding predicted better subsequent object recognition. The effect was specific to the theta band.
Memory	Güntekin et al. (2020)	6–7-year-olds	Visual and auditory memory tasks	0–400 ms (during stimulus presentation)	Remembered (vs. forgotten) items elicited greater theta (4–7 Hz) phase-locking during memory encoding. No such effect was found for theta power.
Memory	Kavanaugh et al. (2021)	11-year-olds receiving outpatient mental health services	The Sternberg spatial working memory test (SWMT)	0–6 s (during encoding, maintenance, and the initial portion of the probe)	Higher frontal theta-gamma coupling predicted higher working memory performance. Theta power was not associated with task performance.
Attention	Orekhova et al. (1999)	8–11-month-olds	1. Attention to an object in the visual field 2. Anticipation of the person in the peek-a-boo game 3. Attention to the reappeared person in the peek-a-boo game	The length of the analysis time window ranged from 4 s to 15 s, depending on infants' behavior.	Infants exhibited a sharp increase in absolute theta (3.6–6 Hz) power over the frontal region during anticipatory attention. Individual differences in frontal theta power during the task predicted infants' ability to maintain internally controlled attention.

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Table A.2 (*continued*)

Construct	Study	Participants	Paradigm	Analysis Time Window	Main Findings
Attention	Wass et al. (2018)	12-month-olds	Solo play with toys and joint play with parents	-1000–0 ms prior to the onset of a look	During solo play with toys, infants who exhibited higher relative theta (3–7 Hz) power over the central region prior to visual fixations showed longer visual attention.
Attention	Begus et al. (2016)	11-month-olds	Dynamic videos of people interacting with objects	The last 1 s of the anticipation period	Infants exhibited increased absolute theta (3–5 Hz) power over the frontal and temporal regions when they could expect to receive information from others. Greater theta power was observed when infants could expect information from a native speaker than from a nonnative speaker
Attention	Jones et al. (2020)	12-month-olds	Dynamic videos of people and objects	The main measure was the percent change in theta power between the first and second halves of the first presentation of each video. Each video was 30–60 s in length.	Infants exhibited increased absolute theta (3–6 Hz) power over the frontal region when viewing the videos. Increases in frontal theta during the first presentation of a video predicted subsequent responses to the same video. Greater increases in theta power over the course of viewing at 12 months predicted higher cognitive skills measured concurrently and prospectively at 2, 3 and 7 years of age.
Attention	Braithwaite et al. (2020)	6-month-olds	Dynamic non-social videos	The main measure was the change in theta power between the first and second halves of the video. Each video was 60 s in length.	Infants showed increased absolute theta (3–6 Hz) power over the frontal region when viewing dynamic non-social videos. Greater theta power increases over the course of viewing at 6 months predicted higher non-verbal cognitive abilities at 9 months.
Attention	Xie et al. (2017)	10- and 12-month-olds	Dynamic videos of dancing and singing characters	The video was 4 min in length. Sustained attention was defined as the periods during which the infant was looking at the screen with heart rate below the pre-stimulus level.	Infants showed increased theta (2–6 Hz) and decreased alpha power spectral density during heart rate-defined sustained attention. The theta effects were localized to the orbital frontal, temporal pole, and ventral temporal brain regions.
Attention	Brandes-Aitken et al. (2023)	3-month-olds	Dynamic videos of dancing and singing characters	The video was 4 min in length. Sustained attention was defined as the periods during which the infant was looking at the screen with heart rate below the pre-stimulus level.	Infants exhibited higher absolute theta (4–6 Hz) power over the frontal region during heart rate-defined sustained attention. Greater theta power during sustained attention predicted increased proportion of time in sustained attention. Greater increases in theta power during sustained attention at 3 months predicted better recognition memory at 9 months.
Attention	Morales et al., (2023)	4–11-year-olds	Three-stimulus auditory oddball task	0–500 ms post-stimulus	Children showed increased absolute delta and theta (4–8 Hz) power over the frontocentral region in response to novel (vs. standard) sounds. These effects increased with age, and greater theta inter-trial phase synchrony in response to novel sounds predicted higher inhibitory control.
Cognitive control	Berger et al. (2006)	6–9-month-olds	Puppet show videos	0–700 ms post-stimulus	Infants exhibited greater absolute power in the theta and alpha ranges over the mediofrontal region when viewing presentation of incorrect (e.g., 1+1=1) versus correct (e.g., 1+1=2) arithmetic solutions.
Cognitive control	Conejero et al. (2018)	16–18-month-olds and adults	Videos showing progressive completion of puzzles	0–750 ms post-stimulus	Children and adults showed greater absolute theta (6–7 Hz) power over the mediofrontal region when observing incorrect (vs. correct) puzzle configurations. Children from more highly educated families showed stronger theta increments.
Cognitive control	Köster et al. (2021)	9-month-olds	Videos of physical and social events	0–2000 ms post-stimulus	Infants showed increased absolute theta (4–5 Hz) power across the scalp when they viewed unexpected (vs. expected) outcomes in physical and social events.
Cognitive control	Schneider and Maguire (2019)	8–9-year-olds, 12–13-year-olds, and adults	Auditory sentence processing tasks	0–1000 ms post-stimulus	Children and adults showed increased absolute theta (4–8 Hz) power over the right frontal and parietal regions to semantically incorrect (vs. correct) sentences
Cognitive control	Orekhova et al. (2006)	7–12-month-olds and 4–6-year-olds	Baseline and two test conditions (exploring toys, attending to speech)	Each condition was ~ 2 min in length.	Participants showed increased absolute theta (3.6–5.6 Hz in infants and 4–8 Hz in preschoolers) power over frontal and posterior brain regions in situations involving higher emotional and cognitive load than during baseline.

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Table A.2 (*continued*)

Construct	Study	Participants	Paradigm	Analysis Time Window	Main Findings
Cognitive control	Meyer et al. (2019)	4-year-olds	Three conditions: No Task, Color-naming Task, Imitation Task	Each trial started with a 1-second fixation cross (1 s) followed by a video clip (~ 7 s in length).	Children exhibited increased absolute theta (3–6 Hz) power over the midfrontal region during tasks with higher cognitive demand (e.g., imitating actions in movie clips vs. passively viewing movie clips). This effect was specific to the theta band.
Cognitive control	Adam et al. (2020)	4–6-year-olds and 6–8-year-olds	An interference task adapted from the "heart and flower" task" (Davidson et al., 2006)	0–1500 ms post-stimulus	Children showed increased absolute theta (4–8 Hz) power over the midfrontal region when resisting acting based on distracting information that could interfere with their ongoing action.
Cognitive control	Morales et al. (2022)	4–9-year-olds	The go/no-go paradigm	0–600 ms post-response	Children exhibited increased absolute delta and theta (4–8 Hz) power over the frontocentral region after making an incorrect (vs. correct) response. The magnitude of these effects increased with age.
Cognitive control	Liu et al. (2014)	8–18-year-olds	The go/no-go paradigm	0–800 ms post-stimulus	Baseline-corrected task-related theta (4–8 Hz) power over the medial prefrontal region during correct no-go trials increased with age from 8 to 18 years. These age-related changes partially mediated improvements in response control ability over time.

References

Adam, N., Blaye, A., Gulbinaite, R., Delorme, A., Farrer, C., 2020. The role of midfrontal theta oscillations across the development of cognitive control in preschoolers and school-age children. Dev. Sci. *23* (5), e12936 https://doi.org/10.1111/desc.12936.

Addante, R.J., Watrous, A.J., Yonelinas, A.P., Ekstrom, A.D., Ranganath, C., 2011. Prestimulus theta activity predicts correct source memory retrieval. Proc. Natl. Acad. Sci. *108* (26), 10702–10707. https://doi.org/10.1073/pnas.1014528108.

Ahveninen, J., Huang, S., Belliveau, J.W., Chang, W.-T., Hämäläinen, M., 2013. Dynamic oscillatory processes governing cued orienting and allocation of auditory attention. J. Cogn. Neurosci. 25 (11), 1926–1943.

Alekseichuk, I., Turi, Z., Amador de Lara, G., Antal, A., Paulus, W., 2016. Spatial Working Memory in Humans Depends on Theta and High Gamma Synchronization in the Prefrontal Cortex. Curr. Biol. *26* (12), 1513–1521. https://doi.org/10.1016/j.cub.2016.04.035.

Anderson, A.J., Perone, S., 2018. Developmental change in the resting state electroencephalogram: Insights into cognition and the brain. Brain Cogn. *126*, 40–52. https://doi.org/10.1016/j.bandc.2018.08.001.

Anderson, P., 2002. Assessment and development of executive function (EF) during childhood. Child Neuropsychol. *8* (2), 71–82.

Angelini, L., Tamburro, G., Lionetti, F., Spinelli, M., Comani, S., Zappasodi, F., Fasolo, M., Aureli, T., 2023. Alpha and theta brain activity in 9-month-old infants during a live referential gaze paradigm. Psychophysiology *60* (3), e14198. https://doi.org/10.1111/psyp.14198.

Arns, M., Peters, S., Breteler, R., Verhoeven, L., 2007. Different brain activation patterns in dyslexic children: Evidence from EEG power and coherence patterns for the double-deficit theory of dyslexia. J. Integr. Neurosci. *6* (01), 175–190.

Arns, M., Conners, C.K., Kraemer, H.C., 2013. A decade of EEG theta/beta ratio research in ADHD: a meta-analysis. J. Atten. Disord. *17* (5), 374–383.

Atallah, B.V., Scanziani, M., 2009. Instantaneous Modulation of Gamma Oscillation Frequency by Balancing Excitation with Inhibition. Neuron *62* (4), 566–577. https://doi.org/10.1016/j.neuron.2009.04.027.

Barczak, A., Haegens, S., Ross, D.A., McGinnis, T., Lakatos, P., Schroeder, C.E., 2019. Dynamic modulation of cortical excitability during visual active sensing. Cell Rep. 27 (12), 3447–3459.

Barry, R.J., Clarke, A.R., Johnstone, S.J., 2003. A review of electrophysiology in attention-deficit/hyperactivity disorder: I. Qualitative and quantitative electroencephalography. Clin. Neurophysiol. *114* (2), 171–183.

Barry, R.J., Clarke, A.R., Hajos, M., McCarthy, R., Selikowitz, M., Dupuy, F.E., 2010. Resting-state EEG gamma activity in children with attention-deficit/hyperactivity disorder. Clin. Neurophysiol. *121* (11), 1871–1877.

Barwick, F., Arnett, P., Slobounov, S., 2012. EEG correlates of fatigue during administration of a neuropsychological test battery. Clin. Neurophysiol. *123* (2), 278–284.

Başar-Eroglu, C., Başar, E., Demiralp, T., Schürmann, M., 1992. P300-response: Possible psychophysiological correlates in delta and theta frequency channels. A review. Int. J. Psychophysiol. 13 (2), 161–179.

Beese, C., Meyer, L., Vassileiou, B., Friederici, A.D., 2017. Temporally and spatially distinct theta oscillations dissociate a language-specific from a domain-general processing mechanism across the age trajectory. Sci. Rep. *7* (1), 11202 https://doi.org/10.1038/s41598-017-11632-z.

Begus, K., Bonawitz, E., 2020. The rhythm of learning: Theta oscillations as an index of active learning in infancy. Dev. Cogn. Neurosci. *45*, 100810.

Begus, K., Southgate, V., Gliga, T., 2015. Neural mechanisms of infant learning: Differences in frontal theta activity during object exploration modulate subsequent object recognition. Biol. Lett. *11* (5), 20150041.

Begus, K., Gliga, T., Southgate, V., 2016. Infants' preferences for native speakers are associated with an expectation of information. Proc. Natl. Acad. Sci. https://doi.org/10.1073/pnas.1603261113.

Bell, M.A., Fox, N.A., 1992. The relations between frontal brain electrical activity and cognitive development during infancy. Child Dev. *63* (5), 1142–1163.

Bell, M.A., Fox, N.A., 1997. Individual differences in object permanence performance at 8 months: Locomotor experience and brain electrical activity. Dev. Psychobiol.: J. Int. Soc. Dev. Psychobiol. *31* (4), 287–297.

Ben-Ari, Y., 2002. Excitatory actions of gaba during development: The nature of the nurture. Nat. Rev. Neurosci. *3* (9), 728–739. https://doi.org/10.1038/nrn920.

Benasich, A.A., Gou, Z., Choudhury, N., Harris, K.D., 2008. Early cognitive and language skills are linked to resting frontal gamma power across the first 3 years. Behav. Brain Res. *195* (2), 215–222.

Benninger, C., Matthis, P., Scheffner, D., 1984. EEG development of healthy boys and girls. Results of a longitudinal study. Electroencephalogr. Clin. Neurophysiol. *57* (1), 1–12.

Berger, A., Posner, M.I., 2022. Beyond Infant's Looking: The Neural Basis for Infant Prediction Errors. Perspect. Psychol. Sci., 17456916221112918 https://doi.org/10.1177/17456916221112918.

Berger, A., Tzur, G., Posner, M.I., 2006. Infant brains detect arithmetic errors. Proc. Natl. Acad. Sci. *103* (33), 12649–12653.

Berry, S.D., Thompson, R.F., 1978. Prediction of Learning Rate from the Hippocampal Electroencephalogram. Science *200* (4347), 1298–1300. https://doi.org/10.1126/science.663612.

Botvinick, M.M., Cohen, J.D., Carter, C.S., 2004. Conflict monitoring and anterior cingulate cortex: An update. Trends Cogn. Sci. *8* (12), 539–546.

Bowers, M.E., Morales, S., Buzzell, G.A., Fox, N.A., 2021. The influence of monetary reward on proactive and reactive control in adolescent males. Dev. Cogn. Neurosci. 48, 100934 https://doi.org/10.1016/j.dcn.2021.100934.

Braithwaite, E.K., Jones, E.J.H., Johnson, M.H., Holmboe, K., 2020. Dynamic modulation of frontal theta power predicts cognitive ability in infancy. Dev. Cogn. Neurosci. *45*, 100818 https://doi.org/10.1016/j.dcn.2020.100818.

Brandes-Aitken, A., Pini, N., Weatherhead, M., Brito, N.H., 2023. Maternal hair cortisol predicts periodic and aperiodic infant frontal EEG activity longitudinally across infancy. Dev. Psychobiol. *65* (5), e22393 https://doi.org/10.1002/dev.22393.

Brandes-Aitken, A., Metser, M., Braren, S.H., Vogel, S.C., Brito, N.H., 2023. Neurophysiology of sustained attention in early infancy: Investigating longitudinal relations with recognition memory outcomes. Infant Behav. Dev. *70*, 101807 https://doi.org/10.1016/j.infbeh.2022.101807.

Brito, N.H., Fifer, W.P., Myers, M.M., Elliott, A.J., Noble, K.G., 2016. Associations among family socioeconomic status, EEG power at birth, and cognitive skills during infancy. Dev. Cogn. Neurosci. *19*, 144–151.

Brooks, H., Goodman, M.S., Bowie, C.R., Zomorrodi, R., Blumberger, D.M., Butters, M.A., Daskalakis, Z.J., Fischer, C.E., Flint, A., Herrmann, N., Kumar, S., Mah, L., Mulsant, B.H., Pollock, B.G., Voineskos, A.N., Rajji, T.K., Mulsant, B.H., Rajji, T.K., Herrmann, N., on behalf of the PACt-MD Study Group, 2020. Theta–gamma coupling and ordering information: A stable brain–behavior relationship across cognitive tasks and clinical conditions. Neuropsychopharmacology *45* (12), 2038–2047. https://doi.org/10.1038/s41386-020-0759-z.

Bullock, T., McClune, M., Enright, J., 2003. Are the electroencephalograms mainly rhythmic? Assessment of periodicity in wide-band time series. Neuroscience *121* (1), 233–252.

Busch, N.A., VanRullen, R., 2010. Spontaneous EEG oscillations reveal periodic sampling of visual attention. Proc. Natl. Acad. Sci. 107 (37), 16048–16053. https://doi.org/10.1073/pnas.1004801107.

Buzsaki, G., 2006. Rhythms of the Brain. Oxford university press.

Buzsáki, G., Wang, X.-J., 2012. Mechanisms of gamma oscillations. Annu. Rev. Neurosci. *35*, 203–225.

Buzzell, G.A., Richards, J.E., White, L.K., Barker, T.V., Pine, D.S., Fox, N.A., 2017. Development of the error-monitoring system from ages 9–35: Unique insight provided by MRI-constrained source localization of EEG. NeuroImage *157*, 13–26. https://doi.org/10.1016/j.neuroimage.2017.05.045.

Buzzell, G.A., Barker, T.V., Troller-Renfree, S.V., Bernat, E.M., Bowers, M.E., Morales, S., Bowman, L.C., Henderson, H.A., Pine, D.S., Fox, N.A., 2019. Adolescent cognitive control, theta oscillations, and social observation. NeuroImage *198*, 13–30. https://doi.org/10.1016/j.neuroimage.2019.04.077.

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., 101201 https://doi.org/10.1016/j.dcn.2023.101201.

Cai, D., Deng, M., Yu, J., Nan, W., Leung, A.W.S., 2021. The relationship of resting-state EEG oscillations to executive functions in middle childhood. Int. J. Psychophysiol. *164*, 64–70. https://doi.org/10.1016/j.ijpsycho.2021.02.021.

Calvin, C.M., Batty, G.D., Der, G., Brett, C.E., Taylor, A., Pattie, A., Čukić, I., Deary, I.J., 2017. Childhood intelligence in relation to major causes of death in 68 year follow-up: Prospective population study. Bmj *357*.

Camacho, M.C., Quiñones-Camacho, L.E., Perlman, S.B., 2020. Does the child brain rest?: An examination and interpretation of resting cognition in developmental cognitive neuroscience. NeuroImage *212*, 116688. https://doi.org/10.1016/j.neuroimage.2020.116688.

Caplan, J.B., Glaholt, M.G., 2007. The roles of EEG oscillations in learning relational information. NeuroImage *38* (3), 604–616. https://doi.org/10.1016/j.neuroimage.2007.07.054.

Cardin, J.A., Carlén, M., Meletis, K., Knoblich, U., Zhang, F., Deisseroth, K., Tsai, L.-H., Moore, C.I., 2009. Driving fast-spiking cells induces gamma rhythm and controls sensory responses. Nature *459* (7247), 663–667.

Carlson, S.M., 2005. Developmentally sensitive measures of executive function in preschool children. Dev. Neuropsychol. *28* (2), 595–616.

Cavanagh, J.F., Frank, M.J., 2014. Frontal theta as a mechanism for cognitive control. Trends Cogn. Sci. *18* (8), 414–421.

Cavanagh, J.F., Cohen, M.X., Allen, J.J., 2009. Prelude to and Resolution of an Error: EEG Phase Synchrony Reveals Cognitive Control Dynamics during Action Monitoring. J. Neurosci. *29* (1), 98–105.

Cavanagh, J.F., Frank, M.J., Klein, T.J., Allen, J.J.B., 2010. Frontal theta links prediction errors to behavioral adaptation in reinforcement learning. NeuroImage *49* (4), 3198–3209. https://doi.org/10.1016/j.neuroimage.2009.11.080.

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., Rennie, C., Robinson, P., Van Albada, S., Kerr, C., 2011. Age trends and sex differences of alpha rhythms including split alpha peaks. Clin. Neurophysiol. *122* (8), 1505–1517.

Chrobak, J.J., Stackman, R.W., Walsh, T.J., 1989. Intraseptal administration of muscimol produces dose-dependent memory impairments in the rat. Behav. Neural Biol. *52* (3), 357–369. https://doi.org/10.1016/S0163-1047(89)90472-X.

Clarke, A.R., Barry, R.J., McCarthy, R., Selikowitz, M., 2001. Age and sex effects in the EEG: development of the normal child. Clin. Neurophysiol. *112* (5), 806–814.

Clarke, A.R., Barry, R.J., Bond, D., McCarthy, R., Selikowitz, M., 2002. Effects of stimulant medications on the EEG of children with attention-deficit/hyperactivity disorder. Psychopharmacology *164*, 277–284.

Cohen, M.X., 2014. A neural microcircuit for cognitive conflict detection and signaling. Trends Neurosci. *37* (9), 480–490. https://doi.org/10.1016/j.tins.2014.06.004.

Cohen, M.X., Cavanagh, J.F., 2011. Single-trial regression elucidates the role of prefrontal theta oscillations in response conflict. Front. Psychol. *2*, 30.

Cohen, M.X., Donner, T.H., 2013. Midfrontal conflict-related theta-band power reflects neural oscillations that predict behavior. J. Neurophysiol. *110* (12), 2752–2763.

Cole, S., Voytek, B., 2019. Cycle-by-cycle analysis of neural oscillations. J. Neurophysiol. 122 (2), 849–861. https://doi.org/10.1152/jn.00273.2019.

Colgin, L.L., 2013. Mechanisms and functions of theta rhythms. Annu Rev. Neurosci. *36* (1), 295–312.

Colgin, L.L., 2015. Theta–gamma coupling in the entorhinal–hippocampal system. SI: Brain Rhythms Dyn. Coord. *31*, 45–50. https://doi.org/10.1016/j.conb.2014.08.001.

Conejero, Á., Guerra, S., Abundis-Gutiérrez, A., Rueda, M.R., 2018. Frontal theta activation associated with error detection in toddlers: Influence of familial socioeconomic status. Dev. Sci. *21* (1), e12494 https://doi.org/10.1111/desc.12494.

Corning, W.C., Steffy, R.A., Chaprin, I.C., 1982. EEG slow frequency and WISC-R correlates. J. Abnorm. Child Psychol. *10* (4), 511–530. https://doi.org/10.1007/BF00920751.

Corning, W.C., Steffy, R., Anderson, E., Bowers, P., 1986. EEG "maturational lag" profiles: Follow-up analyses. J. Abnorm. Child Psychol. *14* (2), 235–249.

Crowley, M.J., van Noordt, S.J.R., Wu, J., Hommer, R.E., South, M., Fearon, R.M.P., Mayes, L.C., 2014. Reward feedback processing in children and adolescents: Medial frontal theta oscillations. Spec. Issue Reward Regul. Process. Adolesc. *89*, 79–89. https://doi.org/10.1016/j.bandc.2013.11.011.

Cuevas, K., Bell, M.A., 2022. EEG frequency development across infancy and childhood. The Oxford Handbook of EEG Frequency. Oxford University Press, pp. 293–323.

Cuevas, K., Raj, V., Bell, M.A., 2012. A frequency band analysis of two-year-olds' memory processes. Int. J. Psychophysiol. *83* (3), 315–322. https://doi.org/10.1016/j.ijpsycho.2011.11.009.

Cunillera, T., Fuentemilla, L., Periañez, J., Marco-Pallarès, J., Krämer, U.M., Càmara, E., Münte, T.F., Rodríguez-Fornells, A., 2012. Brain oscillatory activity associated with task switching and feedback processing. Cogn., Affect., Behav. Neurosci. *12* (1), 16–33. https://doi.org/10.3758/s13415-011-0075-5.

Davidson, R.J., Jackson, D.C., Larson, C.L., 2000. Human electroencephalography. In: Cacioppo, J.T., Tassinary, L.G., Berntson, G.G. (Eds.), Handbook of psychophysiology. Cambridge University Press, pp. 27–52.

Davies, P.L., Segalowitz, S.J., Gavin, W.J., 2004. Development of Response-Monitoring ERPs in 7- to 25-Year-Olds. Dev. Neuropsychol. *25* (3), 355–376. https://doi.org/10.1207/s15326942dn2503_6.

Deary, I.J., Strand, S., Smith, P., Fernandes, C., 2007. Intelligence and educational achievement. Intelligence *35* (1), 13–21.

Debnath, R., Tang, A., Zeanah, C.H., Nelson, C.A., Fox, N.A., 2020. The long-term effects of institutional rearing, foster care intervention and disruptions in care on brain electrical activity in adolescence. Dev. Sci. *23* (1), e12872.

van der Velde, B., White, T., Kemner, C., 2021. The emergence of a theta social brain network during infancy. NeuroImage *240*, 118298.

Diamond, A., 2013. Executive Functions. Annu. Rev. Psychol. *64* (1), 135–168. https://doi.org/10.1146/annurev-psych-113011-143750.

Donoghue, T., Dominguez, J., Voytek, B., 2020. Electrophysiological frequency band ratio measures conflate periodic and aperiodic neural activity. Eneuro *7* (6).

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.

Doppelmayr, M., Klimesch, W., Pachinger, T., Ripper, B., 1998. Individual differences in brain dynamics: Important implications for the calculation of event-related band power. Biol. Cybern. 79, 49–57.

van Driel, J., Ridderinkhof, K.R., Cohen, M.X., 2012. Not all errors are alike: Theta and alpha EEG dynamics relate to differences in error-processing dynamics. J. Neurosci. 32 (47), 16795–16806.

Dugué, L., Marque, P., VanRullen, R., 2015. Theta oscillations modulate attentional search performance periodically. J. Cogn. Neurosci. *27* (5), 945–958.

Eriksen, B.A., Eriksen, C.W., 1974. Effects of noise letters upon the identification of a target letter in a nonsearch task. Percept. Psychophys. *16* (1), 143–149.

Escera, C., Alho, K., Winkler, I., Näätänen, R., 1998. Neural mechanisms of involuntary attention to acoustic novelty and change. J. Cogn. Neurosci. *10* (5), 590–604. https://doi.org/10.1162/089892998562997.

Feinberg, I., Campbell, I.G., 2010. Sleep EEG changes during adolescence: an index of a fundamental brain reorganization. Brain Cogn. *72* (1), 56–65.

Fell, Juergen, Ludowig, Eva, Staresina, Bernhard P., Wagner, Tobias, Kranz, Thorsten, Elger, Christian E., Axmacher, Nikolai, 2011. Medial temporal theta/alpha power enhancement precedes successful memory encoding: evidence based on intracranial EEG. J. Neurosci. *31* (14), 5392. https://doi.org/10.1523/JNEUROSCI.3668-10.2011.

Fellner, M.-C., Gollwitzer, S., Rampp, S., Kreiselmeyr, G., Bush, D., Diehl, B., Axmacher, N., Hamer, H., Hanslmayr, S., 2019. Spectral fingerprints or spectral tilt? Evidence for distinct oscillatory signatures of memory formation. PLOS Biol. *17* (7), e3000403 https://doi.org/10.1371/journal.pbio.3000403.

Fernández, T., Harmony, T., Mendoza, O., López-Alanís, P., Marroquín, J.L., Otero, G., Ricardo-Garcell, J., 2012. Event-related EEG oscillations to semantically unrelated words in normal and learning disabled children. Brain Cogn. *80* (1), 74–82.

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.

Fiebelkorn, I.C., Saalmann, Y.B., Kastner, S., 2013. Rhythmic sampling within and between objects despite sustained attention at a cued location. Curr. Biol. *23* (24), 2553–2558.

Finley, A.J., Angus, D.J., van Reekum, C.M., Davidson, R.J., Schaefer, S.M., 2022. Periodic and aperiodic contributions to theta-beta ratios across adulthood. Psychophysiology *59* (11), e14113. https://doi.org/10.1111/psyp.14113.

Finnigan, S., Robertson, I.H., 2011. Resting EEG theta power correlates with cognitive performance in healthy older adults. Psychophysiology *48* (8), 1083–1087. https://doi.org/10.1111/j.1469-8986.2010.01173.x.

Food and Drug Administration. (2013). *De novo classification request for Neuropsychiatric EEG-Based Assessment Aid for ADHD (NEBA) System*. ⟨https://www.accessdata.fda.gov/cdrh_docs/reviews/k112711.pdf⟩.

Fries, P., 2005. A mechanism for cognitive dynamics: Neuronal communication through neuronal coherence. Trends Cogn. Sci. *9* (10), 474–480.

Fries, P., 2023. Rhythmic attentional scanning. Neuron 111 (7), 954–970. https://doi.org/10.1016/j.neuron.2023.02.015.

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.

Fuentemilla, L., Penny, W.D., Cashdollar, N., Bunzeck, N., Düzel, E., 2010. Theta-coupled periodic replay in working memory. Curr. Biol. *20* (7), 606–612.

Fuentemilla, Ll, Marco-Pallarés, J., Münte, T.F., Grau, C., 2008. Theta EEG oscillatory activity and auditory change detection. Act. Listen *1220*, 93–101. https://doi.org/10.1016/j.brainres.2007.07.079.

Gale, A., Coles, M., Boyd, E., 1971. Variation in visual input and the occipital EEG: II. Psychon. Sci. *23* (1), 99–100.

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.

Gevins, A., Smith, M.E., McEvoy, L., Yu, D., 1997. High-resolution EEG mapping of cortical activation related to working memory: Effects of task difficulty, type of processing, and practice. Cereb. Cortex *7* (4), 374–385. https://doi.org/10.1093/cercor/7.4.374.

Gloss, D., Varma, J.K., Pringsheim, T., Nuwer, M.R., 2016. Practice advisory: The utility of EEG theta/beta power ratio in ADHD diagnosis: Report of the Guideline Development, Dissemination, and Implementation Subcommittee of the American Academy of Neurology. Neurology *87* (22), 2375–2379.

Gou, Z., Choudhury, N., Benasich, A.A., 2011. Resting frontal gamma power at 16, 24 and 36 months predicts individual differences in language and cognition at 4 and 5 years. Behav. Brain Res. *220* (2), 263–270. https://doi.org/10.1016/j.bbr.2011.01.048.

Greenstein, Y.J., Pavlides, C., Winson, J., 1988. Lonf-term potentiation in the dentate gyrus is preferentially induced at theta rhythm periodicity. Brain Res. *438* (1), 331–334. https://doi.org/10.1016/0006-8993(88)91358-3.

Guderian, S., Schott, B.H., Richardson-Klavehn, A., Düzel, E., 2009. Medial temporal theta state before an event predicts episodic encoding success in humans. Proc. Natl. Acad. Sci. *106* (13), 5365–5370. https://doi.org/10.1073/pnas.0900289106.

Güntekin, B., Uzunlar, H., Çalışoğlu, P., Eroğlu-Ada, F., Yıldırım, E., Aktürk, T., Atay, E., Ceran, Ö., 2020. Theta and alpha oscillatory responses differentiate between six-to seven-year-old children and adults during successful visual and auditory memory encoding. Brain Res. *1747*, 147042 https://doi.org/10.1016/j.brainres.2020.147042.

Haartsen, R., Charman, T., Pasco, G., Johnson, M.H., Jones, E.J.H., Baron-Cohen, S., Bedford, R., Blasi, A., Bolton, P., Chandler, S., Cheung, C., Davies, K., Elsabbagh, M., Fernandes, J., Gammer, I., Garwood, H., Gliga, T., Guiraud, J., Hudry, K., The BASIS Team, 2022. Modulation of EEG theta by naturalistic social content is not altered in infants with family history of autism. Sci. Rep. *12* (1), 20758 https://doi.org/10.1038/s41598-022-24870-7.

Hald, L.A., Bastiaansen, M.C.M., Hagoort, P., 2006. EEG theta and gamma responses to semantic violations in online sentence processing. Brain Lang. *96* (1), 90–105. https://doi.org/10.1016/j.bandl.2005.06.007.

Hanslmayr, S., Pastötter, B., Bäuml, K.-H., Gruber, S., Wimber, M., Klimesch, W., 2008. The electrophysiological dynamics of interference during the Stroop task. J. Cogn. Neurosci. 20 (2), 215–225.

Harmony, T., Alvarez, A., Pascual, R., Ramos, A., Marosi, E., Díaz De León, A.E., Valdés, P., Becker, J., 1988. EEG maturation on children with different economic and psychosocial characteristics. Int. J. Neurosci. *41* (1–2), 103–113.

Hashimoto, T., Nguyen, Q.L., Rotaru, D., Keenan, T., Arion, D., Beneyto, M., Gonzalez-Burgos, G., Lewis, D.A., 2009. Protracted developmental trajectories of GABAA receptor α1 and α2 subunit expression in primate prefrontal cortex. Biol. Psychiatry *65* (12), 1015–1023.

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.

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. Neuron 99 (4), 854–865.e5. https://doi.org/10.1016/j.neuron.2018.07.032.

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.

Heusser, A.C., Poeppel, D., Ezzyat, Y., Davachi, L., 2016. Episodic sequence memory is supported by a theta–gamma phase code. Nat. Neurosci. 19 (10), 1374–1380. https://doi.org/10.1038/nn.4374.

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.

Hirsh, J.B., Inzlicht, M., 2010. Error-related negativity predicts academic performance. Psychophysiology *47* (1), 192–196.

Hoffman, K.L., Dragan, M.C., Leonard, T.K., Micheli, C., Montefusco-Siegmund, R., Valiante, T.A., 2013. Saccades during visual exploration align hippocampal 3–8 Hz rhythms in human and non-human primates. Front. Syst. Neurosci. 7, 43.

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. https://doi.org/10.1523/JNEUROSCI.17-16-06470.1997.

Hyman, J.M., Zilli, E.A., Paley, A.M., Hasselmo, M.E., 2010. Working memory performance correlates with prefrontal-hippocampal theta interactions but not with prefrontal neuron firing rates. Front. Integr. Neurosci. *4*, 1162.

Igarashi, K.M., Lu, L., Colgin, L.L., Moser, M.-B., Moser, E.I., 2014. Coordination of entorhinal–hippocampal ensemble activity during associative learning. Nature *510* (7503)), 143–147.

Isler, J.R., Pini, N., Lucchini, M., Shuffrey, L.C., Morales, S., Bowers, M.E., Leach, S.C., Sania, A., Wang, L., Condon, C., Nugent, J.D., Elliott, A.J., Friedrich, C., Andrew, R., Fox, N.A., Myers, M.M., Fifer, W.P., 2022. Longitudinal characterization of EEG power spectra during eyes open and eyes closed conditions in children. Psychophysiology, e14158. https://doi.org/10.1111/psyp.14158.

Jasper, H.H., 1936. Cortical excitatory state and variability in human brain rhythms. Science *83* (2150), 259–260.

Jasper, H.H., 1948. Charting the sea of brain waves. Science *108* (2805), 343–347.

Jelic, V., Shigeta, M., Julin, P., Almkvist, O., Winblad, B., Wahlund, L.-O., 1996. Quantitative Electroencephalography Power and Coherence in Alzheimer's Disease and Mild Cognitive Impairment. Dement. Geriatr. Cogn. Disord. *7* (6), 314–323. https://doi.org/10.1159/000106897.

Jensen, S.K.G., Xie, W., Kumar, S., Haque, R., Petri, W.A., Nelson, C.A., 2021. Associations of socioeconomic and other environmental factors with early brain development in Bangladeshi infants and children. Dev. Cogn. Neurosci. *50*, 100981 https://doi.org/10.1016/j.dcn.2021.100981.

Johnston, W.A., Dark, V.J., 1986. Selective attention. Annu. Rev. Psychol. *37* (1), 43–75.

Jones, E.J., Venema, K., Lowy, R., Earl, R.K., Webb, S.J., 2015. Developmental changes in infant brain activity during naturalistic social experiences. Dev. Psychobiol. *57* (7), 842–853.

Jones, E.J., Goodwin, A., Orekhova, E., Charman, T., Dawson, G., Webb, S., Johnson, M. H., 2020. Infant EEG theta modulation predicts childhood intelligence. Sci. Rep. *10* (1), 1–10.

Jones, M.W., Wilson, M.A., 2005. Theta rhythms coordinate hippocampal–prefrontal interactions in a spatial memory task. PLoS Biol. *3* (12), e402.

Kamzanova, A., Matthews, G., Kustubayeva, A., Jakupov, S., 2011. EEG indices to time-on-task effects and to a workload manipulation (cueing). Int. J. Psychol. Behav. Sci. *5* (8), 928–931.

Karakaş, S., 2020. A review of theta oscillation and its functional correlates. Int. J. Psychophysiol. 157, 82–99. https://doi.org/10.1016/j.ijpsycho.2020.04.008.

Karalunas, S.L., Ostlund, B.D., Alperin, B.R., Figuracion, M., Gustafsson, H.C., Deming, E. M., Foti, D., Antovich, D., Dude, J., Nigg, J., Sullivan, E., 2022. Electroencephalogram aperiodic power spectral slope can be reliably measured and predicts ADHD risk in early development. Dev. Psychobiol. *64* (3), e22228 https://doi.org/10.1002/dev.22228.

Kavanaugh, B.C., Fryc, A., Temereanca, S., Tirrell, E., Oberman, L., Carpenter, L.L., Spirito, A., 2021. A preliminary investigation of childhood anxiety/depressive symptomatology and working memory across multiple units of analysis. Psychiatry Res. *298*, 113786 https://doi.org/10.1016/j.psychres.2021.113786.

Kavcic, V., Zalar, B., Giordani, B., 2016. The relationship between baseline EEG spectra power and memory performance in older African Americans endorsing cognitive concerns in a community setting. Int. J. Psychophysiol. *109*, 116–123. https://doi.org/10.1016/j.ijpsycho.2016.09.001.

Kay, L.M., 2005. Theta oscillations and sensorimotor performance. Proc. Natl. Acad. Sci. *102* (10), 3863–3868.

Kim, H., 2011. Neural activity that predicts subsequent memory and forgetting: A meta-analysis of 74 fMRI studies. Neuroimage *54* (3), 2446–2461.

Klimesch, W., 1999. EEG alpha and theta oscillations reflect cognitive and memory performance: A review and analysis. Brain Res. Rev. *29* (2–3), 169–195.

Klimesch, W., Doppelmayr, M., Schimke, H., Ripper, B., 1997. Theta synchronization and alpha desynchronization in a memory task. Psychophysiology 34 (2), 169–176.

Köster, M., 2024. The theta-gamma code in predictive processing and mnemonic updating. Neurosci. Biobehav. Rev. 158, 105529 https://doi.org/10.1016/j.neubiorev.2023.105529.

Köster, M., Friese, U., Schöne, B., Trujillo-Barreto, N., Gruber, T., 2014. Theta–gamma coupling during episodic retrieval in the human EEG. Brain Res. *1577*, 57–68. https://doi.org/10.1016/j.brainres.2014.06.028.

Köster, M., Haese, A., Czernochowski, D., 2017. Neuronal oscillations reveal the processes underlying intentional compared to incidental learning in children and young adults. PLOS ONE *12* (8), e0182540. https://doi.org/10.1371/journal.pone.0182540.

Köster, M., Finger, H., Graetz, S., Kater, M., Gruber, T., 2018. Theta-gamma coupling binds visual perceptual features in an associative memory task. Sci. Rep. 8 (1), 17688 https://doi.org/10.1038/s41598-018-35812-7.

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.

Köster, M., Langeloh, M., Michel, C., Hoehl, S., 2021. Young infants process prediction errors at the theta rhythm. NeuroImage *236*, 118074. https://doi.org/10.1016/j.neuroimage.2021.118074.

Kota, S., Rugg, M.D., Lega, B.C., 2020. Hippocampal Theta Oscillations Support Successful Associative Memory Formation. J. Neurosci. *40* (49), 9507. https://doi.org/10.1523/JNEUROSCI.0767-20.2020.

Krause, C.M., Salminen, P.-A., Sillanmäki, L., Holopainen, I.E., 2001. Event-related desynchronization and synchronization during a memory task in children. Clin. Neurophysiol. *112* (12), 2233–2240. https://doi.org/10.1016/S1388-2457(01)00684-8.

Krause, C.M., Pesonen, M., Hämäläinen, H., 2007. Brain oscillatory responses during the different stages of an auditory memory search task in children. NeuroReport *18* (3). 〈https://journals.lww.com/neuroreport/Fulltext/2007/02120/Brain_oscillatory_responses_during_the_different.4.aspx〉.

Kraybill, J.H., Bell, M.A., 2013. Infancy predictors of preschool and post-kindergarten executive function. Dev. Psychobiol. *55* (5), 530–538. https://doi.org/10.1002/dev.21057.

Kubota, Y., Karube, F., Nomura, M., Kawaguchi, Y., 2016. The diversity of cortical inhibitory synapses. Front. Neural Circuits *10*, 27.

Kuhlman, W. (1980). *The mu rhythm: Functional topography and neural origin.*

Landau, A.N., Fries, P., 2012. Attention samples stimuli rhythmically. Curr. Biol. 22 (11), 1000–1004.

Landfield, P.W., 1977. Different effects of posttrial driving or blocking of the theta rhythm on avoidance learning in rats. Physiol. Behav. *18* (3), 439–445. https://doi.org/10.1016/0031-9384(77)90257-8.

Lansbergen, M.M., Arns, M., van Dongen-Boomsma, M., Spronk, D., Buitelaar, J.K., 2011. The increase in theta/beta ratio on resting-state EEG in boys with attention-deficit/hyperactivity disorder is mediated by slow alpha peak frequency. Prog. Neuro-Psychopharmacol. Biol. Psychiatry *35* (1), 47–52.

Lara, G.A. de, Alekseichuk, I., Turi, Z., Lehr, A., Antal, A., Paulus, W., 2018. Perturbation of theta-gamma coupling at the temporal lobe hinders verbal declarative memory. Brain Stimul. *11* (3), 509–517. https://doi.org/10.1016/j.brs.2017.12.007.

Lazzaro, I., Gordon, E., Li, W., Lim, C., Plahn, M., Whitmont, S., Clarke, S., Barry, R., Dosen, A., Meares, R., 1999. Simultaneous EEG and EDA measures in adolescent attention deficit hyperactivity disorder. Int. J. Psychophysiol. *34* (2), 123–134.

Le Van Quyen, M., Khalilov, I., Ben-Ari, Y., 2006. The dark side of high-frequency oscillations in the developing brain. Trends Neurosci. *29* (7), 419–427.

Lee, T.L., Lee, H., Kang, N., 2023. A meta-analysis showing improved cognitive performance in healthy young adults with transcranial alternating current stimulation. Npj Sci. Learn. 8 (1), 1. https://doi.org/10.1038/s41539-022-00152-9.

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.

Lenartowicz, A., Loo, S.K., 2014. Use of EEG to diagnose ADHD. Curr. Psychiatry Rep. *16*, 1–11.

Lisman, J.E., Jensen, O., 2013. The Theta-Gamma Neural Code. Neuron *77* (6), 1002–1016. https://doi.org/10.1016/j.neuron.2013.03.007.

Lithfous, S., Tromp, D., Dufour, A., Pebayle, T., Goutagny, R., Després, O., 2015. Decreased theta power at encoding and cognitive mapping deficits in elderly individuals during a spatial memory task. Neurobiol. Aging *36* (10), 2821–2829. https://doi.org/10.1016/j.neurobiolaging.2015.07.007.

Liu, Z.-X., Woltering, S., Lewis, M.D., 2014. Developmental change in EEG theta activity in the medial prefrontal cortex during response control. N. Horiz. Neural Oscil. *85*, 873–887. https://doi.org/10.1016/j.neuroimage.2013.08.054.

Lodder, S.S., van Putten, M.J., 2011. Automated EEG analysis: Characterizing the posterior dominant rhythm. J. Neurosci. Methods *200* (1), 86–93.

Loo, S.K., Makeig, S., 2012. Clinical utility of EEG in attention-deficit/hyperactivity disorder: A research update. Neurotherapeutics *9*, 569–587.

Lum, J.A.G., Clark, G.M., Bigelow, F.J., Enticott, P.G., 2022. Resting state electroencephalography (EEG) correlates with children's language skills: Evidence from sentence repetition. Brain Lang. *230*, 105137 https://doi.org/10.1016/j.bandl.2022.105137.

Luu, P., Tucker, D.M., Derryberry, D., Reed, M., Poulsen, C., 2003. Electrophysiological responses to errors and feedback in the process of action regulation. Psychol. Sci. *14* (1), 47–53.

Luu, P., Tucker, D.M., Makeig, S., 2004. Frontal midline theta and the error-related negativity: Neurophysiological mechanisms of action regulation. Clin. Neurophysiol. *115* (8), 1821–1835. https://doi.org/10.1016/j.clinph.2004.03.031.

Maguire, M.J., Schneider, J.M., 2019. Socioeconomic status related differences in resting state EEG activity correspond to differences in vocabulary and working memory in grade school. Brain Cogn. *137*, 103619 https://doi.org/10.1016/j.bandc.2019.103619.

Maguire, M.J., Schneider, J.M., Melamed, T.C., Ralph, Y.K., Poudel, S., Raval, V.M., Mikhail, D., Abel, A.D., 2022. Temporal and topographical changes in theta power between middle childhood and adolescence during sentence comprehension. Dev. Cogn. Neurosci. *53*, 101056 https://doi.org/10.1016/j.dcn.2021.101056.

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.

Mantini, D., Perrucci, M.G., Del Gratta, C., Romani, G.L., Corbetta, M., 2007. Electrophysiological signatures of resting state networks in the human brain. Proc. Natl. Acad. Sci. *104* (32), 13170–13175. https://doi.org/10.1073/pnas.0700668104.

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.

Marshall, P.J., Fox, N.A., Group, B.C., 2004. A Comparison of the Electroencephalogram between Institutionalized and Community Children in Romania. J. Cogn. Neurosci. *16* (8), 1327–1338. https://doi.org/10.1162/0898929042304723.

Matsuura, M., Okubo, Y., Toru, M., Kojima, T., He, Y., Shen, Y., Kyoon Lee, C., 1993. A cross-national EEG study of children with emotional and behavioral problems: A WHO collaborative study in the Western Pacific region. Biol. Psychiatry *34* (1), 59–65. https://doi.org/10.1016/0006-3223(93)90257-E.

McLaughlin, K.A., Fox, N.A., Zeanah, C.H., Sheridan, M.A., Marshall, P., Nelson, C.A., 2010. Delayed maturation in brain electrical activity partially explains the association between early environmental deprivation and symptoms of attention-deficit/hyperactivity disorder. Biol. Psychiatry *68* (4), 329–336.

McLoughlin, G., Gyurkovics, M., Palmer, J., Makeig, S., 2021. Midfrontal Theta Activity in Psychiatric Illness: An Index of Cognitive Vulnerabilities Across Disorders. Biol. Psychiatry.

McSweeney, M., Morales, S., Valadez, E.A., Buzzell, G.A., Fox, N.A., 2021. Longitudinal age- and sex-related change in background aperiodic activity during early adolescence. Dev. Cogn. Neurosci. *52*, 101035 https://doi.org/10.1016/j.dcn.2021.101035.

McSweeney, M., Morales, S., Valadez, E.A., Buzzell, G.A., Yoder, L., Fifer, W.P., Pini, N., Shuffrey, L.C., Elliott, A.J., Isler, J.R., Fox, N.A., 2023. Age-related trends in aperiodic EEG activity and alpha oscillations during early- to middle-childhood. NeuroImage *269*, 119925. https://doi.org/10.1016/j.neuroimage.2023.119925.

Meng, X., Sun, C., Du, B., Liu, L., Zhang, Y., Dong, Q., Georgiou, G.K., Nan, Y., 2022. The development of brain rhythms at rest and its impact on vocabulary acquisition. Dev. Sci. *25* (2), e13157 https://doi.org/10.1111/desc.13157.

Meyer, M., Endedijk, H.M., van Ede, F., Hunnius, S., 2019. Theta oscillations in 4-year-olds are sensitive to task engagement and task demands. Sci. Rep. *9* (1), 6049. https://doi.org/10.1038/s41598-019-42615-x.

Michel, C., Stets, M., Parise, E., Reid, V.M., Striano, T., Hoehl, S., 2015. Theta- and alpha-band EEG activity in response to eye gaze cues in early infancy. NeuroImage *118*, 576–583. https://doi.org/10.1016/j.neuroimage.2015.06.042.

Michel, C., Matthes, D., Hoehl, S., 2023. Theta power relates to infant object encoding in naturalistic mother-infant interactions. Child Dev.

Michelini, G., Salmastyan, G., Vera, J.D., Lenartowicz, A., 2022. Event-related brain oscillations in attention-deficit/hyperactivity disorder (ADHD): A systematic review and meta-analysis. Int. J. Psychophysiol. 174, 29–42. https://doi.org/10.1016/j.ijpsycho.2022.01.014.

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.

Morales, S., Bowers, M.E., 2022. Time-frequency analysis methods and their application in developmental EEG data. Dev. Cogn. Neurosci. *54*, 101067 https://doi.org/10.1016/j.dcn.2022.101067.

Morales, S., Bowers, M.E., Leach, S.C., Buzzell, G.A., Fifer, W., Elliott, A.J., Fox, N.A., 2022. Time–frequency dynamics of error monitoring in childhood: An EEG study. Dev. Psychobiol. *64* (3), e22215 https://doi.org/10.1002/dev.22215.

Morales, S., Bowers, M.E., Leach, S.C., Buzzell, G.A., McSweeney, M., Yoder, L., Fifer, W., Elliott, A.J., Fox, N.A., 2023. Development of auditory change-detection and attentional capture, and their relation to inhibitory control. Psychophysiology *60* (4), e14211. https://doi.org/10.1111/psyp.14211.

Müller, V., Gruber, W., Klimesch, W., Lindenberger, U., 2009. Lifespan differences in cortical dynamics of auditory perception. Dev. Sci. *12* (6), 839–853. https://doi.org/10.1111/j.1467-7687.2009.00834.x.

Näätänen, R., Paavilainen, P., Rinne, T., Alho, K., 2007. The mismatch negativity (MMN) in basic research of central auditory processing: A review. Clin. Neurophysiol. *118* (12), 2544–2590. https://doi.org/10.1016/j.clinph.2007.04.026.

Newson, J.J., Thiagarajan, T.C., 2019. EEG frequency bands in psychiatric disorders: A review of resting state studies. Front. Hum. Neurosci. *12*, 521.

Nigbur, R., Ivanova, G., Stürmer, B., 2011. Theta power as a marker for cognitive interference. Clin. Neurophysiol. *122* (11), 2185–2194. https://doi.org/10.1016/j.clinph.2011.03.030.

Nigbur, R., Cohen, M.X., Ridderinkhof, K.R., Stürmer, B., 2012. Theta dynamics reveal domain-specific control over stimulus and response conflict. J. Cogn. Neurosci. 24 (5), 1264–1274.

Nissim, N.R., McAfee, D.C., Edwards, S., Prato, A., Lin, J.X., Lu, Z., Coslett, H.B., Hamilton, R.H., 2023. Efficacy of Transcranial Alternating Current Stimulation in the Enhancement of Working Memory Performance in Healthy Adults: A Systematic Meta-Analysis. Neuromodulation: Technol. Neural Interface 26 (4), 728–737. https://doi.org/10.1016/j.neurom.2022.12.014.

van Noordt, S., Heffer, T., Willoughby, T., 2022. A developmental examination of medial frontal theta dynamics and inhibitory control. NeuroImage *246*, 118765. https://doi.org/10.1016/j.neuroimage.2021.118765.

Norton, E.S., MacNeill, L.A., Harriott, E.M., Allen, N., Krogh-Jespersen, S., Smyser, C.D., Rogers, C.E., Smyser, T.A., Luby, J., Wakschlag, L., 2021. EEG/ERP as a pragmatic method to expand the reach of infant-toddler neuroimaging in HBCD: Promises and challenges. Dev. Cogn. Neurosci. *51*, 100988 https://doi.org/10.1016/j.dcn.2021.100988.

Nunez, P.L., Srinivasan, R., 2006. Electric fields of the brain: The neurophysics of EEG. Oxford University Press, USA.

Olvera-Cortés, E., Cervantes, M., González-Burgos, I., 2002. Place-learning, but not cue-learning training, modifies the hippocampal theta rhythm in rats. Brain Res. Bull. *58* (3), 261–270. https://doi.org/10.1016/S0361-9230(02)00769-4.

Orekhova, E.V., Stroganova, T.A., Posikera, I.N., 1999. Theta synchronization during sustained anticipatory attention in infants over the second half of the first year of life. Int. J. Psychophysiol. *32* (2), 151–172.

Orekhova, E.V., Stroganova, T.A., Posikera, I.N., Elam, M., 2006. EEG theta rhythm in infants and preschool children. Clin. Neurophysiol. *117* (5), 1047–1062. https://doi.org/10.1016/j.clinph.2005.12.027.

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.

Ostlund, B.D., Alperin, B.R., Drew, T., Karalunas, S.L., 2021. Behavioral and cognitive correlates of the aperiodic (1/f-like) exponent of the EEG power spectrum in adolescents with and without ADHD. Dev. Cogn. Neurosci. *48*, 100931 https://doi.org/10.1016/j.dcn.2021.100931.

Otero, G.A., 1994. EEG spectral analysis in children with sociocultural handicaps. Int. J. Neurosci. *79* (3–4), 213–220.

Otero, G.A., Pliego-Rivero, F., Fernández, T., Ricardo, J., 2003. EEG development in children with sociocultural disadvantages: A follow-up study. Clin. Neurophysiol. *114* (10), 1918–1925.

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.

Papagiannopoulou, E.A., Lagopoulos, J., 2016. Resting state EEG hemispheric power asymmetry in children with dyslexia. Front. Pediatr. *4*, 11.

Papenberg, G., Hämmerer, D., Müller, V., Lindenberger, U., Li, S.-C., 2013. Lower theta inter-trial phase coherence during performance monitoring is related to higher reaction time variability: A lifespan study. NeuroImage *83*, 912–920. https://doi.org/10.1016/j.neuroimage.2013.07.032.

Pavlides, C., Greenstein, Y.J., Grudman, M., Winson, J., 1988. Long-term potentiation in the dentate gyrus is induced preferentially on the positive phase of θ-rhythm. Brain Res. *439* (1–2), 383–387.

Perone, S., Gartstein, M.A., 2019. Mapping cortical rhythms to infant behavioral tendencies via baseline EEG and parent-report. Dev. Psychobiol. *61* (6), 815–823. https://doi.org/10.1002/dev.21867.

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.

Pierce, L.J., Thompson, B.L., Gharib, A., Schlueter, L., Reilly, E., Valdes, V., Roberts, S., Conroy, K., Levitt, P., Nelson, C.A., 2019. Association of Perceived Maternal Stress During the Perinatal Period With Electroencephalography Patterns in 2-Month-Old Infants. JAMA Pediatr. *173* (6), 561–570. https://doi.org/10.1001/jamapediatrics.2019.0492.

Polich, J., 2007. Updating P300: An integrative theory of P3a and P3b. Clin. Neurophysiol. *118* (10), 2128–2148. https://doi.org/10.1016/j.clinph.2007.04.019.

Pscherer, C., Mückschel, M., Summerer, L., Bluschke, A., Beste, C., 2019. On the relevance of EEG resting theta activity for the neurophysiological dynamics underlying motor inhibitory control. Hum. Brain Mapp. *40* (14), 4253–4265. https://doi.org/10.1002/hbm.24699.

Pscherer, C., Bluschke, A., Prochnow, A., Eggert, E., Mückschel, M., Beste, C., 2020. Resting theta activity is associated with specific coding levels in event-related theta activity during conflict monitoring. Hum. Brain Mapp. *41* (18), 5114–5127. https://doi.org/10.1002/hbm.25178.

Pscherer, C., Bluschke, A., Mückschel, M., Beste, C., 2021. The interplay of resting and inhibitory control-related theta-band activity depends on age. Hum. Brain Mapp. *42* (12), 3845–3857. https://doi.org/10.1002/hbm.25469.

Rajan, V., Bell, M.A., 2015. Developmental changes in fact and source recall: Contributions from executive function and brain electrical activity. Dev. Cogn. Neurosci. *12*, 1–11. https://doi.org/10.1016/j.dcn.2014.10.001.

Reid, V.M., Hoehl, S., Grigutsch, M., Groendahl, A., Parise, E., Striano, T., 2009. The neural correlates of infant and adult goal prediction: Evidence for semantic processing systems. Dev. Psychol. *45* (3), 620.

Richards, J., 2008. Attention in young infants: A developmental psychophysiological perspective. In: Nelson, C., Luciana, M. (Eds.), Handbook of developmental cognitive neuroscience, 2nd ed. MIT Press, pp. 479–497.

Richards, J.E., Casey, B.J., 1991. Heart Rate Variability During Attention Phases in Young Infants. Psychophysiology *28* (1), 43–53. https://doi.org/10.1111/j.1469-8986.1991.tb03385.x.

Ridderinkhof, K.R., Ullsperger, M., Crone, E.A., Nieuwenhuis, S., 2004. The role of the medial frontal cortex in cognitive control. Science *306* (5695), 443–447.

Robertson, M.M., Furlong, S., Voytek, B., Donoghue, T., Boettiger, C.A., Sheridan, M.A., 2019. EEG power spectral slope differs by ADHD status and stimulant medication exposure in early childhood. J. Neurophysiol. *122* (6), 2427–2437.

Roca-Stappung, M., Fernández, T., Becerra, J., Mendoza-Montoya, O., Espino, M., Harmony, T., 2012. Healthy aging: Relationship between quantitative electroencephalogram and cognition. Neurosci. Lett. *510* (2), 115–120. https://doi.org/10.1016/j.neulet.2012.01.015.

Rodríguez-Martínez, E., Ruiz-Martínez, F., Barriga Paulino, C., Gómez, C.M., 2017. Frequency shift in topography of spontaneous brain rhythms from childhood to adulthood. Cogn. Neurodyn *11* (1), 23–33.

Saad, J.F., Kohn, M.R., Clarke, S., Lagopoulos, J., Hermens, D.F., 2018. Is the theta/beta EEG marker for ADHD inherently flawed? J. Atten. Disord. *22* (9), 815–826.

Saby, J.N., Marshall, P.J., 2012. The utility of EEG band power analysis in the study of infancy and early childhood. Dev. Neuropsychol. *37* (3), 253–273.

Sargent, K., Chavez-Baldini, U., Master, S.L., Verweij, K.J.H., Lok, A., Sutterland, A.L., Vulink, N.C., Denys, D., Smit, D.J.A., Nieman, D.H., 2021. Resting-state brain oscillations predict cognitive function in psychiatric disorders: A transdiagnostic machine learning approach. NeuroImage: Clin. *30*, 102617 https://doi.org/10.1016/j.nicl.2021.102617.

Satterfield, J.H., Cantwell, D.P., Satterfield, B.T., 1974. Pathophysiology of the hyperactive child syndrome. Arch. Gen. Psychiatry *31* (6), 839–844.

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.

Schmidt, F.L., Hunter, J., 2004. General mental ability in the world of work: Occupational attainment and job performance. J. Personal. Soc. Psychol. *86* (1), 162.

Schneider, J.M., Maguire, M.J., 2019. Developmental differences in the neural correlates supporting semantics and syntax during sentence processing. Dev. Sci. *22* (4), e12782 https://doi.org/10.1111/desc.12782.

Schneider, J.M., Poudel, S., Abel, A.D., Maguire, M.J., 2023. Age and vocabulary knowledge differentially influence the N400 and theta responses during semantic retrieval. Dev. Cogn. Neurosci. *61*, 101251 https://doi.org/10.1016/j.dcn.2023.101251.

Seidenbecher, T., Laxmi, T.R., Stork, O., Pape, H.-C., 2003. Amygdalar and hippocampal theta rhythm synchronization during fear memory retrieval. Science *301* (5634), 846–850.

Sheridan, M.A., Fox, N.A., Zeanah, C.H., McLaughlin, K.A., Nelson, C.A., 2012. Variation in neural development as a result of exposure to institutionalization early in childhood. Proc. Natl. Acad. Sci. *109* (32), 12927–12932. https://doi.org/10.1073/pnas.1200041109.

Smit, D.J., Boersma, M., Schnack, H.G., Micheloyannis, S., Boomsma, D.I., Hulshoff Pol, H.E., Stam, C.J., de Geus, E.J., 2012. The brain matures with stronger functional connectivity and decreased randomness of its network. PLoS One *7* (5), e36896.

Spironelli, C., Angrilli, A., 2010. Developmental aspects of language lateralization in delta, theta, alpha and beta EEG bands. Biol. Psychol. *85* (2), 258–267.

Staubli, U., Xu, F.B., 1995. Effects of 5-HT3 receptor antagonism on hippocampal theta rhythm, memory, and LTP induction in the freely moving rat. J. Neurosci. *15* (3), 2445–2452.

Strenze, T., 2007. Intelligence and socioeconomic success: A meta-analytic review of longitudinal research. Intelligence *35* (5), 401–426. https://doi.org/10.1016/j.intell.2006.09.004.

Stroganova, T.A., Orekhova, E.V., 2007. EEG and infant states. In: De Haan, M. (Ed.), Infant EEG and event-related potentials. Psychology Press, pp. 251–288.

Stroganova, T.A., Orekhova, E.V., Posikera, I.N., 1998. Externally and internally controlled attention in infants: An EEG study. Int. J. Psychophysiol. *30* (3), 339–351.

Stroganova, T.A., Orekhova, E.V., Posikera, I.N., 1999. EEG alpha rhythm in infants. Clin. Neurophysiol. *110* (6), 997–1012.

Sweeney-Reed, C.M., Zaehle, T., Voges, J., Schmitt, F.C., Buentjen, L., Kopitzki, K., Richardson-Klavehn, A., Hinrichs, H., Heinze, H.-J., Knight, R.T., Rugg, M.D., 2016. Pre-stimulus thalamic theta power predicts human memory formation. NeuroImage *138*, 100–108. https://doi.org/10.1016/j.neuroimage.2016.05.042.

Tajik-Parvinchi, D., Farmus, L., Tablon Modica, P., Cribbie, R.A., Weiss, J.A., 2021. The role of cognitive control and emotion regulation in predicting mental health problems in children with neurodevelopmental disorders. Child.: Care, Health Dev. *47* (5), 608–617. https://doi.org/10.1111/cch.12868.

Tamnes, C.K., Walhovd, K.B., Torstveit, M., Sells, V.T., Fjell, A.M., 2013. Performance monitoring in children and adolescents: A review of developmental changes in the error-related negativity and brain maturation. Dev. Cogn. Neurosci. *6*, 1–13. https://doi.org/10.1016/j.dcn.2013.05.001.

Tan, E., Tang, A., Debnath, R., Humphreys, K.L., Zeanah, C.H., Nelson, C.A., Fox, N.A., 2023. Resting brain activity in early childhood predicts IQ at 18 years. Dev. Cogn. Neurosci. *63*, 101287 https://doi.org/10.1016/j.dcn.2023.101287.

Tarullo, A.R., Obradović, J., Keehn, B., Rasheed, M.A., Siyal, S., Nelson, C.A., Yousafzai, A.K., 2017. Gamma power in rural Pakistani children: Links to executive function and verbal ability. Dev. Cogn. Neurosci. *26*, 1–8. https://doi.org/10.1016/j.dcn.2017.03.007.

Taylor, S.F., Stern, E.R., Gehring, W.J., 2007. Neural systems for error monitoring: Recent findings and theoretical perspectives. Neuroscientist *13* (2), 160–172.

Thatcher, R.W., 1998. Normative EEG databases and EEG biofeedback. J. Neurother. *2* (4), 8–39.

Thut, G., Miniussi, C., Gross, J., 2012. The Functional Importance of Rhythmic Activity in the Brain. Curr. Biol. *22* (16), R658–R663. https://doi.org/10.1016/j.cub.2012.06.061.

Tomalski, P., Moore, D.G., Ribeiro, H., Axelsson, E.L., Murphy, E., Karmiloff-Smith, A., Johnson, M.H., Kushnerenko, E., 2013. Socioeconomic status and functional brain development – associations in early infancy. Dev. Sci. *16* (5), 676–687. https://doi.org/10.1111/desc.12079.

Tort, A.B.L., Komorowski, R.W., Manns, J.R., Kopell, N.J., Eichenbaum, H., 2009. Theta–gamma coupling increases during the learning of item–context associations. Proc. Natl. Acad. Sci. *106* (49), 20942–20947. https://doi.org/10.1073/pnas.0911331106.

Trammell, J.P., MacRae, P.G., Davis, G., Bergstedt, D., Anderson, A.E., 2017. The Relationship of Cognitive Performance and the Theta-Alpha Power Ratio Is Age-Dependent: An EEG Study of Short Term Memory and Reasoning during Task and Resting-State in Healthy Young and Old Adults. Front. Aging Neurosci. *9*. 〈https://www.frontiersin.org/articles/10.3389/fnagi.2017.00364〉.

Tran, T.T., Rolle, C.E., Gazzaley, A., Voytek, B., 2020. Linked sources of neural noise contribute to age-related cognitive decline. J. Cogn. Neurosci. *32* (9), 1813–1822.

Troller-Renfree, S.V., Brito, N.H., Desai, P.M., Leon-Santos, A.G., Wiltshire, C.A., Motton, S.N., Meyer, J.S., Isler, J., Fifer, W.P., Noble, K.G., 2020. Infants of mothers with higher physiological stress show alterations in brain function. Dev. Sci. *23* (6), e12976 https://doi.org/10.1111/desc.12976.

Troller-Renfree, S.V., Costanzo, M.A., Duncan, G.J., Magnuson, K., Gennetian, L.A., Yoshikawa, H., Halpern-Meekin, S., Fox, N.A., Noble, K.G., 2022. The impact of a poverty reduction intervention on infant brain activity. Proc. Natl. Acad. Sci. *119* (5), e2115649119 https://doi.org/10.1073/pnas.2115649119.

Troller-Renfree, S.V., Sperber, J.F., Hart, E.R., Costanzo, M.A., Gennetian, L.A., Meyer, J. S., Fox, N.A., Noble, K.G., 2023. Associations between maternal stress and infant resting brain activity among families residing in poverty in the US. Biol. Psychol., 108683

Trujillo, L.T., Allen, J.J.B., 2007. Theta EEG dynamics of the error-related negativity. Clin. Neurophysiol. *118* (3), 645–668. https://doi.org/10.1016/j.clinph.2006.11.009.

Tzur, G., Berger, A., 2007. When things look wrong: Theta activity in rule violation. Neuropsychologia *45* (13), 3122–3126. https://doi.org/10.1016/j.neuropsychologia.2007.05.004.

Tzur, G., Berger, A., 2009. Fast and slow brain rhythms in rule/expectation violation tasks: Focusing on evaluation processes by excluding motor action. Behav. Brain Res. *198* (2), 420–428. https://doi.org/10.1016/j.bbr.2008.11.041.

Tzur, G., Berger, A., Luria, R., Posner, M.I., 2010. Theta synchrony supports Weber–Fechner and Stevens' Laws for error processing, uniting high and low mental processes. Psychophysiology *47* (4), 758–766. https://doi.org/10.1111/j.1469-8986.2010.00967.x.

Uhlhaas, P.J., Roux, F., Singer, W., Haenschel, C., Sireteanu, R., Rodriguez, E., 2009. The development of neural synchrony reflects late maturation and restructuring of functional networks in humans. Proc. Natl. Acad. Sci. *106* (24), 9866–9871. https://doi.org/10.1073/pnas.0900390106.

Uhlhaas, P.J., Roux, F., Rodriguez, E., Rotarska-Jagiela, A., Singer, W., 2010. Neural synchrony and the development of cortical networks. Trends Cogn. Sci. *14* (2), 72–80. https://doi.org/10.1016/j.tics.2009.12.002.

Van de Vijver, I., Ridderinkhof, K.R., Cohen, M.X., 2011. Frontal oscillatory dynamics predict feedback learning and action adjustment. J. Cogn. Neurosci. 23 (12), 4106–4121.

Vanderwert, R.E., Marshall, P.J., Nelson III, C.A., Zeanah, C.H., Fox, N.A., 2010. Timing of intervention affects brain electrical activity in children exposed to severe psychosocial neglect. PLoS One *5* (7), e11415.

Vanderwert, R.E., Zeanah, C.H., Fox, N.A., Nelson, C.A., 2016. Normalization of EEG activity among previously institutionalized children placed into foster care: A 12-year follow-up of the Bucharest Early Intervention Project. Dev. Cogn. Neurosci. *17*, 68–75. https://doi.org/10.1016/j.dcn.2015.12.004.

Varela, F., Lachaux, J.-P., Rodriguez, E., Martinerie, J., 2001. The brainweb: Phase synchronization and large-scale integration. Nat. Rev. Neurosci. *2* (4), 229–239.

Veen, V. van, Carter, C.S., 2002. The timing of action-monitoring processes in the anterior cingulate cortex. J. Cogn. Neurosci. *14* (4), 593–602.

Verbruggen, F., Logan, G.D., 2008. Response inhibition in the stop-signal paradigm. Trends Cogn. Sci. *12* (11), 418–424.

Vlahou, E.L., Thurm, F., Kolassa, I.-T., Schlee, W., 2014. Resting-state slow wave power, healthy aging and cognitive performance. Sci. Rep. *4* (1), 5101. https://doi.org/10.1038/srep05101.

Von Stein, A., Sarnthein, J., 2000. Different frequencies for different scales of cortical integration: From local gamma to long range alpha/theta synchronization. Int. J. Psychophysiol. *38* (3), 301–313.

Wascher, E., Rasch, B., Sänger, J., Hoffmann, S., Schneider, D., Rinkenauer, G., Heuer, H., Gutberlet, I., 2014. Frontal theta activity reflects distinct aspects of mental fatigue. Biol. Psychol. *96*, 57–65. https://doi.org/10.1016/j.biopsycho.2013.11.010.

Wass, S.V., Noreika, V., Georgieva, S., Clackson, K., Brightman, L., Nutbrown, R., Covarrubias, L.S., Leong, V., 2018. Parental neural responsivity to infants' visual attention: How mature brains influence immature brains during social interaction. PLOS Biol. *16* (12), e2006328 https://doi.org/10.1371/journal.pbio.2006328.

Wechsler, D., 2004. The Wechsler Intelligence Scale for Children, 4th ed. The Psychological Corporation.

Whitford, T.J., Rennie, C.J., Grieve, S.M., Clark, C.R., Gordon, E., Williams, L.M., 2007. Brain maturation in adolescence: Concurrent changes in neuroanatomy and neurophysiology. Hum. Brain Mapp. *28* (3), 228–237.

Wiebe, S.P., Stäubli, U.V., 2001. Recognition Memory Correlates of Hippocampal Theta Cells. J. Neurosci. *21* (11), 3955. https://doi.org/10.1523/JNEUROSCI.21-11-03955.2001.

Williams, I.A., Tarullo, A.R., Grieve, P.G., Wilpers, A., Vignola, E.F., Myers, M.M., Fifer, W.P., 2012. Fetal cerebrovascular resistance and neonatal EEG predict 18-month neurodevelopmental outcome in infants with congenital heart disease. Ultrasound Obstet. Gynecol. *40* (3), 304–309. https://doi.org/10.1002/uog.11144.

Winson, J., 1978. Loss of hippocampal theta rhythm results in spatial memory deficit in the rat. Science *201* (4351)), 160–163.

Xie, W., Mallin, B.M., Richards, J.E., 2017. Development of infant sustained attention and its relation to EEG oscillations: An EEG and cortical source analysis study (n/a). Dev. Sci., e12562. https://doi.org/10.1111/desc.12562.

Xu, X., Buzzell, G.A., Bowers, M.E., Shuffrey, L.C., Leach, S.C., McSweeney, M., Yoder, L., Fifer, B., Myers, M., Elliott, A.J., Fox, N.A., & Morales, S. (in press). Electrophysiological Correlates of Inhibitory Control in Children: Relations with Prenatal Risk Factors and Child Psychopathology. *Development and Psychopathology*. 〈https://doi.org/10.1017/S0954579424000816〉.

Zeanah, C.H., Nelson, C.A., Fox, N.A., Smyke, A.T., Marshall, P., Parker, S.W., Koga, S., 2003. Designing research to study the effects of institutionalization on brain and behavioral development: The Bucharest Early Intervention Project. Dev. Psychopathol. *15* (4), 885–907.

Zhang, Y., Koerner, T., Miller, S., Grice-Patil, Z., Svec, A., Akbari, D., Tusler, L., Carney, E., 2011. Neural coding of formant-exaggerated speech in the infant brain. Dev. Sci. *14* (3), 566–581. https://doi.org/10.1111/j.1467-7687.2010.01004.x.