



The development of peak alpha frequency from infancy to adolescence and its role in visual temporal processing: A meta-analysis

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ABSTRACT

While it has been shown that alpha frequency increases over development (Stroganova et al., 1999), a precise trajectory has not yet been specified, making it challenging to constrain theories linking alpha rhythms to perceptual development. We conducted a comprehensive review of studies measuring resting-state occipital peak alpha frequency (PAF, the frequency exhibiting maximum power) from birth to 18 years of age. From 889 potentially relevant studies, we identified 40 reporting PAF (109 samples; 3882 subjects). A nonlinear regression revealed that PAF increases quickly in early childhood (from 6.1 Hz at 6 months to 8.4 Hz at 5 years) and levels off in adolescence (9.7 Hz at 13 years), with an asymptote at 10.1 Hz. We found no effect of resting state procedure (eyes-open versus eyes-closed) or biological sex. PAF has been implicated as a clock on visual temporal processing, with faster frequencies associated with higher visual temporal resolution. Psychophysical studies have shown that temporal resolution reaches adult levels by 5 years of age (Freschl et al., 2019, 2020). The fact that PAF reaches the adult range of 8–12 Hz by that age strengthens the link between PAF and temporal resolution.

1. Introduction

Brain rhythms measured from an electroencephalogram (EEG) fall into frequency bands emerging from different brain regions and functional states (Berger, 1924). These rhythms are characterized by repeated, synchronous fluctuations of excitability in ensembles of neurons (Buzsáki and Draguhn, 2004; Nunez and Srinivasan, 2006; Thut et al., 2012). These bands include delta (0–3 Hz), theta (4–7 Hz), alpha (8–12 Hz), beta (13–30 Hz), and gamma (30–100 Hz) (Buzsáki, 2006). The emerging consensus is that brain rhythms influence cognitive and perceptual functions. For instance, theta rhythms have been associated with visual attention (engaging the frontal and central regions), whereas alpha rhythms have been associated with visual perception (engaging the occipital region). In particular, alpha frequency has been thought to affect visual temporal processing by influencing whether temporally sequenced visual inputs are integrated into a coherent representation, or segmented into distinct percepts (Battaglini et al., 2020; Ronconi et al., 2018; Samaha and Postle, 2015; Wutz et al., 2018).

Our work has focused on the *development* of visual temporal processing - understanding how young children organize visual information across time into meaningful representations (Freschl et al., 2019, 2020).

Specifically, we investigated the Temporal Integration Window (TIW) which has been hypothesized to organize information across time (Arnett and Di Lollo, 1979; Wutz et al., 2016). That is, information will be *integrated* and perceived as a unitary representation if it falls within the same temporal window, or *segmented* and perceived as distinct representations if it falls in separate windows. Using a paradigm that measured both integration and segmentation within the same participant, we found that temporal windows narrow across development, with TIWs at 191 ms in infants aged 6 and 12 months (Freschl et al. *in prep*), narrowing to 142 ms in toddlers aged 18–36 months (Freschl et al., 2020), reaching adult levels of 70 ms by 5 years of age (Freschl et al., 2019). Our findings suggest that through development, the visual system becomes more tuned to perceiving rapid change across time, at the cost of information accrual.

In order to critically evaluate whether changes in alpha frequency could drive changes in visual temporal processing (or, for that matter, plausibly underlie any other candidate perceptual or cognitive process (Clayton et al., 2018)), a precise tracking of alpha frequency development is required. Toward that end, we conducted a thorough review of the literature measuring alpha frequency, in posterior areas, from birth to adolescence. Determining a precise trajectory requires more than

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measuring power across a frequency *band* as a function of age, but instead pinpointing *peak* alpha frequency (PAF), the particular frequency that exhibits maximum power (i.e., the peak within the band). Very few studies have made this measurement - from a total of 889 potentially relevant papers, we identified only 40 - and only a few directly attempted to map a developmental trajectory (Chiang et al., 2011; Cragg et al., 2011; Marcuse et al., 2008; Marshall et al., 2002; Miskovic et al., 2015; Perone et al., 2018; Stroganova et al., 1999). The goal of this meta-analysis was to specify the developmental trajectory of PAF (defined functionally and topographically, see below) across the entire field while accounting for the potential effects of the methodological variability in resting state (i.e., eyes-closed versus eyes-open) and sex differences.

1.1. The functional role of the alpha rhythm

It is clear that alpha rhythms influence visual processing. The most salient indicator is that modulating visual input, by closing and opening the eyes, modulates alpha band power (an increase, and decrease, respectively) in both infants and adults (Stroganova et al., 1999). Given the different electrophysiological characteristics (power, frequency, phase) of alpha rhythms, it is necessary to explain how they may covary or independently influence aspects of vision (Clayton et al., 2018). For example, alpha power is negatively associated with visual excitability (with a decrease in alpha power leading to an increase in visual excitability) and has been shown to modulate inhibitory processes in vision (Clayton et al., 2018). Romei and colleagues (Romei et al., 2010) looked at the causal relationship between alpha and the inhibition of irrelevant perceptual information. In their task, participants were asked to report whether they perceived a target (black dot) presented on either side of a central fixation cross while receiving transcranial magnetic stimulation (TMS) to both hemispheres at a frequency of 10 Hz (the center of the 8–12 Hz alpha band) and two comparison frequencies, 5 Hz (center of theta band) and 20 Hz (center of beta band). They found that TMS stimulation at the alpha frequency (compared to the control frequencies) impaired target detection when stimulation was applied contralaterally to the target (i.e., the region processing the visual space where the target was presented).

The *phase* of alpha oscillations has also been shown to modulate top-down prediction (Clayton et al., 2018; Sherman et al., 2016). Sherman and colleagues (2016) investigated the neural correlates underlying how expectations bias perceptual decisions. Using a detection task, while recording EEG, participants were told the probability of the presence of a target. They found that during the prestimulus interval, occipital alpha phase rhythmically influenced perceptual decisions, shifting decision criteria. That is, the phase of prestimulus alpha rhythm directly predicted how much expectations biased perceptual decisions.

Alpha *frequency* has also been shown to play a role in regulating temporal processing. Alpha frequency has been thought to clock the parsing of visual, temporal information into discrete events - information that falls within the same alpha cycle is perceived as a unitary representation, and information that falls in a different alpha cycle is perceived as a distinct representation (VanRullen, 2016); a neural correlate of the TIW (Battaglini et al., 2020; Ronconi et al., 2018; Samaha and Postle, 2015; Wutz et al., 2018). In a highly influential study, Samaha and Postle (2015) showed that individual differences in the speed of PAF predicted the speed of temporal processing. In a flash fusion task (in which participants reported whether they saw one or two flashes), individuals with a higher PAF had higher temporal resolution, meaning they perceived two flashes that were presented closely in time. It has also been shown that alpha frequency changes depending on specific task demands, whether temporal integration or segmentation of visual information is required, suggesting a top-down mechanism that can affect both alpha frequency and temporal resolution simultaneously (Wutz et al., 2018).

Similarly, alpha frequency has been shown to modulate crossmodal

temporal integration (Cecere et al., 2015). Using transcranial alternating current stimulation (tACS), Cecere and colleagues (2015) showed that the probability of perceiving a sound-induced double flash illusion (in which a single tone is presented with a flash followed by a second tone presented at various delays) was mediated by the speed of tACS received (which was set to an individual's peak alpha frequency, ± 2 Hz). That is, tACS set to either a faster or slower alpha frequency shortened or lengthened the temporal window to perceive the illusion, respectively. There is also evidence for a causal relationship between alpha frequency and temporal processing. Ronconi et al., (2018) entrained ongoing neural oscillations prior to the onset of a behavioral task that required the participant to either integrate or segment two displays to perceive a target stimulus. Sensory entrainment was set to an individual's peak alpha frequency ± 2 Hz. They found that faster entrainment frequencies improved segmentation while slower entrainment frequencies improved integration. Entrainment aligned ongoing neural oscillations to a slower or faster alpha frequency, directly modulating temporal processing, and ultimately perception.

1.2. Alpha rhythm development

Early EEG studies investigating the development of alpha oscillations looked at changes in absolute or relative power between different age groups and populations using a fixed 8–12 Hz frequency band derived from adults (Hagne, 1968; John et al., 1980; Matoušek and Petersén, 1973). At the same time, though, ever since the classic studies of Lindsley (1939), the conventional wisdom has been that alpha rhythm gradually increases in frequency with age, suggesting that the infant alpha range is initially lower and gradually increases within the first year of life. Given these early findings, it was suggested that alternative frequency bands should be applied to developmental populations.

Developmental work has applied various frequency ranges (Bell, 2002; Fox et al., 2001; Orekhova et al., 2001). Early studies identified 'infant alpha' using different criteria, with some stating that topographical equivalence was sufficient (i.e. any EEG activity in the posterior region should be identified as alpha) (Lindsley, 1939; Smith, 1941), whereas others stated that functional equivalence was sufficient (i.e. that any dominant rhythmic activity in infants, prominent during visual attention, should be identified as alpha) (Davidson and Fox, 1989). Stroganova et al. (1999) suggested following a functional topography approach (Kuhlman and Wn, 1980), in which both functional (prominent during eyes-closed resting state) and topographical (prominent in the occipital region) similarity to adults was necessary to identify the infant equivalents of adult alpha oscillations. Marshall and colleagues (2002) found that 6–9 Hz was a useful and stable alpha range in the later half of the first year of life (around 10 months of age) into early childhood (approximately 4 years of age), and a potentially lower band should be applied for early infancy (e.g. 4–6 Hz).

However, critical developmental changes may occur *within* a band, so using a fixed frequency band is not sufficiently informative (Cragg et al., 2011; Dickinson et al., 2018). Moreover, it has been shown that there is wide variability in alpha frequency between individuals, so using a fixed alpha frequency band biases against individuals who have a *peak* frequency that may fall outside the range (Cohen, 2014; Haegens et al., 2014). This is also true in development, with early studies showing a range of variability between individuals resulting in contrasting findings across studies (e.g. some children reaching 10 Hz by 6 years of age and others by 12 years) (Bell and Wolfe, 2008; Henry and Greulich, 1944; Lindsley, 1939; Smith, 1941). Additionally, changes in absolute power may be affected by changes in other band powers, as well peak frequencies within a band may mediate changes in alpha power (Cragg et al., 2011; Somsen et al., 1997).

PAF gives us a more precise measure of age-related changes and individual differences than overall power within a frequency band (Cragg et al., 2011; Dickinson et al., 2018). And, importantly PAF is implicated in driving the organization of visual information across time,

making it critical to investigate whether age-related changes in PAF drive developmental changes in temporal processing. In adults, it has been suggested that the average dominant frequency within the alpha range (8–12 Hz) is approximately 10 Hz. However, recently it has been shown that adults' PAF spans from 7 to 14 Hz, suggesting high inter-subject variability (Haegens et al., 2014; Klimesch, 1999). In development, Stroganova et al. (1999) was one of the most influential studies that not only looked at the topographical and functional similarity of alpha to adults, but also how occipital PAF developed across infancy (from 8 to 11 months). They found that PAF increased from 6.24 Hz at 8 months of age to 6.78 Hz at 11 months. Only a handful of other studies have directly measured changes in alpha over development, finding that PAF increases from 4 Hz to 8 Hz from 5 months to 4 years of age (Marshall et al., 2002), then increasing from 8 to 9 Hz from 3 to 9 years of age (Perone et al., 2018), reaching 10 Hz at 11 years of age (Miskovic et al., 2015). While certainly informative, the variability in testing methods and the limited age ranges do not allow the specification of a precise trajectory across development from infancy to adolescence.

1.3. Methodological variability

There is variability in how resting state is defined (Anderson and Perone, 2018), whether recordings were made, for instance, with eyes closed, eyes open in a dimly lit room, or eyes open with passive viewing of a visual stimulus (e.g. bubbles animation). Generally, visual stimulation results in a decrease in posterior alpha power. However, the functional meaning of these differences and which method should be used is still under debate. Alpha activity obtained during eyes-closed resting state has been known to be negatively associated with arousal (measured by skin conductance level) and that the transition from an eyes-closed to an eyes-open resting state results in an increase in arousal (as well as a decrease in alpha activity) in both children (Barry, Clarke et al., 2009) and adults (Barry et al., 2007). However, recently it has been shown that during eyes-closed resting state, not all components of the alpha band reflect arousal levels. That is, not all alpha band components correlate negatively with arousal and thereby may reflect other mechanisms unrelated to arousal, such as potential cognitive or perceptual mechanisms (Barry et al., 2020). Since eyes-open resting state results in an increase in arousal as well as a decrease in alpha activity, it has been suggested that eyes-closed is a better measure of spontaneous brain activity (Barry et al., 2007; van Diessen et al., 2015); however, it may not always be appropriate for developmental or clinical populations.

The distinction between eyes-closed versus open resting state is especially relevant in developmental EEG studies since obtaining eyes-closed resting (without being asleep) in infants and very young children is difficult. Oftentimes, infant resting state is obtained during sleep or while engaged in a visual animation whereas only older children can be instructed to keep their eyes closed for an extended time. This makes it challenging to compare age groups, as it is unlikely that sleep resting state is measuring the same spontaneous rhythmic activity as an eyes closed but awake condition or a visual animation condition (Anderson and Perone, 2018). Some work has shown high statistical reliability of PAF in eyes-closed and eyes-open (presented with a fixation cross) conditions in young adults, and that PAF under these two conditions is strongly correlated (Grandy et al., 2013; Grandy et al., 2013). However, other, recent work has shown reduced PAF during an eyes-open condition while fixating a fixation cross, but found no difference in PAF under an eyes-open in a dark room versus eyes-closed condition, suggesting that visual input (light), and not simply closing the eye, modulates PAF (Webster and Ro, 2020). Given these contrasting findings, our meta-analysis tests the effect of resting state on PAF.

1.4. Sex differences in alpha rhythm

PAF has been shown to be directly related to the development of structural brain maturation (Jann et al., 2012; Valdés-Hernández et al., 2010), where biological sex differences are apparent. For example, boys show increased white matter growth in childhood than girls, while both sexes show white matter growth in adolescence (De Bellis et al., 2001; Kaczurkin et al., 2019; Simmonds et al., 2014; Wang et al., 2012). As well, sex differences have been found in visual temporal processing with males having higher temporal frequency thresholds than females in an attentional tracking task (Roudaia and Faubert, 2017). Given this relationship between the alpha rhythm, structural and functional brain maturation, and temporal processing, it is important to understand how the alpha rhythm develops in males and females. Studies looking at sex differences in neural oscillations have focused mainly on differences in overall power. However, this may miss important individual differences and sex differences. This may be one of the reasons why the literature on sex differences in neural oscillations shows contrasting results, with some studies suggesting that females' alpha power matures earlier than males (Matousek and Petersén, 1973; Petersén and Eeg-Olofsson, 1971) some suggesting they mature later, (Clarke et al., 2001; Matthis et al., 1980), and others suggesting no difference (Gasser et al., 1988). Studies investigating sex differences in PAF have also shown mixed findings. For example, Cragg and colleagues (2011) longitudinally tracked the development of PAF from 10 to 13 years and found no difference between males and females and Miskovic et al. (2015) did not find differences in children 7–11 years old. In contrast, Chiang and colleagues (2011) found that up until the age of 16, males had higher PAF compared to females. Again here, it is possible that differences across studies stem from differences in populations and methodologies.

1.5. The current study

Taken together, there is ample evidence showing that PAF increases over development. This meta-analysis will not only pin down the precise developmental trajectory of PAF based on 3882 participants across 40 studies, but also investigate the relationship between the development of PAF and age-related changes in visual temporal processing. Additionally, our results will allow us to further understand (1) how methodological variability (i.e. eyes-open versus eyes-closed measurements) impacts resting state data, (2) whether there are sex differences in PAF, and (3) how these changes align with behavioral findings in perceptual development.

2. Method

2.1. Study identification

We identified studies following the guidelines in the PRISMA statement (Moher et al., 2009). The literature search was conducted in PubMed with the following key terms (sets of 'or' terms appear between curly braces, and '*' indicates a wildcard to capture different word endings): {alpha, iAPF, PAF, APF, α } AND {ERP, evoked potential*, event related potential*, EEG, QEEG, RSEEG, electroencephalograph*} AND {infan*, development*, preschool, baby, babies, toddler*, adolescent*, child*, newborn*, neonate*} AND {typical, typicals, neurotypical, normal, control, controls, comparison group, healthy} with the language limited to English. This search was conducted on July 11, 2022, and yielded 889 potentially relevant studies.

Each of these abstracts was then reviewed to determine if the associated paper should be given a full-text review. An abstract 'passed' if it indicated that the study: 1. Measured alpha using EEG (if an abstract mentioned evoked potentials as a main measure, using EEG, it was included so that we could later determine if the paper mentioned a baseline, resting state measure), 2. Included a developmental population (from infancy to adolescence, up to 18 years of age), and 3. Included a

typically developing group (alone, or as a comparison to an atypically developing sample). At this stage, to err on the side of inclusivity, studies that did not mention resting state, or that measured alpha frequency during sleep, were included. We also included measures of PAF that were recorded across all brain regions at this stage. Later, after full review, if it turned out that a paper did not report resting state measures, the participants were indeed asleep, or did not measure alpha frequency in occipital regions, it was rejected.

All authors served as the team reviewing studies. As training, we independently screened a sample of approximately 10% of the abstracts (70 abstracts) and coded each as relevant (if they met all three criteria) or irrelevant (if one or more of the criteria was not met, e.g. resting state peak alpha frequency measured, but only in adults). We then discussed and reconciled any discrepancies. We then broke into pairs to screen the remainder of the abstracts. Each pair screened a separate set of abstracts from the other pair, and within a pair, each member screened abstracts independently. Throughout the process, any places of disagreement or

uncertainty were discussed by the full group until consensus was reached (see Fig. 1 for a flow diagram of study identification).

2.2. Coding

As a result of the initial abstract triage, 456 papers were identified for full review. The authors again broke into pairs for this review. If a paper indeed measured PAF, in occipital regions, in a typical population between birth and 18 years of age, all relevant variables were then extracted, otherwise, the study was rejected as irrelevant. At this stage, the vast majority of studies were rejected because, in spite of their abstracts passing our screening, they did not in fact measure PAF. In the end, 40 studies remained in our final set, yielding a total of 109 samples, across 3882 participants (see Table 1).

The following variables were coded - if reported - for each of these studies: study location, race/ethnicity breakdown of the participants, recording channels (e.g. occipital regions: O1 and O2), and whether the

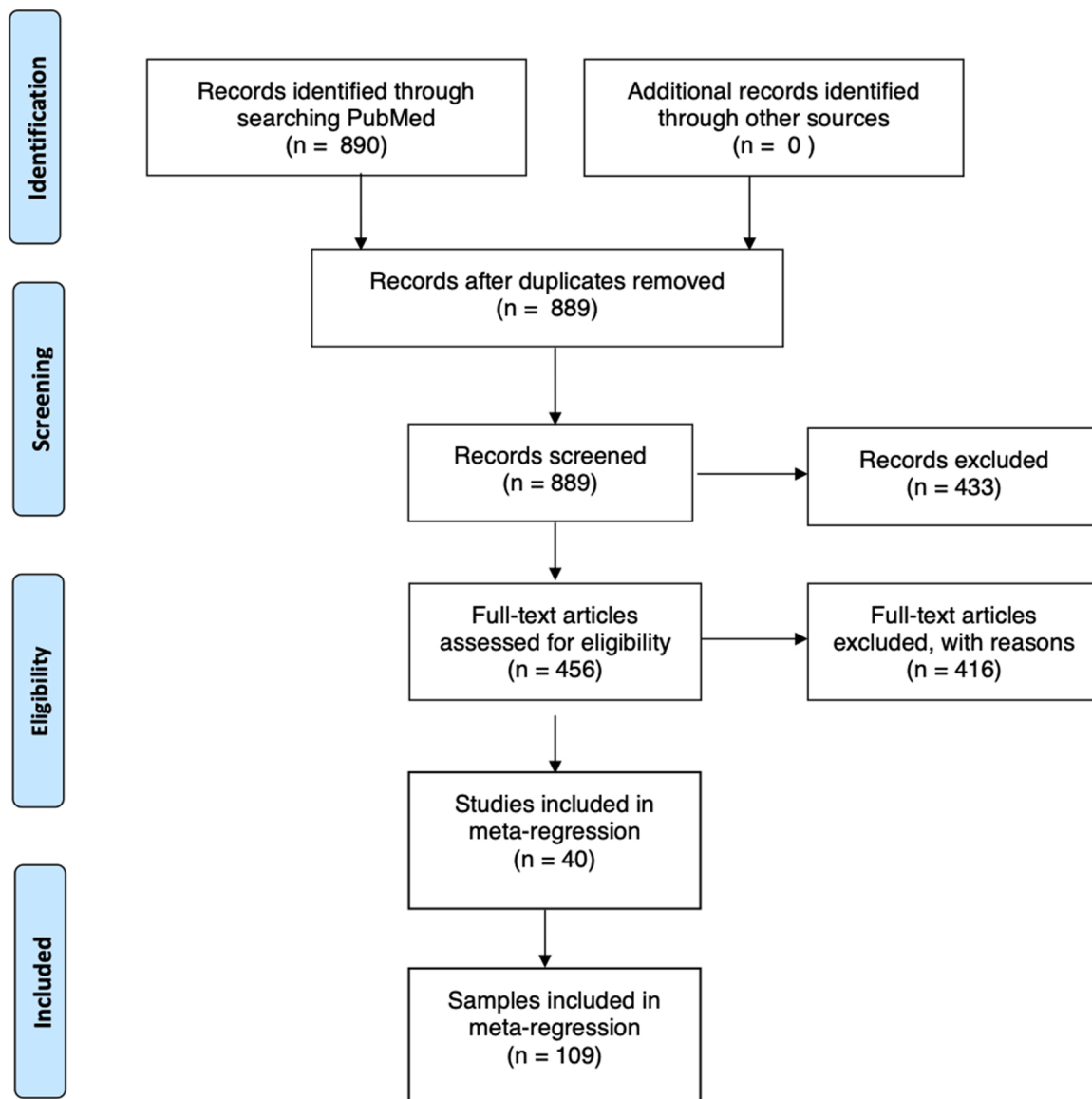


Fig. 1. Flow diagram for identifying articles following the guidelines in the PRISMA statement (Moher et al., 2009). PubMed search results yielded 889 abstracts with duplicates removed (1 abstract) to be screened for potential eligibility on July 11, 2022. A total of 433 abstracts were excluded from full-text screening for not meeting criteria (investigating EEG alpha rhythm activity in a typically developing population). This yielded 456 articles eligible for full-text review, and only those studies were retained that identified occipital peak alpha frequency, during resting state. 40 studies met all criteria to be included in the meta-regression. Across these 40 studies, 109 samples were included.

Table 1

List of studies included in the meta-regression with first author, year of publication, study topic, age range studied, measured (or extracted) PAF range, resting state procedure, and mean proportion of girls reported. List of studies sorted chronologically by year of publication. Studies that longitudinally tracked the development of peak alpha frequency are denoted with an asterisk (*).

Study	Topic	Age range	Peak Alpha Frequency range (Hz)	Resting state procedure	Mean proportion of girls	Race/Ethnicity	Study region
Samson-Dollfus and Goldberg (1979)	Maturation of EEG patterns in typical development	6–15 years	8.83–9.81	Eyes closed	Not reported	Not reported	Europe
Hårdle et al. (1984)	EEG patterns in response to opening and closing of the eye in children with an intellectual disability	12.5 years	10.68 (eyes closed); 9.58 eyes open	Eyes closed and eyes open	Not reported	Not reported	Europe
Ogawa et al. (1984)	Ontogenic development of autoregressive component waves of EEG	36 months–15 years	7.88–10.17	Eyes closed	0.35	Not reported	Asia
Balzar et al. (1986)	Quantitative EEG patterns in children with and without renal disease	12 years	9.96	Eyes closed	0.50	Not reported	Europe
Amador et al. (1989)	EEG maturation using a broad band model and xi-alpha model	5–12 years	7.72–10.59	Eyes closed	Not reported	Not reported	North America
Bjørngaas et al. (1996)	Quantitative EEG patterns in children with Type 1 Diabetes	13 years	9.49	Eyes closed	Not reported	Not reported	Europe
Koeda and Takeshita (1998)	Coherence differences in Preterm Diplegia	11 years	9.8	Eyes closed	Not reported	Not reported	Asia
Martinović et al. (1998)	Gender differences in EEG maturation in preadolescent twins	8–14 years	9.78–10.28	Eyes open (lit room)	0.5	Not reported	Europe
Stroganova et al. (1999)	Development of alpha in infants	8.71–11.39 months	6.24–6.78	Eyes open (dark room)	0.44	Not reported	Europe
Pellouchoud et al. (1999)	EEG and mental effort during video games	12 years	9.79	Eyes open (lit room)	0.43	Not reported	North America
Koukkou et al. (2000)	Development of EEG in adolescents with schizophrenia	11–14 years	9.84–10.14	Eyes closed	0.34	Not reported	Europe
Clarke et al. (2001)	EEG differences in ADHD subtypes	10 years	7.63	Eyes closed	0.2	Not reported	Australia
Ehlers et al. (2001)	EEG development in children with parental history of alcoholism	9–12 years	9.39–9.70	Eyes closed	Not reported	Not reported	North America
*Marshall et al. (2002)	EEG development in young children	5 months - 4 years	4–8 Hz	Difference (eyes closed - eyes open)	0.41	All participants Caucasian	North America
*Marcuse et al. (2008)	Development of peak alpha frequency in adolescents	15–16 years	9.92–10	Eyes closed	0.41	Not reported	North America
Lazarev Pontes and deAzevedo (2009)	EEG characteristics in children with autism	11 years	9.46	Eyes closed	0	Not reported	South America
Barry et al. (2009)	Effects of caffeine on resting state in children	10 years	9.57	Eyes closed	0.37	Not reported	Australia
Chiang et al. (2011)	Development and sex differences of alpha rhythms	6–18 years	8.71–9.65	Eyes closed	0.50	Not reported	Australia
*Cragg et al. (2011)	EEG development in early adolescence	10–13 years	9.7–10.1	Eyes closed	0.48	mixed ethnicity with majority (75% of european decent)	Europe
Kulandaivel and Holmes (2011)	EEG power spectral analysis in infants with seizures	9–21 months	4.73–4.97	Eyes open	Not reported	Not reported	North America
Sander et al. (2012)	Development of amplitude of alpha oscillations and working memory capacity	12 years	9.53	Eyes closed	Not reported	Not reported	Europe
Benz et al. (2013)	Regional stability in resting state EEG in adolescence	12 years	9.4–9.65	Eyes closed	0.45	Not reported	Europe
Miskovic et al. (2015)	Development of resting state EEG	7–11 years	8.89–7.79	Eyes closed	0.46	67.7% Caucasian; 13.8% African American	North America
Matlis et al. (2015)	Characteristics of brain rhythms in children with autism	6 years	8.53–8.93	Eyes closed	0.47	Not reported	North America
Adebimpe et al. (2015)	EEG resting state in individuals with epilepsy	9 years	9.75	Eyes closed	Not reported	Not reported	Europe
Alahmadi et al. (2016)	Resting state in EEG in children	9.95–10.03 months	7.65 – 7.7	Eyes open (lit room)	0.56	Not reported	Multi-site
Mierau et al. (2016)	Relationship between sensorimotor ability, cognitive performance and alpha frequency	5 years	8.01	Eyes closed	0.36	Not reported	Europe
Dickinson et al. (2018)	Peak alpha frequency in autism	6 years	9.27	Eyes open (with stimulus)	0.34	Not reported	North America
Shephard et al. (2018)	Resting state activity in children with ASD and ADHD	10 years	8.61	Eyes open (lit room)	Not reported	Not reported	Europe
Perone et al. (2018)	EEG development in early to middle childhood	3–9 years	7.8–9.4	Difference (eyes closed - eyes open)	0.68	Not reported	North America
Piispala et al. (2018)	Alpha activity in children who stutter during a visual task	8 years	9.5	Eyes open (lit room)	0	Not reported	Europe

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Table 1 (continued)

Study	Topic	Age range	Peak Alpha Frequency range (Hz)	Resting state procedure	Mean proportion of girls	Race/Ethnicity	Study region
Lefebvre et al. (2018)	Alpha waves in children with ASD	9 years	10.68	Difference (eyes closed - eyes open)	0.76	Not reported	Europe
Kwok et al. (2019)	Alpha activity and its role in language ability	5 years	8.0–8.9	Eyes closed; Eyes open (lit room)	Not reported	Not reported	North America
*Dickinson et al. (2019)	EEG development in children with autism	1–2 years	7.3–8.1	Eyes open (lit room)	0.56	Not reported	Multi-site
Chang et al. (2020)	EEG development in girls with ADHD	8 years	8.0	Eyes closed	1.0	Not reported	Asia
Lanthier et al. (2020)	EEG peak alpha frequency in adolescents with Scoliosis	13 years	9.49–9.77	Eyes open (lit room); Eyes closed	1.0	Not reported	North America
Lyakso et al. (2020)	EEG parameters and speed features in children	4–10 years	7.8–9.5	Difference (eyes closed - eyes open)	Not reported	Not reported	Europe
Umemoto et al. (2021)	EEG resting alpha power in adolescents with major depressive disorder	15 years	9.9	Difference (eyes closed - eyes open)	1.0	77% Caucasian; 14% Asian; 0% African American; 8.6% mixed ethnicity	North America
Ronconi et al. (2022)	Relationship between individual alpha frequency and audio-visual integration in children with autism	12 years	10.0	Eyes closed	0.14	Not reported	Europe
Garcés et al. (2022)	Resting state EEG in individuals with autism	9–18 years	9.3–10.0	Difference (eyes closed - eyes open)	Not reported	Not reported	Europe

study was performed with repeated measures/longitudinal (Benz et al., 2013; Kwok et al., 2019; Lanthier et al., 2020; Lyakso et al., 2020; Marcuse et al., 2008; Dickinson et al., 2018; Cragg et al., 2011; Marshall et al., 2002) or cross-sectional design. Within each study, we treated each investigated age group as independent, and extracted sample size (including number of females, if reported), mean age (reported in months), and how resting state measurements were obtained. This was coded using three main categories: *Eyes-closed*, *Eyes-open* (within this category, we further noted whether the study used a lit room with no visual stimulation, a dark room, or visual stimulation), and *Difference measure* (i.e., the difference between an eyes-closed and eyes-open measure). When frequency information was only presented graphically, PAF was estimated from the graph using an online tool, Web-PlotDigitizer (of the 40 studies in our final set, 12 were coded in this way). If PAF was reported separately for the two hemispheres, we used an average value (Higgins et al., 2019).

2.3. Data analysis

Results from each study were used to estimate mean peak alpha frequency at a particular age. We performed a weighted asymptotic nonlinear regression: $y = a - be^{-cx}$ (where a represents the asymptote, $b = a - RO$ where RO represents the intercept, c is the rate constant, and e is the base of the natural logarithm). A common weighting scheme is to weight each study relative to its standard deviation, i.e. inversely proportional to the root of the variance and proportionally to the root of sample size. In the 40 studies in our final set, standard deviation was rarely reported, but sample size was, so we were able to use the root of the sample size as weights for the regression.

If the study had multiple independent groups (e.g. multiple age groups), these were treated as independent samples and entered separately into the regression analysis (Higgins et al., 2019). In our sample, we had a total of eight studies that performed repeated measures on the same group or longitudinal design. For example, repeated measures design included comparing an eyes-closed versus an eyes-open condition within the same participants (Benz et al., 2013; Kwok et al., 2019; Lanthier et al., 2020; Lyakso et al., 2020) or longitudinally tracked PAF (Marcuse et al., 2008; Cragg et al., 2011; Marshall et al., 2002; Dickinson

et al., 2019). These studies were also entered as independent samples into the model. (Variability explained by study design (e.g. longitudinal and repeated measures) was low with an intraclass correlation coefficient of 0.02, suggesting that the differences between the results of the dependent versus independent samples only contributed 2% of the overall variance).

In addition, we investigated the relationship between differences in EEG testing methods (eyes-open versus eyes-closed) and PAF. Also, given contrasting results regarding sex differences found in previous EEG studies measuring both power and frequency (Clarke et al., 2001; Cragg et al., 2011; Gasser et al., 1988; Matoušek and Petersén, 1973), we analyzed the relationship between sex (calculated as proportion of girls in the total sample) and PAF. It should be noted that the utility of this comparison is low since most reported samples were close to balanced, therefore the variability among samples is low. It is important to note that none of the studies reported EEG results disaggregated by sex.

Finally, to test for a potential publication bias over time, we performed a linear regression to predict PAF based on year of publication.

3. Results

To understand the effects of variability in resting state methodology on the development of PAF, we first collapsed any procedure that included eyes-open resting methods into one group (due to low sample size in each eyes-open category). We then used AIC model selection to investigate the relationship between age, eyes-closed versus eyes-open resting state methods, and PAF. The best fit model included only age with an $\Delta AICc = -4.46$ (with 90.3% probability that this model is correct), indicating that the variability in resting state methodology did not significantly influence PAF.

We then conducted a weighted asymptotic nonlinear regression of PAF as a function of age. We found a developmental increase in PAF, beginning at 5.68 Hz at 5.17 months of age (corresponding to the youngest age group included in this analysis) to 9.97 Hz at 18 years (corresponding to the oldest age group), with a predicted asymptote of 10.13 Hz (95% confidence interval around the asymptote: 9.68, 10.58 Hz), a value right in the center of the standard specification of the adult alpha band of 8–12 Hz (Klimesch, 1999) (Fig. 2). Overall, this

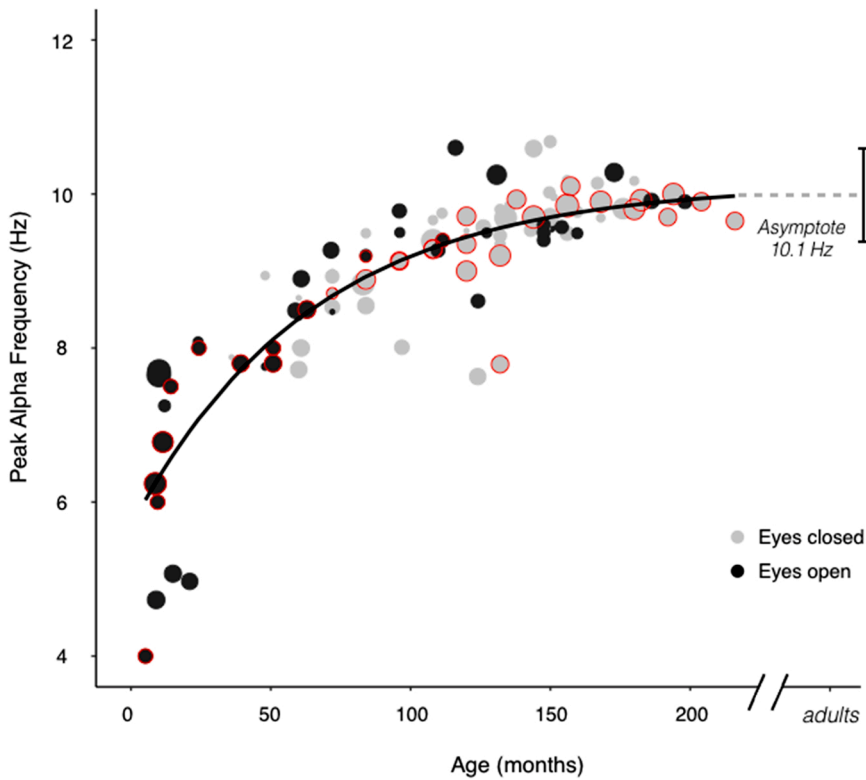


Fig. 2. Mean peak alpha frequency (PAF) as a function of age across all studies. An asymptotic nonlinear regression, weighted by root sample size, revealed a developmental increase from infancy to adolescence with an asymptote of 10.1 Hz (matching adult levels) and a starting value at 5.7 Hz. Grey and black points indicate eyes-closed or eyes-open resting state condition, respectively (though this was deemed not to be a significant factor). Points outlined in red represent PAF studies that explicitly measured the development of PAF. The error bar indicates the 95% confidence interval around the asymptote. Across the 40 studies, 109 samples (3882 participants) were included in this meta-regression.

amounts to a nearly 1 Hz increase in PAF every time a child doubles in age. These results were consistent with the few studies that explicitly investigated the development of peak alpha frequency across different age groups (Marshall et al., 2002; Stroganova et al., 1999; Cragg et al., 2011; Chiang et al., 2011; Miskovic et al., 2015; Marcuse et al., 2008; Perone et al., 2018). We ran a separate nonlinear regression analysis on these studies, which revealed a developmental increase in PAF from 5.4 Hz at 5 months to an asymptote of 9.9 Hz at approximately 16 years of age, consistent with our overall regression.

Then, given contrasting findings regarding sex differences and alpha activity, we tested the effect of sex on PAF. We conducted a Kendall rank correlation, weighted by root sample size, and found no significant relationship between sex and PAF ($\tau = 0.06$, $p = 0.45$). Also, to test for year of publication bias on PAF, we ran a linear regression model, with age as a covariate, which revealed that the effect of year of publication on PAF was not significant ($t = -0.40$, $p = 0.35$) (but not surprisingly, there was a significant effect of age ($t = 14.79$, $p < 0.001$)). Consistent with previously noted biases in the literature (Henrich et al., 2010), we found that only four of the 40 studies included the race or ethnicity breakdown of their sample. Three out of the four studies had mostly, or all, White participants. In addition, we also coded the region where the studies took place. The majority were conducted in Europe (18 studies) and North America (13). The remaining studies took place in Asia (3 studies), Australia (3), South America (1), or were multi-sited (2).

4. Discussion

Previous studies on the development of alpha oscillations focused mainly on differences in overall alpha power across various age groups, which misses both individual differences (Haegens et al., 2014), and shifts in peak alpha frequency (Cragg et al., 2011; Somsen et al., 1997). PAF, the frequency that exhibits maximum power within the alpha band, is a more appropriate and precise measure to capture age-related differences. While it has been assumed that the peak frequency of the alpha rhythm increases over development, only a handful of studies have

tested this directly, and each only within a limited age range (Marshall et al., 2002; Stroganova et al., 1999; Cragg et al., 2011; Chiang et al., 2011; Miskovic et al., 2015; Marcuse et al., 2008; Perone et al., 2018). Here we conducted a meta-analysis of studies that measured occipital peak alpha frequency in a typically developing (birth to 18 years) population.

In our meta-analysis, we cast a wide net to include all studies that reported PAF in children, even if their main hypotheses were unrelated to the development of alpha frequency, per se. Our screening of 889 abstracts yielded 456 potentially relevant studies, from which 40 (yielding 109 samples) were identified, which contributed to our meta-analysis. This meta-analysis revealed a non-linear increase in PAF from infancy (6.1 Hz at 6 months), to early childhood (8.4 Hz at 5 years), to adolescence (10 Hz at 18 years); put together, we found a nearly 1 Hz increase in PAF every time a child doubles in age. These results are consistent with the small set of prior studies that explicitly investigated the development of PAF (Fig. 2: data from these studies are indicated in red) (Marshall et al., 2002; Stroganova et al., 1999; Cragg et al., 2011; Chiang et al., 2011; Miskovic et al., 2015; Marcuse et al., 2008; Perone et al., 2018). One limitation of our main analysis is that only one study measured PAF in early infancy at 5 months of age - highlighting a gap in the literature from birth to about 8 months. This limits our understanding of the emergence of PAF, and future work is necessary to understand PAF in this early age range.

Additionally, we found no systematic effect of resting state testing condition (eyes-closed versus eyes-open), and no effect of biological sex on PAF. Our findings also show that few studies highlight race or ethnicity, in which three out of the four studies that reported race, were mostly, or all White participants. Additionally, the majority of studies were biased toward Western regions (Europe and North America) (Henrich et al., 2010).

A precise tracking of PAF development allows one to better evaluate claims that alpha rhythms may underlie or affect particular visual processes. Our own psychophysical work tracked the development of visual temporal processing, from infancy to early childhood and found that the

temporal resolution of mid-level vision (responsible for parsing patterns) increased over development, with Temporal Integration windows (TIWs) narrowing from 188 ms in infants aged 6–12 months (Freschl et al. *in prep.*), to 142 ms in toddlers aged 18–36 months (Freschl et al., 2020), to 70 ms (adult levels) by 5 years of age (Freschl et al., 2019). Our current tracking of alpha development mirrors this trajectory (Fig. 3). This correspondence supports the argument that the alpha rhythm is a driver of the organization of visual information across time (Samaha and Postle, 2015; Wutz et al., 2018).

Strengthening the link between the development of the alpha rhythm and the development of temporal processing is the structural maturation of the systems that underlie processing efficiency. Both processing efficiency (supported by structural maturation and an increase in white matter) and alpha frequency have been implicated as neural correlates of visual temporal processing (Wutz et al., 2016; Wutz and Melcher, 2014). Through development, the brain undergoes drastic structural changes with synaptic proliferation, reaching density levels twice as much as the adult brain by 2 years of age, followed by synaptic pruning, reaching adult levels by early adolescence (Johnston et al., 2009). The development of white matter, involving an increase in synaptic myelination, axonal growth, and white matter tract organization, enhances efficient communication and connectivity of neural networks, playing a critical role in the development of cognitive and perceptual processes (Barnea-Goraly et al., 2005). PAF has been shown to be directly related to these changes in white matter, with individuals with higher PAF having increased white matter myelination/axonal growth (Jann et al., 2012; Valdés-Hernández et al., 2010). PAF has also been associated with the development of corticothalamic connections (Valdés-Hernández et al., 2010), in which synchronized activity in the thalamus and posterior cortical regions has been shown to play a role in the generation of alpha oscillations (Clayton et al., 2018). Taken together, the development of alpha is directly related to the development of structural connections and neural efficiency, which, in turn, affects the temporal tuning of visual processes.

Understanding the development of PAF and its role in age-related changes in temporal processing may also elucidate temporal processing differences in neurodevelopmental disorders like autism. Our work has looked at the development of temporal processing in 1.5–3-year-old toddlers with autism spectrum disorder (ASD). We found that toddlers with ASD have shorter TIWs, higher temporal resolution, than age-matched, typically developing (TD) peers (Freschl et al., 2020), as if

they were more advanced along this developmental trajectory. If PAF is a driver of temporal resolution, then we would expect it to be similarly advanced. Unfortunately, there has not yet been much work directly on PAF in ASD, and the work that does exist has been challenging to reconcile. It has been shown that children (6–17 years old) with autism have atypical alpha oscillations, though findings have been inconsistent with some studies showing increased (Edgar et al., 2019) or decreased (Dickinson et al., 2018) PAF, or no difference at all, compared to neurotypical children (Cornew et al., 2012). However, it has been consistently shown that children with ASD do not show the same age-dependent increase in PAF compared to TD children (Cornew et al., 2012; Dickinson et al., 2018; Edgar et al., 2019). This would predict that temporal resolution in children with autism would plateau, while TD children become more tuned towards adult levels.

4.1. Implications of resting state conditions

Resting state alpha rhythm is functionally defined by visual disengagement during a wakefulness state. However, what constitutes resting state in the context of a particular study and population varies (Anderson and Perone, 2018). The resting state methodology varied across studies in our meta-analysis with some using eyes-closed and others using variants of eyes-open methods (e.g. eyes-open with visual animations or in a light vs. dark room). All infant studies that were reviewed (5–24 months of age) used only eyes-open resting state methods which could potentially confound the results. It has been unclear how this impacts EEG signatures. Could observed age-related changes in alpha be due just to shifts in resting state methodology?

Our results showed that the variability in resting state measures did not influence the development of peak alpha frequency. This is consistent with previous work showing high reliability and stability of peak alpha frequency in both eyes-closed and eyes-open conditions in young adults, and that PAF under these two conditions are strongly correlated (Grandy et al., 2013; Grandy et al., 2013). This means that eyes-open resting state methods in infants may be an appropriate and comparable (to the ideal eyes-closed measure) resting state method, at least for measuring peak alpha frequency. These results may also support the notion that peak alpha frequency is a more reliable measure of the development of alpha rhythms (as opposed to overall alpha power) since it seems not to be influenced by resting state method. That said, given the limited work explicitly investigating PAF and resting state methods,

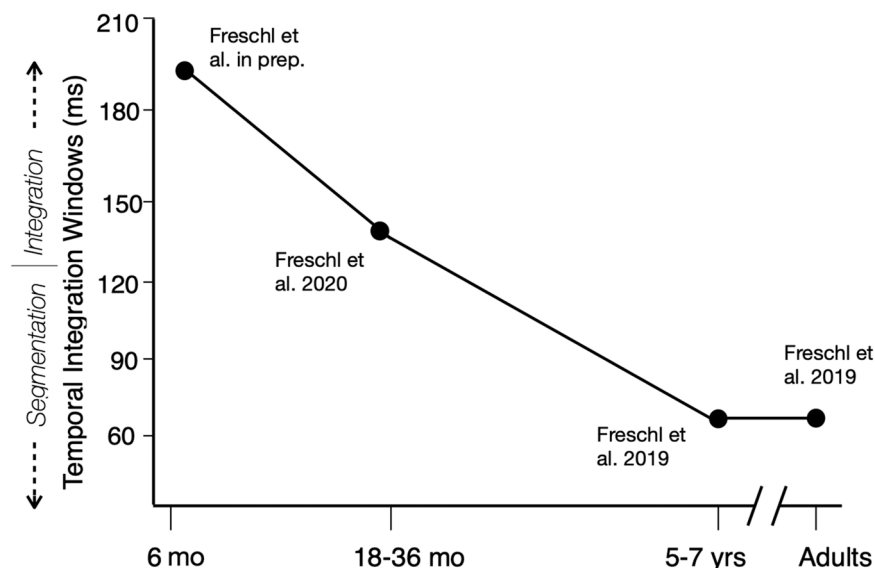


Fig. 3. Developmental trajectory of Temporal Integration Windows (TIWs) from 6 months of age to adulthood. Infants' (6-months-old) TIWs are at 197 ms and narrow to 142 ms in toddlerhood, and reach adult levels of 70 ms by 5 years of age, reflecting increases in temporal resolution. PAF has been implicated as a driver of visual temporal processing, and the PAF trajectory produced by our meta-analysis is consistent with these changes in TIWs.

this should be a focus of future research.

We have also conducted an analysis of whether there has been any systematic change in PAF measurement as a function of when the study was conducted. We found that year of publication did not have a significant effect on PAF. This suggests that any differences or advancements in EEG (e.g. advancements in digitized analysis) did not play a role in measurements of PAF.

4.2. Sex differences in alpha rhythm

The few developmental studies that investigated sex differences in alpha rhythms have shown contrasting findings. Studies have shown that males have higher alpha power than females (Clarke et al., 2001; Matthis et al., 1980), lower (Matousek, 1973; Petersén and Eeg-Olofsson, 1971) or that there is no difference (Gasser et al., 1988). In terms of alpha frequency, findings are mixed as well, showing that males have higher alpha frequency than females (Chiang et al., 2011; van Albada et al., 2010), lower (Martinović et al., 1998), or no difference (Cragg et al., 2011; Ehlers et al., 2001; Marcuse et al., 2008; Miskovic et al., 2015).

The results of our meta-analysis revealed no significant effect of sex on PAF. One limitation of this analysis is that only 26 studies (out of the total 40) reported a sex ratio in their participant demographics (i.e., the proportion of participants that were girls). However, of these 26 studies, PAF and sex were not directly measured in which reported PAF was not disaggregated by sex. This limits our analysis to only measuring the correlation between mean PAF and proportion of girls who participated in each study.

Additionally, only six studies directly analyzed the relationship between sex and PAF - reporting PAF for boys and girls separately. It is important to note that these six studies had a limited age range which together spanned only from 7 to 16 years, so it is unclear what the relationship between sex and PAF is in children younger than 7.

That said, our results are in line with studies that did not find an effect of biological sex on PAF (Cragg et al., 2011; Ehlers et al., 2001; Marcuse et al., 2008; Miskovic et al., 2015). Given that higher PAF is related to an increase in white matter (Jann et al., 2012; Valdés-Hernández et al., 2010), and that males show increased growth in white matter compared to females from childhood to adolescence (Kaczurkin et al., 2019), it would not be surprising if future studies would show a faster PAF and temporal processing development in males. However, in our previous psychophysical work, group-level gender analyses revealed no differences in visual temporal processing between boys and girls in 2-year-old toddlers or 5–7-year-old children (Freschl et al., 2019, 2020). This discrepancy may stem from studies finding sex differences in white matter development in older children (e.g. 8 years and older), whereas studies investigating younger children (4 years and older) found no difference between sexes (Krogsrud et al., 2016). Future work should further investigate the relationship between PAF and structural maturation in both males and females across even younger age groups which may shed light on temporal processing between sexes.

4.3. Conclusion and future directions

Our meta-analysis yielded a precise developmental trajectory of peak alpha frequency (PAF) from infancy to adolescence. It revealed a developmental increase from approximately 6 Hz in early infancy to an asymptote of 10 Hz (the middle of the standard 8–12 Hz alpha band) by 18 years of age; just under 1 Hz increase with each doubling in age. Precise specification of the PAF trajectory helps to constrain theories that attribute some aspect, or change, in visual processing underlying alpha frequencies. Here, we focused on the claim that alpha frequency ‘paces’ visual temporal resolution (Samaha and Postle, 2015), and found that the age-related increases we have measured in our psychophysical work on temporal resolution (Freschl et al., 2019, 2020) are consistent with the age-related changes in PAF shown by this meta-analysis. Future

work explicitly measuring the development of PAF and visual temporal resolution is necessary to investigate our proposed relationship between PAF and visual temporal processing in development.

Although we did not find an effect of sex on PAF, there were limited studies that reported sex and even fewer that investigated sex differences and PAF. Given this, we suggest that future work not only report sex, but also investigate potential maturational differences between sexes to help reconcile conflicting findings in the literature, and to further our understanding of the functional differences between the male and female brain. As well, our review revealed that only a few studies reported race or ethnicity, and the ones that did reveal that the vast majority of participants were White (Henrich et al., 2010). Future research should include race or ethnicity as a part of their demographics to increase transparency of who is included in the study, and importantly, increase recruitment from non-White populations in psychology research (Roberts et al., 2020).

Finally, we did not find an effect of resting state methodology (i.e. eyes-closed versus eyes-open), suggesting that resting state measures do not present a confound to developmental comparisons of alpha frequency. However, we do think future developmental work should explicitly compare resting state methods to further corroborate this finding.

Looking forward, given the limited studies measuring PAF in early infancy, we think it is important for future work to measure PAF in this age range to fully understand the emergence of PAF. Additionally, we think it would be useful to determine the developmental trajectory of peak frequency in other bands. Particularly, a longitudinal analysis of peak frequency across bands could provide more precise measures of age-related changes and thereby help to inform theories that implicate these brain rhythms in modulating perceptual and cognitive processes and their individual and group differences.

Data statement

Data included in the regression and correlation analyses can be found in the [supplemental table](#) (see [Supplemental Materials](#)) and [Table 1](#) (see [Methods section](#)).

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

The data included in the analyses can be found in the [Supplemental Materials](#) and [Table 1](#) (found in the [methods section](#)).

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.dcn.2022.101146](https://doi.org/10.1016/j.dcn.2022.101146).

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