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

Enda Tan[a,b *], Sonya V. Troller-Renfree[c], Santiago Morales[d], George A. Buzzell[e], Marco McSweeney[a], Martín Antúnez[a], Nathan A. Fox[a,b]

[a] Department of Human Development and Quantitative Methodology, University of Maryland, College Park; College Park, MD, 20740, USA.

[b] Neuroscience and Cognitive Science Program, University of Maryland, College Park; College Park, MD, 20740, USA.

[c] Teachers College, Columbia University; New York, NY, 10027, USA.

[d] Department of Psychology, University of Southern California; Los Angeles, CA, 90007, USA.

[e] Department of Psychology, Florida International University; Miami, FL, 33199, USA.

* Correspondence concerning this paper should be addressed to Enda Tan, Department of Human Development and Quantitative Methodology, 3119 Benjamin Building, College Park, MD 20742. E-mail: endatan@umd.edu

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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: On the one hand, children and adolescents who exhibit higher theta power during resting state tend to have lower cognitive abilities. On the other hand, task-related EEG research has consistently found positive associations between theta power during cognitive tasks and behavioral performance. Why does theta power, measured during resting state versus cognitive tasks, exhibit distinct correlations with cognitive functioning? This review provides a coherent account of the functional properties of theta across contexts. We first present evidence that higher theta power during resting state predicts lower executive functioning, attentional abilities, language skills, and IQ. Next, we review research showing that theta activity plays a crucial role in memory, attention, and cognitive control, and that higher theta power during cognitive tasks predicts better behavioral performance. Finally, we discuss potential explanations for the differential correlations between resting/task-related theta and cognitive functioning, and propose future directions for clarifying these relations.

Keywords: electroencephalography (EEG), theta, neural oscillations, cognitive functioning, child development

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 direct measure of the electrical activity of the brain and provides unique insights into the dynamics of neurocognitive processes (Davidson et al., 2000). Over the past decades, developmental EEG research has made significant progress by adopting more sophisticated analysis approaches (Buzzell et al., 2023). A particularly fruitful area of research has focused on the analysis of oscillatory EEG activity (Cuevas & Bell, 2022; Saby & Marshall, 2012). Oscillatory EEG activity reflects rhythmic changes in local field potentials (LFPs), which are influenced by fluctuations in the excitability of neurons (Nunez & Srinivasan, 2006; Thut et al., 2012). These neural oscillations are thought to play a crucial role in the development of cortical networks and the coordination of 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 transformed from the time domain into the frequency domain, and divided into frequency bands bearing the names of Greek letters (e.g., theta, alpha, beta). These frequency bands are defined based on frequency characteristics, functional properties, and topographical distribution (Kuhlman, 1980). The energy within each band is quantified by spectral power (i.e., signal amplitude squared; Thatcher, 1998). Among various frequency bands, the theta band stands out for its prominence in the power spectrum and its unique position as a transition point traditionally used to distinguish low- and high-frequency bands (Klimesch, 1999; Saad et al., 2018).

A growing number of studies have shown that theta activity exhibits distinct functional properties during resting state versus cognitive tasks. On the one hand, greater theta power during a resting state recording has been associated with lower cognitive skills in children and adolescents (e.g., Maguire & Schneider, 2019; Perone et al., 2018), suggestive of a negative relation between resting theta power and cognitive functioning. On the other hand, 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, exhibit distinct correlations with cognitive performance? This article provides an integrated account of the functional properties of theta activity across contexts. 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 the divergent patterns of associations. Finally, we synthesize evidence across the resting-state and task-related EEG literatures, and explore potential explanations for the divergent associations observed across contexts.

2. The development of oscillatory EEG activity

Developmental EEG research has found that frequency bands that share 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 these age-related differences, the boundaries of different frequency bands are typically defined at lower values in younger (vs. older) children (Saby & Marshall, 2012). For example, although the exact boundaries are somewhat debated, the theta frequency ranges tend to be ~4-8 Hz in adults and ~3-5 Hz in infants (Orekhova et al., 1999). As children age, the boundaries of different frequency bands progressively increase. Besides increasing frequency boundaries over time, an alternative strategy for setting frequency boundaries across age groups involves the use of individual alpha peak frequency (IAF; Lansbergen et al., 2011). For instance, because individuals exhibit greater alpha power when their eyes are closed (vs. open) (Gale et al., 1971; Jasper, 1936), one way of defining the IAF is to identify the specific frequency within the alpha range that exhibits the greatest power differences between eyes-closed and eyes-open conditions. The boundaries of different frequency bands can then be established using proportions of the IAF (e.g., theta: .4×IAF-.8×IAF, alpha: .8×IAF-1.2×IAF, beta: 1.2×IAF-30 Hz; Perone et al., 2018; see also Klimesch, 1999).

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 (i.e., 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). Although there is always some energy within each frequency band across age groups, the relative power of different frequency bands changes as children age (Figure 1). During early childhood, the power spectrum of resting EEG is dominated by slower (e.g., delta, theta) oscillations (Cellier et al., 2021; Schaworonkow & Voytek, 2021). During this period, the peak of oscillatory activity falls within the low theta range (e.g., 3-4 Hz; Lodder & van Putten, 2011). From infancy through adolescence, relative power in lower-frequency bands decreases and 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 falls within the alpha range (8-12 Hz; Chiang et al., 2011; Klimesch, 1999).

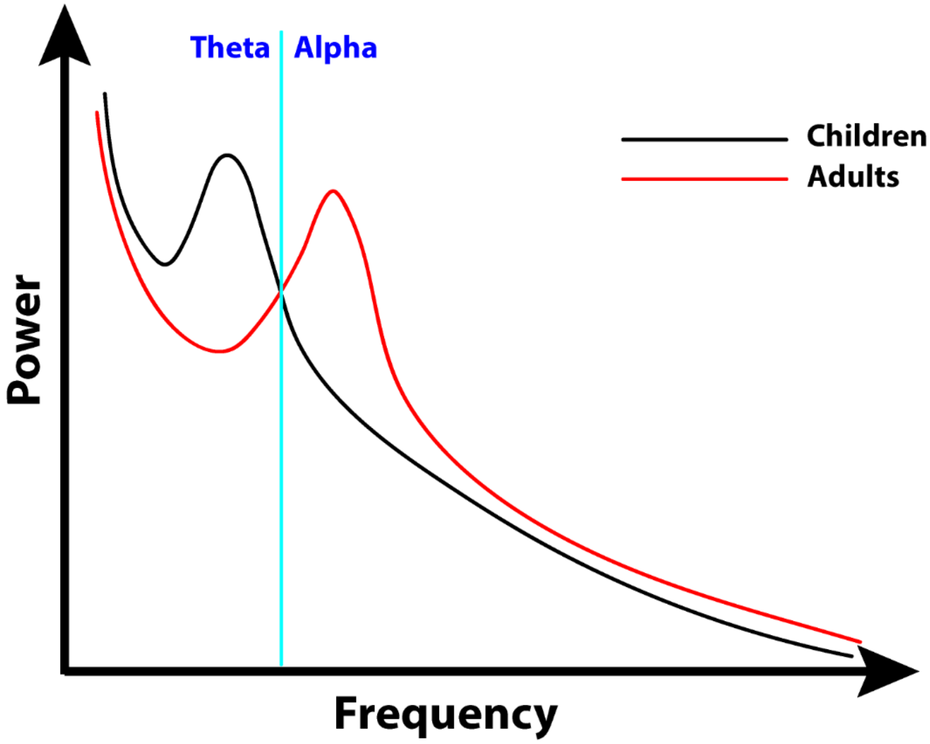

Figure 1. Age-related shift of peak oscillatory activity from the theta range to the alpha range. Adapted from Cellier et al. (2021).

The age-related changes in relative EEG power have been attributed to the maturation of the gamma-aminobutyric acid (GABA) neurotransmitter system, synaptic pruning, and grey matter reduction (Feinberg & Campbell, 2010; Hashimoto et al., 2009; Smit et al., 2012; Whitford et al., 2007). In more mature brains, higher-frequency oscillations depend on the rapid interaction between excitatory pyramidal cells and inhibitory interneurons (Atallah & Scanziani, 2009; Cardin et al., 2009). These interneurons exert inhibitory effects through the neurotransmitter GABA (Buzsáki & 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, neural oscillations primarily rely on recurrent, long-lasting potentials known as giant depolarizing potentials (GDPs), which are too slow to generate high-frequency oscillations. Consequently, neural oscillations in less mature brains are dominated by lower-frequency rhythms. As the brain matures, the intracellular concentration of chloride decreases, enabling 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- (vs. higher) frequency oscillations are typically associated with long-distance neural communication (Von Stein & Sarnthein, 2000), the age-related decline in lower-frequency EEG power is also believed 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.

3. Resting-state 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 reflects a maturational lag in brain development (Corning et al., 1982, 1986; Matsuura et al., 1993). This hypothesis is supported by research showing that children who have experienced environmental adversities exhibit increased EEG power in lower-frequency bands and decreased EEG power in higher-frequency bands. For example, compared with typically-developing children, children who had 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 (Debnath et al., 2020; Marshall et al., 2004; Vanderwert et al., 2016). This 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 decreases 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 & Schneider, 2019; Otero, 1994; Otero et al., 2003; Tomalski et al., 2013) and in children exposed to higher (vs. lower) caregiver stress (Brandes-Aitken, Pini, et al., 2023; Jensen et al., 2021; Pierce et al., 2019; Troller-Renfree et al., 2020, 2023). Critically, these patterns of brain activity appear to be malleable through randomized control trials targeting environmental factors (Debnath et al., 2020; Troller-Renfree et al., 2022; Vanderwert et al., 2010, 2016). Collectively, these studies demonstrate that resting-state brain activity is sensitive to environmental influences on brain development, supporting the hypothesis 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 be associated 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. For recent reviews on EEG activity in other frequency bands, see Anderson & Perone (2018) and Cuevas & Bell (2022).

3.1 Executive functioning

Executive functioning refers to a set of cognitive skills responsible for the regulation of thought and behavior (Anderson, 2002; Carlson, 2005; Diamond, 2013). These skills include working memory (the ability to hold and manipulate information in mind), inhibitory control (the ability to inhibit prepotent responses), and cognitive flexibility (the ability to shift between tasks or mental sets). Although 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. For example, 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, consistent with past research showing the links between environmental adversities and resting EEG. In addition, higher resting theta power was associated with lower working memory across all participants, whereas higher resting alpha power was associated with higher vocabulary in participants from low-income homes. These results provide evidence for the negative associations between resting theta power and working memory in children and adolescents.

The links between resting theta and executive functioning have also been shown in studies using power ratio measures. In one study, 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 the frontal and posterior regions decreased from 3 to 9 years. Importantly, children exhibiting a higher theta/beta power ratio during resting state showed lower performance on working memory, inhibitory control, and cognitive flexibility tasks. These associations held even after individual differences in age and verbal ability were controlled for, highlighting the robustness of the associations. In another study, Cai and colleagues (2021) examined resting EEG power over the frontal brain region in 7-9-year-old children. They found that, after controlling for age and verbal ability, greater alpha/theta and beta/theta ratios (theta frequency range: 4 Hz – IAF-2 Hz) during resting state predicted higher inhibition skills, and that greater resting beta/theta ratios predicted higher planning skills. Together, these findings provide evidence for links between resting theta power ratios and different 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 power changes in the other frequency band. 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 & Dark, 1986). This allows individuals to allocate limited mental resources to important tasks, promoting adaptive behaviors. A growing number of studies have demonstrated that higher resting theta power is associated with lower attentional abilities. In infancy, Perone and Gartstein (2019) 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 6-12 month-olds. 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 have been commonly reported 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). That said, it is important to note that the associations between resting theta/beta ratio and ADHD have not consistently replicated across studies (for reviews, see Arns et al., 2013; Lenartowicz & Loo, 2014; Loo & 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 & Thiagarajan, 2019). Therefore, the use of resting theta/beta ratio in the assessment of ADHD remains a topic of debate (Gloss et al., 2016; Saad et al., 2018), and further research is needed to clarify the relations between resting theta/beta ratio, ADHD, and other mental health conditions. We will return to this issue in Section 5.1.

3.3 Language

In addition to executive functioning and attentional abilities, higher resting theta power has also been associated with lower language skills in children and adolescents. In infants, a recent study found no associations between absolute resting theta (4-6 Hz) power at birth and language skills at 15 months (Brito et al., 2016). However, in older children, Lum and colleagues (2022) found that absolute resting theta (4-8 Hz) power over the left central-prefrontal regions was negatively associated with performance on a sentence repetition task in 9-11-year-olds. The association was specific to the theta band. Similarly, in a longitudinal study, 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 held even after controlling for individual differences in general cognitive abilities, age, home literacy environment, and phonological skills. These studies 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 example, Papagiannopoulou and Lagopoulos (2016) found that, compared with typically developing children, 8-year-old children diagnosed with dyslexia showed increased resting relative theta (3.6-7.4 Hz) power over the left frontal brain region. Similarly, Arns and colleagues (2007) found that 10-16-year-old children diagnosed with dyslexia showed increased absolute resting theta (4-7.5 Hz) power over the frontal and right temporal brain regions. Collectively, these studies provide converging 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 provide a global measure of intellectual ability across cognitive domains, including perceptual reasoning, verbal comprehension, working memory, and processing speed (Wechsler, 2004). IQ tests have been widely used across educational and clinical settings, and IQ scores have been shown to predict real-life outcomes including academic achievement (Deary et al., 2007), job performance (Schmidt & Hunter, 2004), socioeconomic status (Strenze, 2007), and health outcomes (Calvin et al., 2017). A recent study suggests 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 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. 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, suggesting that early experiential factors affect long-term cognitive development through changes in early brain activity. Importantly, these effects were specific to the theta band, and post-hoc analyses on different domains of the IQ test replicated the effects across the perceptual reasoning, working memory, and processing speed domains. These findings provide evidence that early individual differences in resting theta power have meaningful implications for predicting cognitive outcomes into adulthood.

3.5 Interim discussion

The studies reviewed above provide evidence that increased resting theta power is associated with early environmental adversities, and that children and adolescents who exhibit higher resting theta power tend to show lower executive functioning, attentional abilities, language skills, and IQ. These findings demonstrate a negative association between resting theta power and cognitive functioning in childhood and adolescence. We note that there are considerable methodological variations among the studies reviewed above, including the paradigms used to assess resting EEG (e.g., eyes closed/open, dark room, passive viewing of bubbles), the brain regions examined, the use of absolute versus relative power, and the use of power versus power ratio scores. These variations make direct comparisons between studies difficult. That said, the fact that negative associations emerge despite the methodological differences across studies suggests that the overall inverse relation between resting theta power and cognitive functioning is robust. We also note that the associations between resting theta power and cognitive functioning are less consistent in adults than in children and adolescents (Finnigan & 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 magnitude of these relations may change with age in late adulthood (Lithfous et al., 2015; Trammell et al., 2017; Vlahou et al., 2014). The nonlinear nature of the relations across development underscores the importance of considering age when utilizing resting EEG power as an index of brain development.

Although the relations between resting EEG power and cognitive functioning were found to be specific to the theta band in some studies (e.g., Lum et al., 2022; Tan et al., 2023), it is important to note that significant correlations between resting EEG power and cognitive functioning have been reported in other frequency bands (for recent reviews, see Anderson & Perone, 2018; Cuevas & Bell, 2022). For example, greater resting alpha power has been associated with higher executive functioning in infants (Bell & Fox, 1992, 1997; but see Kraybill & Bell, 2013), and greater resting gamma power has been associated with 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). These effects are in line with the theta/alpha and theta/beta findings reported above, 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. We will return to this issue 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 typically use time-frequency analysis to characterize the temporal dynamics of brain activity in response to events of interest (Morales & Bowers, 2022). In contrast to resting EEG research, which has typically found negative associations between theta power and cognitive functioning, task-related EEG research has consistently found positive associations between theta power and cognitive functioning. In the following sections, we review evidence that task-related theta actively contributes to key cognitive processes (including memory, attention, and cognitive control), that engagement of cognitive processes is associated with increased theta power, and that greater theta power during cognitive tasks predicts better behavioral performance.

4.1 Memory

Non-human animal research has demonstrated that theta activity plays a pivotal role in memory formation (Colgin, 2013). At the single-cell level, studies have shown that 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 fundamental cellular mechanism for memory formation (Hölscher et al., 1997; Pavlides et al., 1988). By contrast, stimulating hippocampal cells during the trough of theta oscillations or at other frequencies is much less likely to induce LTP (Greenstein et al., 1988). These findings suggest that theta oscillations contribute to memory formation by modulating the synaptic activity of hippocampal neurons. At the behavioral level, rodent studies have shown that increased hippocampal theta power during olfactory and spatial memory tasks predicted better task performance (Olvera-Cortés et al., 2002; Wiebe & Stäubli, 2001), and that increased hippocampal theta activity prior to classical conditioning predicted faster rates of learning (Berry & Thompson, 1978). In addition, enhancing hippocampal theta through pharmacological manipulation and electrical stimulation resulted in higher performance on olfactory/spatial memory and avoidance memory tasks (Landfield, 1977; Staubli & Xu, 1995), whereas disrupting hippocampal theta through lesion or pharmacological manipulation resulted in spatial memory impairments (Chrobak et al., 1989; Winson, 1978). Collectively, these studies provide evidence for the causal roles of hippocampal theta in memory formation.

Although animal memory research has predominantly focused on hippocampal theta, theta rhythms can be generated in other brain areas (e.g., cingulate cortex, entorhinal cortex, prefrontal cortex; for reviews, see Colgin, 2013; Kahana et al., 2001). Theta activity is thought to play a key role in promoting information transmission across different brain regions. For example, rodent research has shown that increased theta coupling between the hippocampus and medial prefrontal cortex (mPFC) during spatial memory tasks was associated with better behavioral performance (Hyman et al., 2010; Jones & Wilson, 2005). Increased theta coupling has also 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 rodents. These findings support the hypothesis that theta activity contributes to memory processes by facilitating coordination across task-related brain areas.

The links between task-related theta and memory processes have also been demonstrated in human participants. In adults, episodic memory research has shown that greater absolute theta power over the frontal and parietal regions during, or prior to, the encoding of items is associated with more successful recall and recognition of these items (for a review, see Herweg et al., 2020). Similar links have been found in infants, children, and adolescents. For instance, Begus and colleagues (2015) recorded 11-month-olds' EEG activity while they were exploring novel objects, and then 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 naturalistic mother-infant interaction paradigm, Michel and colleagues (2023) found that 9-10-month-old infants who exhibited greater absolute theta (3.5-5 Hz) power during object encoding subsequently showed higher performance in object recognition. In 2-year-olds, greater absolute theta (3-5 Hz) power during verbal recall was associated with higher recall performance (Cuevas et al., 2012). During middle childhood, greater theta inter-trial phase-synchrony (reflecting the consistency of oscillatory phase angle across trials) and greater correlations of theta activity between brain regions during memory tasks predicted more successful recall (Blankenship & Bell, 2015; Güntekin et al., 2020). In older children and adolescents, increased absolute theta power has been observed across brain regions during memory encoding and retrieval (Cuevas et al., 2012; Köster et al., 2017; Krause et al., 2001, 2007; Rajan & Bell, 2015). Together, these findings suggest that, similar to non-human animals, task-related theta plays an active role in memory processes in humans.

The links between task-related theta and memory also involve more complex interactions with gamma oscillations. Theta-gamma coupling refers to the phenomenon in which the power of gamma oscillations is modulated by the phase of theta oscillations (Figure 2). This interplay between the two rhythms is thought to contribute to memory processes by providing temporal references for organizing items within memory and facilitating information transmission across brain areas (for reviews, see Colgin, 2015; Lisman & Jensen, 2013). For instance, theta rhythms are thought to contribute to the binding of individual items in short-term memory (Lisman & Idiart, 1995). According to this theory, individual memory items are represented in neurons firing at the gamma frequency, and the entire set of items held in short-term memory are represented in theta cycles. As a result, the capacity of short-term memory is determined by the number of gamma cycles that can fit inside a theta cycle (e.g., 7±2; Miller, 1956). Consistent with this idea, research with human adults has found that resting theta/gamma cycle length ratio was positively associated with short-term memory capacity (Kamiński et al., 2011; but see Malenínská et al., 2021), and that down-regulating individual theta frequency via transcranial alternating current stimulation (tACS) resulted in an increase in short-term memory (Vosskuhl et al., 2015; see also Wolinski et al., 2018). These findings support the theta-gamma phase coupling theory of short-term memory.

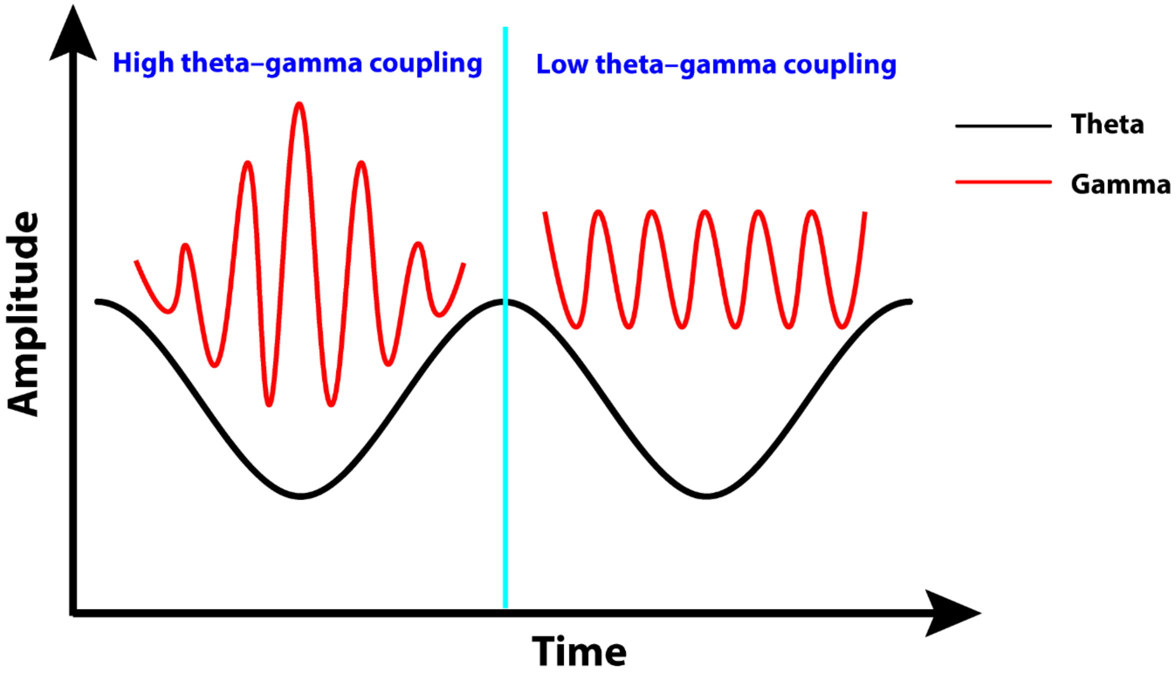

Figure 2. Theta-gamma coupling. Left: high theta-gamma coupling. Right: low theta-gamma coupling. Adapted from Brooks et al. (2020).

The involvement of theta-gamma coupling in memory processes is also supported by research showing links between the strength of theta-gamma coupling and memory performance. In rodents, increased theta-gamma coupling has been observed during odor-place and item-context association memory tasks, and stronger theta-gamma coupling has been associated with more successful learning (Igarashi et al., 2014; Tort et al., 2009). In human adults, increased theta-gamma coupling has been found across working memory and long-term memory tasks, and stronger theta-gamma coupling during these tasks predicted better memory performance (Friese et al., 2013; Fuentemilla et al., 2010; Köster et al., 2014; Mormann et al., 2005; Rutishauser et al., 2010; Vivekananda et al., 2021). Moreover, applying bursts of gamma oscillations over the peaks (vs. troughs) of theta oscillations in the prefrontal cortex resulted in enhanced spatial working memory (Alekseichuk et al., 2016), whereas applying gamma bursts over the troughs (vs. peaks) 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 coupling during working memory tasks predicted higher working memory performance (Kavanaugh et al., 2021). Together, these findings highlight the importance of theta-gamma coupling in memory processes.

4.2 Attention

Attention and memory are closely related mental processes. Memory research has shown 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 this pre-stimulus effect is that differences in theta activity reflect fluctuations in attention, which can influence memory encoding (Kim, 2011). However, closer examination of the data (e.g., trial-by-trial analysis) revealed that attentional fluctuations could not fully explain the pre-stimulus theta effects observed 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, task-related theta has been shown to play a crucial role in attentional processes. For instance, human and non-human animal research has demonstrated 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). To account for this phenomenon, it is proposed that theta activity shapes spatial attention by organizing neural activity into distinct attentional states, including a “sampling” state with increased perceptual sensitivity for the attended location, and a “shifting” state for directing attention to other locations (Fiebelkorn & Kastner, 2019). In addition to spatial attention, theta activity is also believed to contribute to sustained attention by supporting cognitive control and facilitating long-range communication across brain areas (Clayton et al., 2015).

In adults, increased theta power over the frontal region has been commonly observed during tasks that require increased attention (Barwick et al., 2012; Gevins et al., 1997; Kamzanova et al., 2011; Wascher et al., 2014). The links between task-related theta and attentional processes have also been demonstrated in infants. For example, using a live interaction paradigm, Orekhova and colleagues (1999) showed 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 12-month-old infants exhibiting higher relative theta (3-7 Hz) power over the central region prior to visual fixations showed longer visual attention during the task. Together, these live interaction studies provide evidence for links between task-related theta and attentional processes in infants.

The associations between task-related theta and attention-related processes have also been demonstrated 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) found that 12-month-old infants exhibited increased absolute theta (3-6 Hz) power over the frontal region when viewing dynamic movies of people and objects; this type of viewing has been linked to attention, learning, and memory processes (Stroganova & Orekhova, 2007). Importantly, 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 provide evidence that task-related theta is implicated in attention-related processes early in life, and that individual differences in theta activity during tasks are associated with cognitive abilities.

In infancy, sustained attention is characterized by a reduction in heart rate (Richards, 2008; Richards & Casey, 1991). The links between theta and attentional processes have also been demonstrated in studies using heart-rate deceleration as an index of sustained attention. Using dynamic videos as stimuli, Xie and colleagues (2017) demonstrated that 10- and 12-month-old infants showed increased theta (2-6 Hz) and decreased alpha power spectral density (PSD) during heart-rate defined sustained attention (vs. inattention) episodes. 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) demonstrated that 3-month-old infants exhibited higher absolute theta (4-6 Hz) power over the frontal region during heart-rate defined sustained attention, and that greater increases in theta power during sustained attention at 3 months predicted better recognition memory at 9 months. These findings provide further evidence for the links between task-related theta and attentional processes in infancy, and support the hypothesis that early individual differences in task-related theta predict subsequent cognitive functioning.

Attention-related theta activity has also been explored using the oddball paradigm. In this paradigm, brain responses elicited by a frequently repeated sound (i.e., standard sound) are compared with those elicited by an infrequent sound (i.e., deviant sound). 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). In children, adolescents, and adults, studies using a two-stimulus oddball task (which involves standard and deviant sounds) have consistently found increased absolute theta power and theta inter-trial phase synchrony in response to deviant (vs. standard) sounds over the frontal region (Bishop et al., 2011; Fuentemilla et al., 2008; Müller et al., 2009). The magnitude of these effects increased with age, suggesting that theta-related attentional processes undergo important changes over time. Similarly, using a three-stimulus auditory oddball task (which involves a third category of 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 (Morales et al., 2023). These effects increased with age, and increased theta inter-trial phase synchrony in response to novel sounds predicted higher inhibitory control. Together, these studies provide evidence that task-related theta is involved in attention-related processes beyond infancy, and that these processes undergo developmental changes throughout childhood and adolescence.

4.3 Cognitive control

Cognitive control refers to the ability to monitor one own's behaviors for conflicts (competition between multiple potential actions), mistakes, and feedback, and to make behavioral adjustments 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 & Inzlicht, 2010; Tajik-Parvinchi et al., 2021). Cognitive control has been associated with increased theta activity over medial-frontal cortex (for reviews, see Cavanagh & Frank, 2014; Cohen, 2014). Functionally, theta activity is thought to play a crucial role in communicating the need for cognitive control across task-related brain regions through synchronized phase entrainment (Fries, 2005; Varela et al., 2001). Indeed, evoked theta and theta phase resetting are thought to contribute to event-related potential (ERP) components that are commonly observed when individuals engage in 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 the anterior cingulate cortex (ACC; Luu et al., 2003; Veen & Carter, 2002) and the posterior cingulate cortex

(PCC; Buzzell et al., 2017), and these brain regions have been linked to cognitive control in fMRI studies (for reviews, see Botvinick et al., 2004; Taylor et al., 2007).

In adults, increased theta power has been observed when individuals detect errors in the environment, including arithmetic errors (Tzur et al., 2010; Tzur & Berger, 2007, 2009) and semantic errors (Hald et al., 2006). Similar effects have been observed in infants (for reviews, see Begus & Bonawitz, 2020; Berger & Posner, 2022). For example, Berger and colleagues (2006) found that 6-9-month-old 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. Similarly, Conejero and colleagues (2018) found that 16-18-month-old children showed greater absolute theta (6-7 Hz) power over the mediofrontal region when observing incorrect (vs. correct) puzzle configurations, with children from more highly educated families showing stronger theta increments. In another study, Köster and colleagues (2021) presented 9-month-old infants with physical and social events with unexpected or expected outcomes, and found increased absolute theta (4-5 Hz) power across the scalp when infants viewed unexpected (vs. expected) outcomes (see also Köster et al., 2019; Reid et al., 2009). Increased theta power in response to errors has also been found in older children and adolescents. For example, Schneider and Maguire (2019) demonstrated 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. Together, these findings provide evidence that task-related theta is implicated when individuals process errors in the environment.

Increased midfrontal theta power has also been observed in adults when they engage in control processes related to their own behaviors, including response conflicts (Cohen &

Cavanagh, 2011; Cohen & Donner, 2013; Nigbur et al., 2011), error monitoring (Cavanagh et al., 2009; Luu et al., 2004; Trujillo & Allen, 2007), task switching (Cunillera et al., 2012), and feedback processing (Cavanagh et al., 2010). In infants and children, increased theta power has been observed in situations requiring higher cognitive control. For instance, Orekhova and colleagues (2006) found that 7-12-month-old infants and 4-6-year-old children showed increased absolute theta (3.6-5.6 Hz in infants and 4-8 Hz in children) power during toy exploration and social interaction with an adult; these situations presumably require increased top-down control. Notably, the distribution of theta power varied across age groups and situations, suggesting that different brain networks were engaged across ages and situations. Similarly, Meyer and colleagues (2019) found that 4-year-old children exhibited increased absolute theta (3-6 Hz) power over the midfrontal region when engaging in tasks requiring higher levels of top-down control (e.g., imitation task vs. no task). This effect was specific to the theta band. Finally, Adam and colleagues (2020) found that 4-6-year-old and 6-8-year-old children showed increased absolute theta (4-8 Hz) power over the midfrontal region when resisting acting on distracting information that could interfere with their ongoing action. In adolescence, a recent study showed that theta activity 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). Taken together, these findings demonstrate that midfrontal theta is implicated in cognitive control processes across infancy, childhood, and adolescence.

Age-related changes in theta activity during cognitive control have been observed in studies using the Go/No-Go paradigm and the flanker paradigm. In the Go/No-Go paradigm, participants are instructed to either respond (i.e., pressing a designated key) or withhold a response (not pressing the key) based on whether a go or no-go signal is presented (Verbruggen & 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 & Eriksen, 1974). These two paradigms have been widely used to assess inhibitory control and error processing. Using the Go/No-Go paradigm, Morales and colleagues (2022) showed that 4-9-year-old children exhibited increased absolute delta and theta (4-8 Hz) power over the frontocentral region after making 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 increased with age from 8-18 years, and that these age-related changes partially mediated improvements in response control ability over time. In a similar vein, studies using the flanker paradigm have found age-related increases in theta-related ERPs and source activity across late childhood and adolescence (Buzzell et al., 2017; Davies et al., 2004; for a review, see Tamnes et al., 2013). Together, these findings suggest that developmental changes in theta-related control processes take place throughout childhood and adolescence.

4.4 Interim discussion

The studies reviewed above provide evidence for the involvement of task-related theta in various cognitive processes, including memory, attention, and cognitive control. In contrast to resting theta research, which has typically found negative associations between theta power and cognitive functioning, task-related theta research has consistently found positive associations between increased theta power and cognitive performance. As noted above, the cognitive processes reviewed in this section are intertwined with each other. For instance, cognitive control plays a crucial role in guiding attention, and attention is essential for effective memory encoding. On the other hand, memory can affect attention, and attention influences our ability to detect errors, resolve conflict, or process feedback within the internal or external environment. Although the overlap between these cognitive processes suggests that theta activity may represent a common neural mechanism across domains, careful examination of the spatial-temporal-spectral characteristics of theta activity during different tasks suggests that theta may represent distinct mechanisms across domains (for detailed discussion, see Cohen, 2014; Saby & Marshall, 2012).

We also note that, although the links between task-related theta and cognitive functioning have been most robustly found in the cognitive domains reviewed above, changes in theta power have also been reported during other processes including language (Fernández et al., 2012; Maguire et al., 2022; Schneider et al., 2023; Schneider & Maguire, 2019; Spironelli & 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 are relatively higher-level processes supported by memory, attention, and cognitive control, research should clarify whether (and how) theta activity is uniquely linked to these higher-level processes above and beyond its involvement in the processes reviewed in this section.

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

We have reviewed evidence that resting theta and task-related theta exhibit distinct associations with cognitive functioning. Specifically, early exposure to environmental adversities has been associated with higher theta power during resting state. Children who exhibit higher resting theta power tend to show lower executive functioning, attentional abilities, language skills, and IQ scores, and increased resting theta power has been associated with ADHD and dyslexia. In contrast, human and non-human animal studies have demonstrated that theta activity contributes to a wide range of cognitive processes. Theta power tends to increase when individuals engage in memory encoding, attention, and cognitive control, and higher theta power during these cognitive processes predicts higher behavioral performance. Why does theta activity observed in different contexts exhibit distinct functional properties? In the following sections, we explore potential explanations for this divergence, and propose future directions for clarifying this question.

5.1 Narrowband versus broadband EEG activity

One possible explanation for the differential relations between resting theta and task-related theta is that these two measures represent distinct processes in the brain. Indeed, past research has shown that resting theta and task-related theta exhibit distinct developmental trajectories. While resting theta power tends to decrease 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 before adolescence (Liu et al., 2014; Morales et al., 2022; Papenberg et al., 2013; Schneider & Maguire, 2019; see also Crowley et al., 2014; Uhlhaas et al., 2009; van Noordt et al., 2022). These different developmental trajectories support the idea that resting theta and task-related theta may represent distinct neurocognitive processes. In line with this idea, Klimesch (1999) proposed that increased theta power during memory tasks may reflect a narrowband increase in theta synchronization in cortico-hippocampal feedback loops, which play a crucial role in information encoding (Kota et al., 2020). By contrast, resting theta may reflect irregular slow activity (ISA), which leads to a broadband increase in lower-frequency power but may 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 be driven by changes in either narrowband theta activity or broadband power distribution across the entire spectrum. To understand the differential correlations between resting/task-related theta and cognitive functioning, it is important to differentiate between narrowband and broadband 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. This broadband component contributes to the ‘1/f’ slope of the power spectrum (Figure 3), and 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). Periodic activity, on the other hand, 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. The periodic and aperiodic EEG components have been shown to exhibit distinct properties and dynamics across tasks (He, 2014).

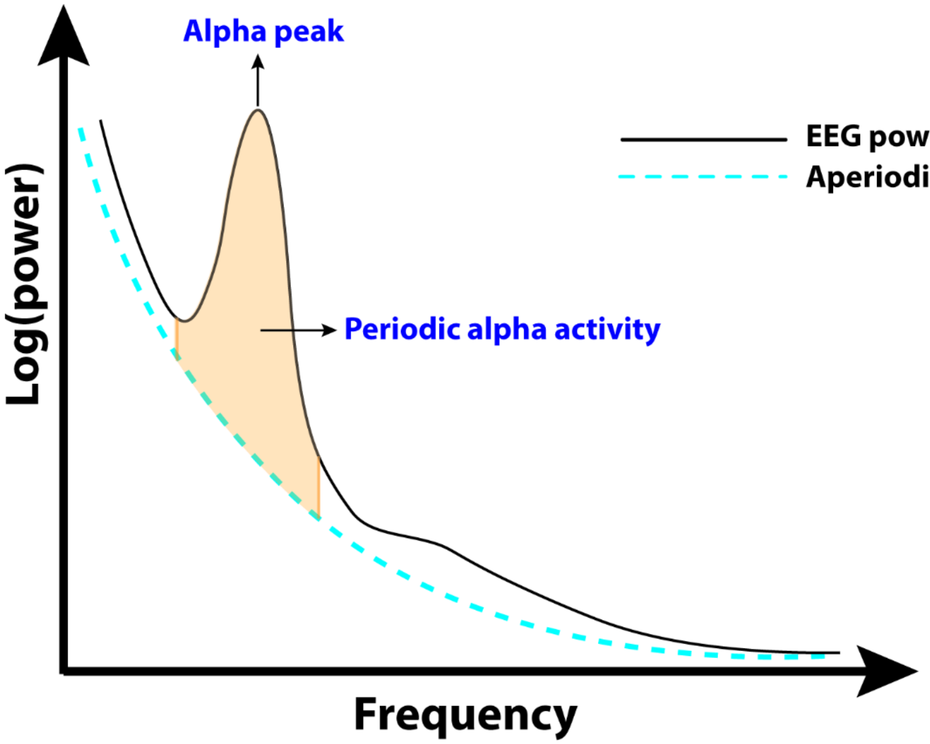

Figure 3. Aperiodic and periodic EEG activity. Adapted from Donoghue et al. (2020).

The separation of these two 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 example, the age-related shift in resting EEG power from lower to higher frequency bands has been shown to be more attributable to 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 or flatter with age across development starting in infancy (McSweeney et al., 2021, 2023; Schaworonkow & Voytek, 2021). In addition, compared with pre-defined frequency band power, aperiodic activity has been shown to better explain individual differences in theta/beta ratio (Donoghue, Dominguez, et al., 2020) and better predict ADHD status in children (Robertson et al., 2019; see also Karalunas et al., 2022; Ostlund et al., 2021). Indeed, a recent study found that, although resting alpha power was associated with cognitive processing speed in adults, this association 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).

Why are resting theta and task-related theta differentially correlated with cognitive functioning? One possibility is that resting theta's negative correlations with cognitive functioning stem from individual differences in aperiodic activity, whereas task-related theta's positive correlations with cognitive functioning may be attributable to periodic theta activity. Indeed, resting EEG studies have shown that early adversities and lower cognitive functioning are associated with not only an increase in theta power, but also 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 may be explained by changes in aperiodic activity across the whole spectrum. By contrast, task-related theta studies suggest that theta plays a unique (and potentially causal) role in memory, attention, and cognitive control. These studies tend to focus on specific time windows during which cognitive processes occur and theta power increases. In addition, most of these studies examine condition differences and utilize baseline correction methods that would likely reduce the confounding effects of aperiodic components (Morales & Bowers, 2022). Thus, the positive correlations between task-related theta and cognitive functioning are more likely to be driven by periodic theta activity. Consistent with this idea, recent studies have shown that theta power remained associated with memory encoding even with the 1/f background signal subtracted from the power spectrum, suggesting that memory encoding is specifically associated with periodic theta activity (Caplan & Glaholt, 2007; Fellner et al., 2019; Lega et al., 2012).

5.2 Atypical 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 represent the same underlying mechanism, then an alternative explanation for the negative correlations between resting theta power and cognitive functioning arises. It is possible that increased theta power during resting state reflects the engagement of cognitive effort in the absence of specific tasks. Indeed, developmental studies have used a wide range of paradigms to measure children's "resting" brain activity, including eyes-open/eyes-closed conditions, lights on/off, and passive viewing of videos (e.g., bubbles, moving shapes, colorful balls spinning in a bingo wheel) (Anderson & Perone, 2018; Norton et al., 2021). Although children are not tasked with anything specific during these procedures, these resting-state paradigms may require increased cognitive control for children to remain still and inhibit physical movement (Camacho et al., 2020). Considering that engagement of cognitive control is associated with increased theta power, children who exhibit increased theta power during these "resting" periods may be those who need more mental effort to control their behavior than do their peers. Hence, increased theta power during resting periods may reflect maladaptive functioning and lower cognitive abilities.

In line with this idea, Saad and colleagues (2018) proposed that increased resting theta power observed in children with ADHD may indicate high cognitive load and the unnecessary engagement of mental effort in the absence of specific cognitive tasks. Similarly, Orekhova and colleagues (2006) suggested that theta activity could act as an attentional gating mechanism, selectively filtering in task-related inputs and filtering out task-irrelevant inputs (Vinogradova, 1995). Lower theta power during resting state may indicate increased readiness of the brain to process new information, whereas higher theta power during resting state may suggest the presence of competing mechanisms or pathological processes that interfere with the admission of new information. We also note that, as reviewed above, the negative associations between resting theta and cognitive functioning appear to be more robust in children than in adults (Finnigan & Robertson, 2011; Kavcic et al., 2016; Sargent et al., 2021; cf. Jelic et al., 1996; Roca-Stappung et al., 2012). This age effect is consistent with the hypothesis that more mental effort is needed for children (vs. adults) to stay still and inhibit movement during "resting" periods, making resting theta power early (vs. later) in life more indicative of individual differences in cognitive functioning.

Relatedly, individuals with higher overall levels of theta activity across contexts may also exhibit lower relative theta increases during cognitive processes. If task-related changes in (rather than the overall levels of) theta activity are more important for cognitive functioning, then individuals with higher resting theta and lower task-related theta increases will show lower cognitive performance. Indeed, as discussed above, task-related theta studies typically focus on changes in theta activity across conditions. Hence, the positive associations between task-related theta and cognitive functioning may be more attributable to task-related theta power increases as opposed to the overall levels of theta. Future research should test this possibility by examining the relations between resting theta power, overall theta power during tasks, task-related changes in theta power, and cognitive functioning.

5.3 Future directions

To clarify the relations between resting/task-related theta and cognitive functioning, future research should investigate whether these theta measures reflect broadband or narrowband activity. Although the use of relative (vs. absolute) power in some previous studies have shed light on how changes in theta power, relative to power across all frequency bands, are associated with cognitive functioning, even relative theta power can be affected by changes in aperiodic slope. We therefore 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.

Future research should also examine how the relations between resting/task-related theta and cognitive functioning change across development. If the negative associations between resting theta power and cognitive functioning are attributable to the engagement of cognitive effort during resting-state procedures, then these associations should decrease as children age. This is because older (vs. younger) children presumably need less mental effort to inhibit movements and stay still during resting-state procedures. As a result, resting theta power in older (vs. younger) children is less likely to reflect meaningful individual differences in cognitive capacity. Future studies should also investigate how resting theta and task-related theta are related to each other. In a recent study, Pscherer and colleagues (2021) examined both resting theta and task-related theta during inhibitory control in individuals ages 8-30 years. They found that absolute resting theta power was positively associated with task-related theta power in individuals above 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 represent mechanisms that are relatively independent at younger ages, and that these mechanisms become more intertwined with age. We call for future research to test these relations in other cognitive domains and with a wider age range.

To clarify the nature of theta activity, future studies should also explore the neural generators of theta across different contexts. For example, cortical source analysis of EEG signals (Beese et al., 2017; Xie et al., 2017) and co-recording of EEG and fMRI (Mantini et al., 2007) have provided insights into the origins of oscillatory EEG activity in the brain. These methods can facilitate the differentiation of 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 resting state and tasks. A deeper understanding of the differences between resting theta and task-related theta can also be obtained by carefully examining the spectral characteristics of theta activity across contexts. For example, if theta activity consistently shows similar peak frequencies during resting state, but shows different peak frequencies across resting state and tasks, then this will support the hypothesis that resting theta and task-related theta represent distinct processes in the brain.

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