Biological Psychology 191 (2024) 108824

Contents lists available at ScienceDirect

Biological Psychology

journal homepage: www.elsevier.com/locate/biopsycho

Development of EEG alpha and theta oscillations in the maintenance stage of working memory

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ARTICLE INFO

Keywords:
EEG oscillations
Periodic components
Aperiodic components
Working memory
Development

ABSTRACT

Several studies have shown developmental changes in EEG oscillations during working memory tasks. Although the load-modulated theta and alpha activities in adults are well-documented, the findings are inconsistent if children possess the adult-like brain oscillations that are similarly modulated by memory load. The present study compares children's and adults' true theta and alpha EEG oscillations, separated from aperiodic components, in the maintenance stage of working memory. The EEG was recorded in 25 Chinese-speaking children (14 male, $M_{age} = 9.4$ yrs) and 31 adults (19 male, $M_{age} = 20.8$ yrs) in Hong Kong while they performed an *n*-back task that included four conditions differing in load (1- vs. 2-back) and stimulus type (Chinese character vs. visual pattern). The results show that aperiodic activities (i.e., broadband power and slope) during the maintenance stage in the *n*-back task were significantly higher in children than adults. The periodic theta and alpha oscillations also changed with age. More importantly, adults showed significant periodic theta increase with memory load, whereas such an effect was absent in children. Regardless of age, there was a significant alpha power decrease with load increase, and a significant theta power enhancement when maintaining visual patterns than Chinese characters. In adults, load-modulated alpha peak shift (towards higher frequency) was linked to higher behavioral efficiency in the *n*-back task. In children, higher load-modulated theta enhancement was linked to better behavioral efficiency. The findings suggest that the load-modulated theta power during working memory maintenance matures from childhood to adulthood.

Working memory (WM) refers to the ability to store and simultaneously manipulate information for a short time, i.e., a few seconds (Baddeley, 1992). Working memory is an essential component in executive functions and its use permeates everyday life. Deficits in working memory are associated with many neurological disorders other than dementia, such as learning disorders (Jeffries & Everatt, 2004) and ADHD (Rhodes et al., 2012). Working memory undergoes great improvement from childhood to young adulthood. A developmental increase in the working memory's capacity is enabled by changes in the anatomical and functional structure of the brain. One manifestation of such changes is in neural oscillations, which refers to the rhythmic pattern of brain activities. It has been established that oscillation power in different frequency ranges plays a distinct role in working memory in adults (Pavlov & Kotchoubey, 2022). It remained unclear if children possess adult-like oscillatory functions for working memory. State-of-the-art algorithms are available to parameterize power spectra into periodic and aperiodic components (e.g., Donoghue et al., 2020), which makes it possible to separate "true" oscillations (e.g., theta and alpha power and peak frequency) from broadband power and slope. Periodic and aperiodic components have different functions in working memory; how these EEG power spectral parameters track behavioral performance also show differences between young and older adults (Donoghue et al., 2020). Evidence regarding function of periodic and aperiodic components during working memory in children is lacking.

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https://doi.org/10.1016/j.biopsycho.2024.108824
Received 17 February 2024; Received in revised form 19 May 2024; Accepted 27 May 2024

Studies are needed to shed light on the development of the function of neural oscillations underlying working memory.

Good working memory performance relies on the solid maintenance of information for a short period of time. Memory maintenance is the last component in working memory in the temporal sequence, i.e., the active maintenance of the information processed. Electroencephalogram (EEG) oscillations at theta and alpha rhythms in the late time window (> 300 ms) inform the neurological underpinnings of working memory maintenance (Gómez et al., 2018). Theta power (in the 3–7 Hz range) rises sharply when working memory is required, is maintained throughout the memory task, and decreases when working memory is no longer required, possibly serving the function of cognitive control. The findings on event-related theta synchronization are echoed in experiments that manipulate cognitive load, in that the frontal midline theta oscillations increase with memory load (e.g., Brzezicka et al., 2019; Maurer et al., 2015; Ratcliffe et al., 2022). On the other hand, it has been observed that alpha power (in the 8–12 Hz range) shows a pattern inverse to that of theta power in memory retention. Researchers show event-related alpha desynchronization (Klimesch et al., 1997), and alpha power decreases with memory load (Maurer et al., 2015). Therefore, alpha oscillations may serve the function of inhibiting irrelevant information (see also Pavlov & Kotchoubey, 2022 for a review of inconsistent findings).

Likewise, individual alpha peak frequency (IAF) has been linked to WM performance as a trait that is variable in the resting state (Clark et al., 2004; Klimesch, 1999) and during task performance in young adults (Haegens et al., 2014b). These studies show that participants with better WM performance have a higher alpha peak. In addition, IAF has been observed to change in function of cognitive demand. Several studies have indicated that IAF increases with memory load in adults (Haegens et al., 2014a; Sghirripa et al., 2021).

A few studies have investigated how brain oscillations in the theta and alpha rhythm underlying working memory change from childhood to adulthood. The findings are equivocal. Using a delayed match-to-sample paradigm (DMS), Güntekin et al. (2020) showed a qualitative difference between children and adults in the role of alpha oscillations in working memory, in that there was an increase in post-stimulus alpha power in children, but a decrease in adults. Sander et al. (2012) also showed that early teenagers' alpha oscillations increased with memory load but not as consistently as it did in young adults. In contrast to the load-modulated alpha enhancement, there is also evidence suggesting load-modulated alpha reduction in children. Researchers have found alpha desynchronization in the retention stage of working memory in children (Ciesielski et al., 2010; Doesburg et al., 2010; Gomarus et al., 2006), and the desynchronization was more pronounced in the high load condition (Ciesielski et al., 2010; Gomarus et al., 2006).

In contrast to development of alpha functions, relatively less evidence exist regarding the development of theta oscillations in working memory. Güntekin et al. (2020) found children possessed the same theta function as adults in working memory; both had higher theta synchronization in response to remembered items in comparison with forgotten items. Gómez et al. (2023) also showed event-related theta synchronization in the maintenance stage of working memory in participants across a wide age span (from children to young adults), and the degree of synchronization showed a slight decrease from children to adults. However, this study did not manipulate memory load.

In sum, evidence regarding the development of brain oscillations in theta and alpha band during working memory tasks is inconsistent, calling for further investigations. The approach of parametrizing EEG power spectra into aperiodic and periodic components, which are conflated in the traditional fixed-band-width approach, helps to resolve the inconsistencies. For example, previously observed alpha deduction could be attributed to deduction of broadband power or flattening of the power spectra, rather than deduction of "true" alpha power. Moreover, the function of aperiodic components in working memory has not been investigated in the child population.

The *n*-back task is a task used widely to investigate the cognitive processes underpinning WM. The *n*-back task can be considered as a continuous recognition task, in which a series of items (e.g., letters, words, visual patterns) are presented sequentially. Participants are asked to judge whether or not the current item matches the item previously presented (*n* trials back). The *n*-back is a complex task comprising a number of WM components such as encoding, recognition, updating, and maintenance (Chen et al., 2008; Pelegrina et al., 2020); the active maintenance of the target in WM for future comparison with upcoming items, is examined in the present study using the 1- and 2-back conditions. Scharinger et al. (2017) compared *n*-back versus span tasks for the induced EEG activities. The results showed that the theta power increase induced by the WM load (in the late time window corresponding to the memory maintenance stage) was more pronounced in the *n*-back task in comparison with the span tasks. Therefore, the present study adopted the *n*-back task to investigate the development of the neural oscillations underlying the maintenance stage of working memory indexed by load modulation.

The present study aims to answer four questions. The first is whether there is any age-related difference in true EEG theta and alpha oscillations during the maintenance stage in visual working memory after aperiodic components are removed. The second is whether memory load modulation of the periodic and aperiodic components differ between children and young adults. The third is whether the load modulation of parameters in power spectra explains individual differences in working memory performance in children and adults. We hypothesized that there are age-related differences in the aperiodic components in power spectra, with children having steeper slope, higher broadband power (offset), and alpha peak frequency, similar to the developmental pattern of spontaneous neural oscillations during resting state (Cellier et al., 2021), and also that children would have higher oscillatory theta and alpha power than adults. In addition, we hypothesized that the memory load modulation is greater for adults than children indicating the matured neural function for working memory maintenance, and that the load modulation of parameters would be associated with behavioral performance within each age group.

Another research question is whether there is experience-induced neural specialization in the development of neural oscillatory function for working memory maintenance. The present study includes two types of stimuli (i.e., print symbols and novel visual patterns) to separate general brain maturation from experience-induced neural specialization. Novel visual patterns are equally unfamiliar to children and adults; thus, the age-related differences in this condition can be attributed to general brain maturation. In contrast, normal-reading adults have more experience with print symbols than children, be it through explicit learning or mere exposure. The differences between age groups can be attributed to a combination of general maturation and print-related experience. Previous studies have shown that print-related experiences induce specific neural responses to print symbols such as print tuning, which is indicated by the early N1 component generated by the contrast between print and non-print symbols (e.g., Maurer et al., 2006), and print decoding, i.e., different EEG representation patterns for print and non-print symbols (Lui et al., 2021). Therefore, we hypothesized that the age-related differences in load-modulated power spectra parameters vary between novel visual patterns versus print symbols (i.e., Chinese characters), reflecting neural specialization for print.

Method

Participants

Thirty-one adults ($N_{male} = 19$; $Mean_{age} = 20.8$ yrs, SD = 1.1) and 25 children ($N_{male} = 14$; $Mean_{age} = 9.4$ yrs, SD = 0.6) were included in the data analysis. None of the participants was diagnosed with neurological disorders. All adult and child participants were native Cantonese speakers. Originally, 40 university students, as adult participants, were recruited by advertisements that were distributed by university mass mail. Forty-eight child participants were recruited through parents responding to invitation letters distributed by schoolteachers. The demographic information and cognitive profiles of child participants were described in our previous study (Huo et al., 2021). Most of the participating children came from middle-class families with annual incomes exceeding the local median. All the children were typically developing and, according to the parents' reports, had not been diagnosed with any neural developmental disorders. Additionally, twenty-three children and nine adults with poor EEG data quality were excluded from the present study. The details of excluding participants are presented below in the EEG data preprocessing section.

Experimental design and procedures

Participants were seated in a quiet room and were asked to complete the *n*-back task while the EEG was recorded. The whole EEG session lasted about 30 min. The *n*-back task featured a two-way load by type within-participants design. The load factor had two levels: 1-back and 2-back. The type factor featured two types of stimuli, i.e., Chinese characters and visual patterns. The condition sequence was counterbalanced across participants in each age group. In the Chinese character conditions, 60 Grade-2 level characters with a varying number of strokes (from 4 to 13) were selected as stimuli. At each load level, twenty characters appeared twice, and those appearing the second time were targets. As Fig. 1 shows, the targets appeared immediately after the same characters in the 1-back task and appeared in the second position after the same characters in the 2-back task. The same set of characters was used in both the 1-back and 2-back conditions, but the target characters were mostly different so participants could not predict whether a character was a target or not based on its status in an earlier task. Each condition contained 60 non-targets and 20 targets, and they were divided into two blocks of 40 characters. The characters were sequenced in a way that there was no obvious semantic relatedness or orthographic similarity between each pair of consecutive non-target characters. In the visual pattern conditions, 30 3 × 3 checkerboard patterns were created. Each pattern contained three black squares and six white ones (Fig. 1). Similar to the character *n*-back task, both the visual pattern 1-back and 2-back conditions consisted of two blocks of 40 items (30 non-targets and 10 targets each). The patterns were sequenced in such a way that each pair of consecutive non-target patterns did not look similar.

The *n*-back task was administered using E-Prime 3.0 (Psychology Software Tools, Pittsburgh, PA). Each stimulus appeared for 500 ms, followed by a 3500-ms fixation until the next stimulus appeared. The participants needed to press "1" on the keyboard as accurately and quickly as possible when they detected a target, and they did not need to press any key for non-targets. The experimental session was preceded by a practice block with 14 stimuli (including 4 targets) to make sure that they understood the task requirements. Participants were able to repeat the practice if needed.

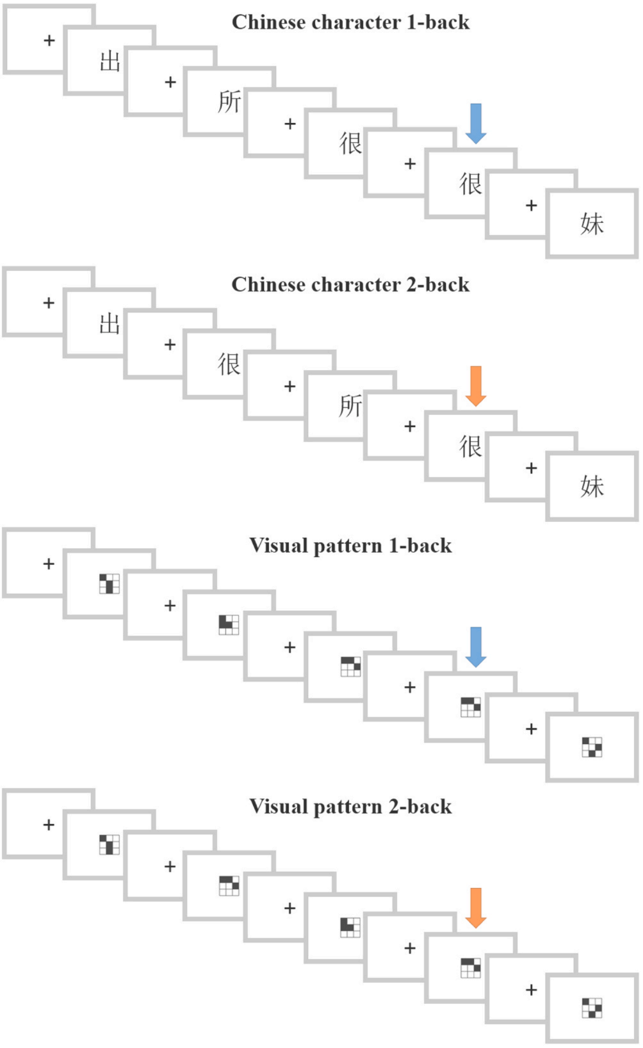

Fig. 1. Example stimuli in the *n*-back task. Here, targets in each task are marked by arrows for illustration.

EEG recording and preprocessing

EEG data were recorded at 500 Hz (online filter: 0.1–100 Hz; Cz as recording reference) using an EGI (Electrical Geodesics, Inc.) 128-channel system in a soundproofed room. Impedances were controlled under 50 kΩ during acquisition. The EEG recordings were offline filtered (0.1–70 Hz; notch filter: 50 Hz). Bad channels and segments were excluded, and the remaining data were submitted to independent component analysis for eye movement correction. The excluded channels were then spline-interpolated. All data were re-referenced to the average reference and then epoched to include the last 1-s interval of the fixation period (i.e., before the onset of the next item). Only epochs following non-target stimuli (without motor artefacts from key pressing) and not exceeding the thresholds (± 100 uV for children and ± 80 uV for adults) were adopted for further analysis. EEG preprocessing was performed using Brain Vision Analyzer software (BrainVision Analyzer, Version 2.2.2, Brain Products GmbH).

The participant selection criteria were the following: 1) *d*' in the *n*-back task greater than 1 in at least two out of four conditions (2 rejected [0 adult]); 2) no more than 30 bad channels (13 rejected [3 adults]); 3) no fewer than 15 usable epochs for each condition (17 rejected [6 adults]). Child participants were a subset of the sample in Wang et al. (2022), in which a relatively loose criterion for EEG data quality (segment no. ≥ 10) was applied to ensure a proper sample size for regression analysis. The downside to the loose criterion was that it added noise to the effect of interest, i.e., load modulation. Therefore, in this study we applied a stricter criterion (segment no. ≥ 15) to select a subsample (25/28) with better EEG data quality.

The selection of ROI was based on previous studies showing that the EEG theta oscillations in the midfrontal area (Maurer et al., 2015) and alpha oscillations in the occipital-parietal area (Hu et al., 2019; Sander et al., 2012) were the most sensitive to the change of memory load.

Estimating aperiodic signal and periodic oscillations

The fast Fourier transform was applied to each EEG epoch and trial obtained from the *n*-back task, then averaged across trials. The power spectrum was estimated for frequency range that maximized the model fit (r^2), i.e., 2–25 Hz for parietal-occipital alpha and 2–16 Hz for midfrontal theta. We used the open-source, Python-based Fitting Oscillations and One-Over-F (FOOOF) toolbox to estimate the periodic and aperiodic signals (Donoghue et al., 2020). We restricted the FOOOF algorithm to four oscillatory peaks within the said frequency range to reduce the risk of overfitting (Cellier et al., 2021). In addition, we constrained the minimum peak width to approximately twice the frequency resolution (2 Hz). The periodic and aperiodic components were extracted using the FOOOF algorithm for all electrodes in each of the four conditions and then averaged for the prespecified clusters.

For the occipital-parietal site, all children's dominant frequencies fell into the alpha range (8–12 Hz) (a total 100 [25 *2 *2] power spectra). For the adults, one participant in 3 conditions (i.e., 3 power spectra which is 2.4 % of the 124[31 *2 *2] total) had no peak. For the midfrontal site, 21 children's dominant frequencies fell into the theta range in all four conditions. For the rest 4 child participants, the dominant frequencies fell into the alpha range (8–12 Hz) for a total of 16 power spectra (16 %). For the adults, 16 participants' dominant frequencies fell into the theta range (4–7 Hz) in all four conditions. Fifteen adults' dominant frequencies fell within the alpha range in a total of 33 power spectra (26.6 %). We assumed no periodic oscillation other than the aperiodic activity if no peak frequency was detected in the bands of interest, and thus the peak power was set to 0 for the theta or alpha range. We conducted a control analysis to verify that the results were not a result of missingness of central peak; periodic theta and alpha power were obtained as the residual of the log-log linear regression of raw power on frequency (Gao et al., 2017), which then served as dependent variables in the subsequent statistical analysis. The results are consistent across approaches (see supplementary materials). Only entries with an estimated central frequency (CF) in the alpha range were analyzed for effects on alpha CF. Because of many missing cases, the CF in the midfrontal theta was not further analyzed.

Statistical analysis

In the current experimental design, type (Chinese character, visual pattern) and load (1-back, 2-back) were two within-participants factors, while group (children, adults) was a between-participants factor. Three-way mixed ANOVA was conducted on the following variables, respectively: 1) behavioral efficiency calculated as performance divided by response time (rt) (Laureiro-Martínez et al., 2014),

$$\frac{d'}{\mathrm{rt}} \times 100$$

in which d' was calculated based on the hit and false alarm rates (Haatveit et al., 2010) while rt was averaged over correct hit responses, 2) aperiodic components of the midfrontal power spectra including broadband power (offset_m) and slope_m, 3) periodic components in the theta range including peak power in the midfrontal site, 4) aperiodic components of the parietal-occipital power spectra, i.e., offset_p and slope_p, and 5) periodic components in the alpha range in the occipital-parietal region, i.e., alpha peak power and alpha central frequency. An FDR-corrected *t*-test was performed in case of significant main effect and interaction. In addition, planned paired-samples *t*-tests comparing 1- and 2-back conditions on each neural measure were conducted for each type of stimuli in each age group. The results of planned FDR-corrected *t*-tests of load effect by age and experiment on periodic and aperiodic components are shown in supplementary materials, along with the topographic maps.

Regression models were built to examine the role of load-modulated power spectra parameters, as trait-like variables, in explaining the individual differences of working memory performances. Following Donoghue et al. (2020)'s practice, ordinal least square regression was conducted to predict behavioral efficiency using load-modulated aperiodic components (Model 1) and aperiodic components (Models 2 and 3) within each age group. Stimulus type, load, and their interaction effects were included as control variables. Model 1, 2, and 3 each was compared against the null model to examined if and how much unique variance the EEG parameters contribute to explaining the individual variations in behavioral performance in the n-back task. Analyses were conducted for the EEG oscillations extracted from midfrontal and parietal-occipital sites in parallel. The periodic activities analyzed in midfrontal site was in the theta band (theta central frequency was not analyzed due to missing values), and parietal-occipital site the alpha band.

Null Model: behavioral efficiency ~ stimulus type*load.

Model 1: behavioral efficiency ~ stimulus type*load + $\mathrm{offset}_{\text{2back-1back}}$ + $\mathrm{slope}_{\text{2back-1back}}$.

Model 2: behavioral efficiency ~ stimulus type*load + peak $\mathrm{power}_{\text{2back-1back}}$.

Model 3: behavioral efficiency ~ stimulus type*load + central $\mathrm{frequency}_{\text{2back-1back}}$.

Results

Behavioral performance

Table 1 shows the behavioral performance on the *n*-back task in different conditions in children and adults. Three-way repeated measure ANOVA on behavioral efficiency indicated a significant stimulus type effect, $F(1, 51) = 110.07, p < .001$, and a significant load effect, $F(1, 51) = 129.90$, $p < .001$. The age effect was also significant, $F(1, 51) = 118.68$, $p < .001$. The FRD-corrected *t*-tests showed that behavioral efficiency in the Chinese character condition was higher than the visual pattern condition, $p < .01$, and that the low load was better than the high load condition, $p < .01$, and that the adults performed better than the children, $p < .01$.

The interaction between load and type also reached statistical significance, $F(1, 51) = 26.23$, $p < .001$. Results of simple effect analysis showed that the load effect in the visual pattern condition was more pronounced (Cohen's $d = 1.54$) than in the Chinese character condition (Cohen's $d = 0.70$). Finally, the three-way interaction (Age × Load × Type) was non-significant, $p = .146$.

Midfrontal brain oscillations during working memory maintenance

The aperiodic components in the midfrontal and occipital-parietal cites and the periodic components in the theta and alpha bands in the maintenance stage of the *n*-back tasks are shown in Table 2. The three-way ANOVA on theta peak power showed a significant load effect, $F(1, 54) = 6.19$, $p < .05$, a significant age effect, $F(1, 54) = 9.54$, $p < .01$, a

Table 1
Descriptive statistics of behavioral performance in the *n*-back task in children and adults.

	Children (N = 25)		Adults (N = 31)	
	Mean	SD	Mean	SD
	response time (ms)			
C1b	793.15	194.28	470.53	73.64
C2b	926.42	211.20	534.83	129.40
V1b	821.93	173.40	503.24	84.07
V2b	1017.25	213.26	629.15	173.33
	d'			
C1b	3.66	0.81	4.24	0.22
C2b	3.12	1.13	4.13	0.27
V1b	3.06	1.13	4.04	0.40
V2b	1.60	0.73	3.11	0.77
	efficiency			
C1b	0.51	0.19	0.92	0.16
C2b	0.38	0.18	0.81	0.19
V1b	0.40	0.19	0.83	0.15
V2b	0.16	0.08	0.54	0.19

Note. C, Chinese character; V, visual pattern; 1b, 1-back; 2b, 2-back.

Table 2
Descriptive statistics of parametrized EEG oscillations in the maintenance stage of the *n*-back task.

	Chinese 1-back		Chinese 2-back		Visual 1-back		Visual 2-back	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
	Children (N = 25)							
$offset_m$	1.32	0.17	1.30	0.19	1.35	0.21	1.36	0.18
$slope_m$	1.44	0.20	1.40	0.22	1.42	0.22	1.45	0.21
peak $power_{theta}$	0.31	0.16	0.32	0.16	0.37	0.26	0.37	0.23
$offset_p$	1.60	0.19	1.57	0.20	1.60	0.20	1.57	0.20
$slope_p$	1.78	0.17	1.73	0.17	1.77	0.17	1.75	0.14
cf_{alpha}	9.49	0.52	9.59	0.63	9.59	0.49	9.45	0.48
peak $power_{alpha}$	0.93	0.18	0.92	0.18	0.92	0.21	0.91	0.19
	Adults (N = 31)							
$offset_m$	0.64	0.22	0.61	0.24	0.58	0.20	0.59	0.24
$slope_m$	0.99	0.24	1.00	0.26	0.97	0.24	0.99	0.27
peak $power_{theta}$	0.16	0.19	0.21	0.21	0.16	0.15	0.26	0.25
$offset_p$	0.63	0.30	0.62	0.32	0.57	0.22	0.62	0.19
$slope_p$	1.18	0.27	1.20	0.33	1.17	0.25	1.20	0.23
cf_{alpha}	10.99	0.94	10.92	0.97	10.83	0.94	10.87	0.99
peak $power_{alpha}$	0.67	0.41	0.66	0.40	0.69	0.41	0.62	0.40

Note. m, midfrontal; p, parietal-occipital; cf, central frequency

significant stimulus type effect, $F(1, 54) = 4.28$, $p < .05$, and a significant interaction effect between load and age, $F(1, 54) = 5.32$, $p < .05$. The uncorrected *t*-tests showed that children had significantly higher theta power than adults, $p < .001$, that theta power was higher in the 2-back condition than in the 1-back condition, $p < .05$, and that theta power was higher in the visual pattern condition than the Chinese character condition, $p < .05$ (Fig. 2a-d). The FRD-corrected follow-up *t*-tests of the interaction between load and age showed that the load effect was significant in adults, $p < .05$, but not in children, $p > .05$ (Fig. 2e). The topographic maps illustrating the interaction between age and load are shown in Fig. 4a. The ones for the main effect of stimulus type is shown in Fig. 4b. For aperiodic components, the three-way ANOVA on $offset_m$ only showed a significant age effect, $F(1, 54) = 229.91$, $p < .001$. The uncorrected *t*-test showed that the children had significantly higher broadband power in the midfrontal site than adults, $p < .001$. The three-way ANOVA on $slope_m$ only showed a significant age effect, $F(1, 54)$

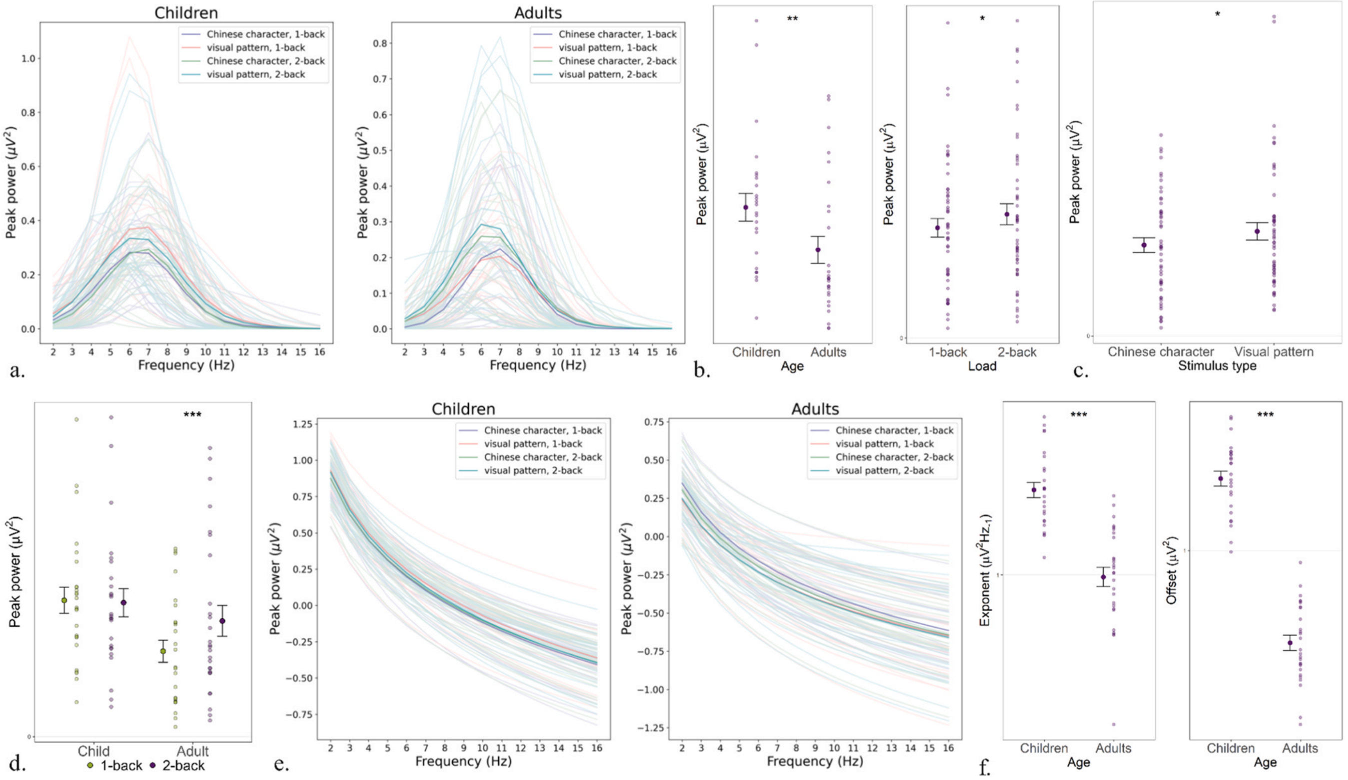

Fig. 2. Age-related shifts in spectral EEG parameters during memory maintenance from the midfrontal area. a, Visualization of individualized oscillations as parameterized by the algorithm, selected as the highest-power oscillation in the theta (3–7 Hz) range for each participant in each condition. There are clear differences in oscillatory properties between age groups that are quantified in b, between memory load that are quantified in c, and between stimulus types that are quantified in d. The difference in load modulation between age groups is quantified in e. b, Comparison of parameterized aperiodic-adjusted theta power ($p = .003$) split by age group. c, Comparison of parameterized aperiodic-adjusted theta power ($p = .016$) split by load. d, Comparison of parameterized aperiodic-adjusted theta power ($p = .043$) split stimulus type. e, Comparison of parameterized aperiodic-adjusted theta power split by load in children ($p > 0.05$) and adults ($p < .001$). f. Visualization of individualized aperiodic power spectra as parameterized by the algorithm from the midfrontal area. g, Comparison of the aperiodic midfrontal offset ($p < .001$) and exponent ($p = 0.001$) by age group. * , $p < .05$; * *, $p < .01$; * ** , $p < .001$.

$= 57.57$, $p < .001$. The uncorrected t-test showed that the children had significantly steeper power spectra than adults in the midfrontal site, $p < .001$ (Fig. 2f and g). The reconstructed power spectra at the sites of interest are shown in supplementary materials.

Occipital-parietal brain oscillations during working memory maintenance

The three-way ANOVA on alpha peak power showed a significant age effect, $F(1, 54) = 9.10$, $p < .01$, and a significant load effect, $F(1, 54) = 4.29$, $p < .05$. The uncorrected t-tests showed that children had significantly stronger alpha power than adults, $p < .001$, and that alpha power was weaker in the 2-back load condition than in the 1-back load condition, $p < .05$, (Fig. 3a and b). The topographic maps of periodic alpha by load are shown in Fig. 4c, and the ones for the effect of age are in Fig. 4d.

The three-way ANOVA on alpha central frequency showed a significant age effect, $F(1, 53) = 48.82$, $p < .001$. The uncorrected t-test showed that children had a significantly lower alpha peak than adults, $p < .001$ (Fig. 3c).

For aperiodic components, the three-way ANOVA on offset$_p$ showed a significant age effect, $F(1, 54) = 34.91$, $p < .001$. The uncorrected t-test showed that children had significantly stronger broadband power than adults in the parietal-occipital site, $p < .001$. The three-way ANOVA on slope$_p$ showed a significant age effect, $F(1, 54) = 101.77$, $p < .001$. The uncorrected t-test showed that children had significantly steeper power spectra than adults, $p < .001$ (Fig. 3d and e). The two-way interaction between age and load reached statistical significance at a marginal level, $F(1, 54) = 3.86$, $p = .055$. The FRD-corrected t-tests of load effect showed that children had flatter power spectra in the high load condition than the low load condition. This finding was at the marginal level of significance, $p = .07$.

Association between load-modulated power spectra parameters and behavioral performance

The regression coefficients of load-modulated (2back-1back) EEG power spectra parameters including aperiodic slope and offset (obtained from model 1), peak power (obtained from model 2), and central frequency (obtained from model 3) on behavioral efficiency are shown in Table 3. For children, the load-related theta enhancement was significantly linked to higher behavioral efficiency, $\beta = .19$, $p < .05$ (Fig. 5 left). The model with load-related theta enhancement explained significantly additional 5.8 % of variance of behavioral efficiency compared to the null model, $p < .01$. For adults, the load-related alpha frequency shift forward was significantly linked to higher behavioral efficiency, $\beta = .23$, $p < .01$ (Fig. 5 right). The model with the EEG parameter explained significantly additional 3.0 % of variance of behavioral efficiency, $p < .05$.

Discussion

The present study examined developmental effects in EEG theta and alpha oscillations in working memory maintenance. After accounting for the aperiodic components in power spectra, which showed drastic differences between children and adults, true periodic oscillations during working memory maintenance also differed between the two groups. More importantly, children and adults further differed in how memory load modulated power spectra parameters. For the theta band, we found that adults showed enhanced periodic theta power with increase of load, whereas children showed no such effect. For the alpha band, we found a significant alpha power decrement with the increase of load regardless of age, suggesting that theta and alpha oscillations play distinct roles in working memory. The different directions of effect indicate different functions of theta and alpha activities in working memory maintenance.

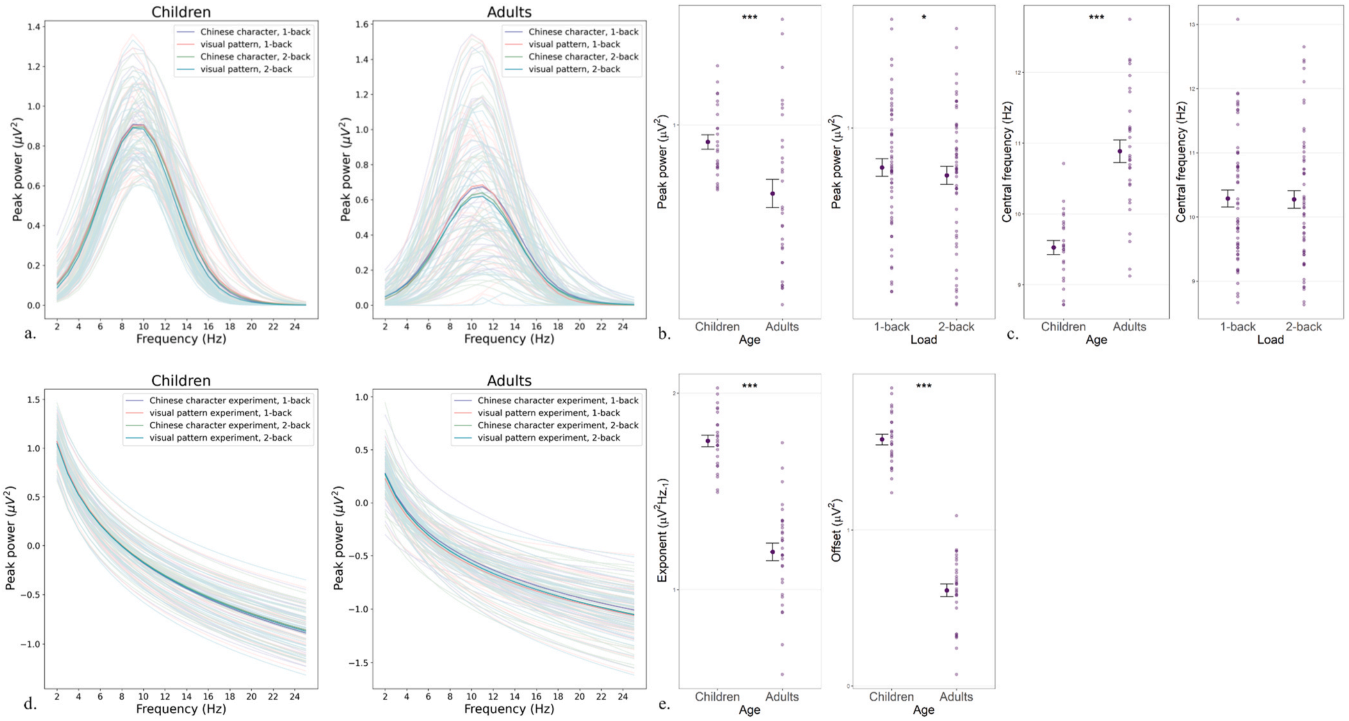

Fig. 3. Age-related shifts in spectral EEG parameters during memory maintenance from occipital temporal area. a, Visualization of individualized oscillations as parameterized by the algorithm, selected as the highest-power oscillation in the alpha (814 Hz) range for each participant averaged across two stimulus types. There are clear differences in oscillatory properties between age groups that are quantified in b, and between memory load that are quantified in c. b, Comparison of parameterized alpha center frequency ($p < .001$), aperiodic-adjusted alpha power ($p = .004$) split by age group. c, Comparison of parameterized, aperiodic-adjusted alpha power ($p = .043$) split by load. d, Visualization of individualized aperiodic power spectra as parameterized by the algorithm from the occipital temporal area. e, Comparison of the aperiodic occipital-parietal offset ($p < .001$) and exponent ($p < .001$), by age group. * , $p < .05$; * *, $p < .01$; * ** , $p < .001$.

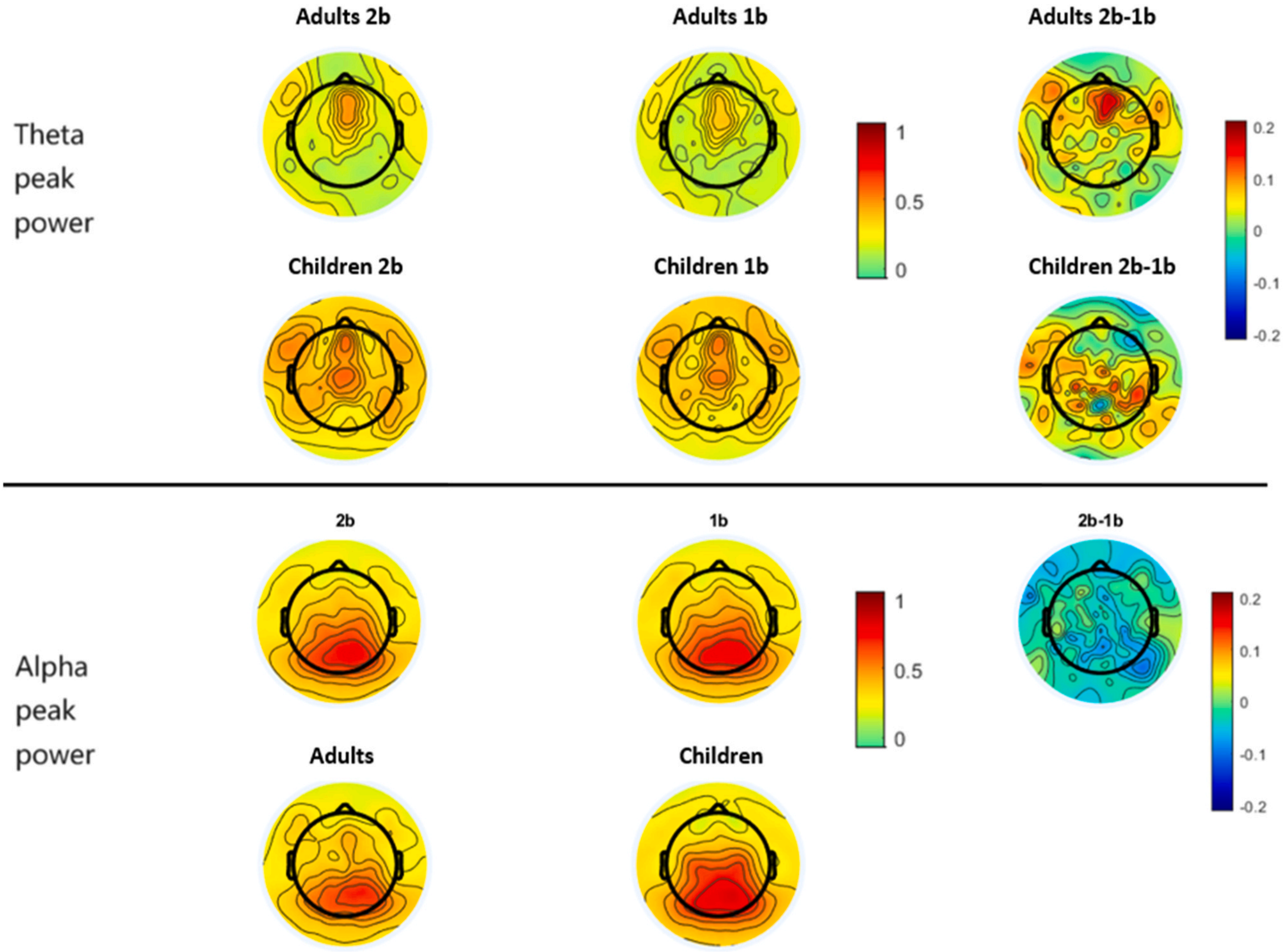

Fig. 4. Topographic map of peak theta (top) and alpha (bottom) power adjusted for aperiodic components in the retention stage of working memory for children and adults. For each participant, the oscillation power within the band was normalized between 0 and 1 and then averaged across all participants, so that a maximal relative power of 1 would indicate that all participants have the same location of maximal band-specific power. Note that theta and alpha have maximal values lower than 1, reflecting individual variability. The difference maps in the most right reflect the averaged differences of normalized scores between 2b and 1b conditions. For theta, adults had significant load-related enhancement, $p < .05$, whereas such effect was not found in children (a). There was a significant theta enhancement in the visual pattern experiment, $p < .05$ (b). For alpha, there was a load-related decrement regardless of age and experiment, $p < .05$ (c), and a developmental decrease, $p < .05$ (d).

The results of within-group individual differences showed that the load-modulated theta enhancement was positively correlated with behavioral performance in children, while shift in alpha peak frequency with increase of memory load tracked higher behavioral efficiency in adults. The results suggest that there are qualitative differences between children and adults regarding the function of brain oscillations in working memory, supporting the midfrontal theta functional maturation account of working memory development.

Behavioral performance

The behavioral results showed that working memory performance was better in adults than children, that there was significant decrease of performance with the increase of load, and that performance was better when the stimuli were verbally decodable. These findings were all expected and confirmed the validity of this task. However, there were no significant group differences in load modulation and stimulus effect. This suggests that behavioral performance might not be sensitive enough to detect the developmental differences in cognitive processes underlying working memory.

Development of periodic theta and alpha activities during memory maintenance

The maintenance stage of working memory is the focus of the current study. We found midfrontal theta increased with memory load in adults, replicating the well-established finding of theta enhancement in working memory maintenance (e.g., Maurer et al., 2015; Ratcliffe et al., 2022). Using the same paradigm, we did not find such load modulation in children at the group level. The lack of load modulation on theta during working memory maintenance is consistent with some previous findings in typically developing children (Lenartowicz et al., 2014). Lenartowicz et al. (2014) attributed the lack of load modulation in typically developing children to the choice of task, i.e., DMS. DMS is relatively easy and does not require information manipulation in the maintenance stage. Our study employed a more difficult task and still did not find any load effect on theta activities in children. This finding suggests that the role of theta oscillations in working memory has not matured in nine-year-old children at the group level, regardless of the task.

In terms of the distribution of the true theta oscillations, the maps of peak theta power show that the midfrontal area was the most responsive in the enhancement of theta rhythm in adults. In contrast, children's theta distribution was less localized with additional activation in

Table 3

Regression coefficients of load-modulated power spectra parameters and additional variance explained of behavioral efficiency in the *n*-back task in adults and children.

		β	t	p	ΔR^2
			Adults		
Midfrontal	offset_m	0.03	0.45	.65	0.001
	slope_m	0.02	0.31	.76	
	$\text{peak power}_{theta}$	0.04	0.52	.60	0.001
Occipital-parietal	offset_p	-0.09	-1.28	.20	0.009
	slope_p	-0.10	-1.36	.18	
	$\text{peak power}_{alpha}$	-0.06	-0.80	.43	0.003
	$\mathbf{cf_{alpha}}$	**0.23**	**3.26**	**.001**	**0.059****
			Children		
Midfrontal	offset_m	0.16	1.88	.06	0.01
	slope_m	0.04	0.48	.64	
	$\mathbf{peak\ power_{theta}}$	**0.19**	**2.10**	**.04**	**0.03***
Occipital-parietal	offset_p	0.11	1.35	.18	0.01
	slope_p	-0.03	-0.29	.77	
	$\text{peak power}_{alpha}$	0.05	0.58	.56	0.002
	cf_{alpha}	0.03	0.40	.69	0.001

Note. m, midfrontal; p, parietal-occipital; cf, central frequency; the regression coefficients of offset and slope were obtained in model 1; the coefficients of peak power were obtained in model 2; the coefficients of cf were obtained in model 3; $\Delta R^{2,}$ *additional variance explained in comparison to the null model.*

temporal and occipital sites, which could tentatively indicate lack of neural specialization for working memory tasks in children (Johnson, 2011). The immaturity of children's brains with respect to working memory is also reflected in functional MRI studies; working memory tasks were found to recruit the neural network involving the prefrontal cortex in adults but such a result pattern was not found in children (Ciesielski et al., 2006; Thomason et al., 2009).

Regarding the brain-behavior association, we found a positive correlation between the load modulation on theta and behavioral efficiency in children; that is, the better the children performed, the more the midfrontal theta increased from the 1-back to 2-back conditions, resembling the matured brain. Although we did not find a significant load effect in children at the group level, the identification of individual differences indicates the variability of functional brain maturation in children of the same age (Luna et al., 2015). The load-modulated theta specifically underpins higher-order brain functions, e.g., information maintenance and effort control (Liu et al., 2014). The load modulation of periodic theta power could potentially serve as a neurological marker for the development of working memory.

With respect to the load-modulated alpha, both adults and children showed a decrease (tendency) in the alpha peak power in the 2-back condition. These findings add to the body of literature showing that alpha power reduces in response to the increase of cognitive load. Reduced parietal alpha oscillations could mean the release of inhibition, which is necessary when the task gets more difficult (Klimesch, 2012).

Regarding the effect of neural specialization for print, we found a significant print effect on periodic theta power showing enhanced activity in the visual pattern condition regardless of age and memory load. Theta power has the function of cognitive control. It can be inferred that maintaining Chinese characters, verbally encodable symbols, requires less resources from the central executive system. This suggests that the brains of Chinese participants, regardless of age, are more efficient at processing print than novel stimuli, and thus show a specialization for print. However, our hypothesis that adults with more literacy practice would show a higher level of print specialization was not confirmed. One speculation is that the neural specialization for print is a complex process that is driven by the interaction between multiple factors including maturation, literacy experience, skill improvement, etc. (Johnson, 2011). As a result, there might be a non-linear relationship between literacy experience and neural specialization (Price & Devlin, 2011). This relationship might have been obscured by the design of the current study, which only included two groups, i.e., high and low literacy. A larger sample with greater variance in literacy experience is needed to investigate the complex relationship between neural specialization for print and literacy experience.

We also found a large age effect on periodic theta and alpha activities regardless of load and stimulus types. First, adults showed weaker periodic power than children during memory maintenance in working memory. There are several hypotheses to the age-related decrement of oscillatory power. The first set attributes the amplitude decrement to age-related changes in anatomical and physiological factors, such as the conductivity of living skull tissue, cerebral blood flow, and neurohormones (Bazanova & Vernon, 2014). The alternative hypothesis

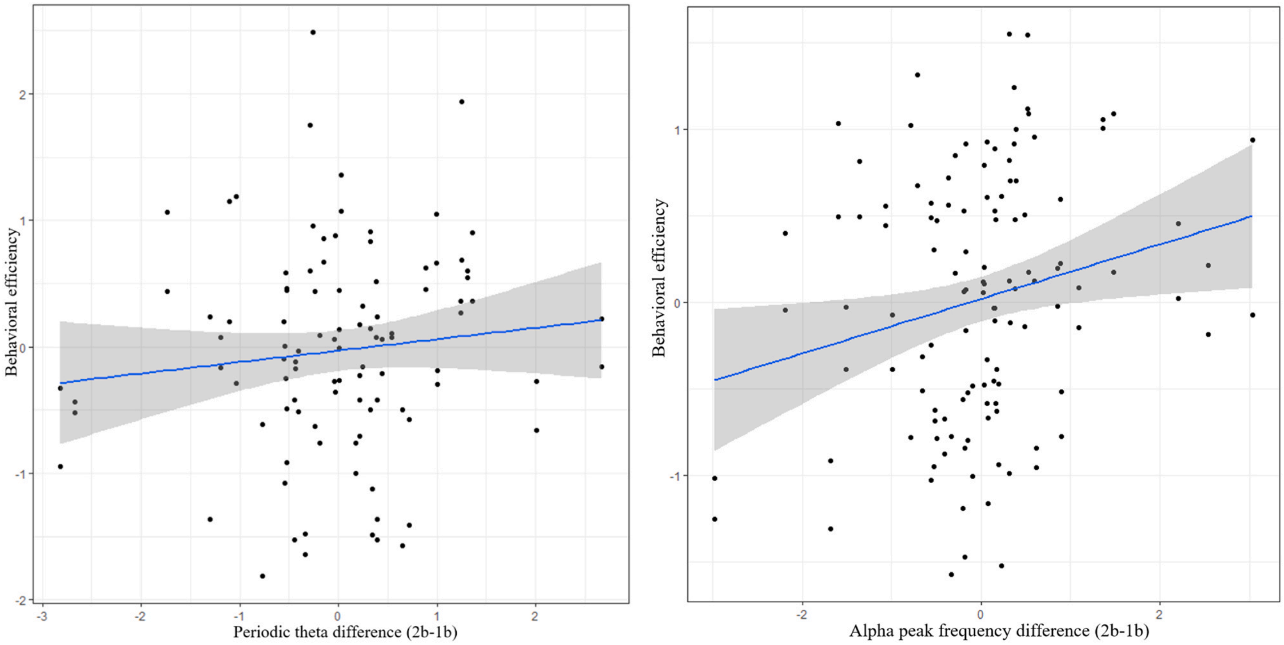

Fig. 5. Associations between standardized load-modulated power spectra parameters and behavioral efficiency (standardized residuals after being regressed on load and stimulus type) for children (left) and adults (right).

attributes the age-related amplitude decrement to increased neural efficiency (Klimesch, 2012). This would mean that the decrease in focal alpha amplitude reflects the activation of a distinct cortical area that is responsible for inhibiting the processing of irrelative information. The age-related alpha power decrement was inconsistent with the findings of Cellier et al. (2021) on resting-state oscillations that from 3 to 24 years old, age was not related to true dominant oscillatory power and was negatively related to broadband power (offset). This potentially suggests that the age-related periodic power decrement during task performance was not due to anatomical and physiological factors, which would be accounted for in the change of offset. In turn, the lower power during task performance could lend support to the neural efficiency hypothesis, in that adults' brains work more efficiently by suppressing irrelevant information during working memory. Yet since we did not analyze the resting-state brain oscillations of this sample, this interpretation is only a tentative one.

Second, the oscillation central frequency, also referred to as individual alpha peak frequency (IAF), was higher in adults than children, which is consistent with previous findings on resting-state oscillations (Cellier et al., 2021). The faster peaked alpha could be driven by physiological factors that change with age. For instance, there is an increase in central frequency with enhanced progesterone activity at puberty (see Bazanova & Vernon, 2014 for a review).

IAF has been shown to be modulated by task demand in young adults, which has been observed to increase with memory load (Haegens et al., 2014). Although we did not replicate this finding at the group level, the current findings showed that the load modulation of alpha peak frequency was linked to good performance in the *n*-back task. This is consistent with the findings that good performance is associated with increased peak frequency, but a drop in performance and fatigue are related to a decrease in IAF (Klimesch, 1999; Ng & Raveendran, 2007). This association was not significant in children, indicating a qualitative difference between children and adults as to how brain oscillations track individual working memory performance.

Development of aperiodic activities during memory maintenance

We found robust developmental effects on aperiodic activities across two topographical sites. Specifically, the power spectrum flattens and the broadband power decreases from children to adults. This pattern is consistent with findings from developmental studies on resting-state oscillations (Cellier et al., 2021). These age-related effects could be attributed to the anatomical and physiological differences between children and adults, as previously discussed. We did not find robust effects of stimulus type, comparable to those in periodic components, on aperiodic components. Altogether, the findings suggest that aperiodic components are trait-like variables, which vary across different age groups (Cellier et al., 2021) and between typical and atypical populations (Peisch & Arnett, 2022) but show little variation across experimental manipulations within individuals (Dave et al., 2018); periodic components, particularly peak power, are state-like variables that can change systematically in accordance to task demands.

The present study has several limitations. First, memory load is confounded with task difficulty. Therefore, the load effect could reflect the neurological underpinning of effort control rather than working memory, i.e., more effort was expended when the task became more difficult. The current study is not sufficient to depict a developmental trajectory of brain oscillations underlying working memory maintenance from pre-teen children to young adults, since other age groups such as early adolescents and late adolescents are missing. Studies including multiple age groups with a larger sample are needed to plot developmental trajectories of load-modulated EEG oscillations in working memory and to better uncover the neurological mechanism that drives the development of executive functions.

Despite the limitations, the present study makes significant contributions by revealing the differences between children's and adults' EEG oscillations during working memory maintenance. The results indicate that children's brains are immature in modulating theta oscillations in response to the increase in memory load. Meanwhile, the children's brains started to show load-modulated alpha activities comparable to that of adults. These findings have implications for understanding the mechanism and diagnosis of neurological disorders that have manifestations in working memory, such as attention deficit disorders and learning disorders.

Declaration of Generative AI and AI-assisted technologies in the writing process

We did not use any Generative AI and AI-assisted technologies in preparation of this manuscript.

CRediT authorship contribution statement

Ka Chun Wu: Writing – review & editing, Project administration, Methodology, Investigation. **Jianhong Mo:** Project administration, Investigation. **Urs Maurer:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **Shuting Huo:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Jie Wang:** Writing – review & editing, Validation, Investigation, Conceptualization. **Tak Kwan Lam:** Writing – review & editing, Visualization, Software, Formal analysis. **Brian W. L. Wong:** Writing – review & editing, Project administration, Investigation.

Declaration of Competing Interest

The authors declare that no competing interests exist.

Data availability

Preprocessed data and data analysis script is available via the link https://github.com/quentinlampsy/FOOOF-CUHK/tree/master.

Acknowledgements

This research was supported by the Health and Medical Research Fund (HMRF) of the Food and Health Bureau, Hong Kong (04152496) and by the General Research Fund of the Research Grants Council, Hong Kong (RGC-GRF 14600919); both grants were awarded to the corresponding author.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.biopsycho.2024.108824.

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