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Age-related changes in brain oscillatory patterns during an *n*-back task in children and adolescents

Carlos M. Gómez [a], Rocío Linares [b], Elena I. Rodríguez-Martínez [a], Santiago Pelegrina [b,*]

[a] *University of Sevilla, Experimental Psychology Department, Human Psychobiology Lab., Sevilla, Spain*
[b] *University of Jaén, Department of Psychology, Jaén, Spain*

A R T I C L E I N F O

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A B S T R A C T

The development of brain oscillatory responses and their possible role in the working memory (WM) performance of children, adolescents and young adults was investigated. A set of 0- and 1-back tasks with letter stimuli were administered to a final sample of 131 subjects (between 6 and 20 years of age). A decrease in response times (RTs) and an increase of the sensitivity index *d*-prime (d') were seen with increased age. RTs increased and d' decreased with load, indicating higher difficulty for higher loads. Event-related synchronization (ERS) and event-related desynchronization (ERD) were obtained by the convolution of Morlet wavelets on the recorded EEG. Statistical analyses were performed of the absolute and relative power of brain oscillations defined by topography, frequency and latency. Posterior alpha and beta ERD, and frontocentral theta ERS, were induced by the stimuli presented during the *n*-back task. While relative theta ERS increased with age, absolute theta ERS, absolute and relative alpha and, absolute beta ERD, decreased with age. Age-related improvement in behavioral performance was mediated by relative theta. Alpha and beta ERD were more pronounced for the most difficult task (1-back) and for the target condition. Globally, there was high consistency of the effects of target type and task load across development. Theta ERS maturation is a crucial step for improving WM performance during development, while alpha and beta ERD maturation seem to be less critical for behavioral performance improvement with age, possibly due to a sufficient level of alpha-beta ERD for good performance in young children.

1. Introduction

Working memory (WM) is a temporary storage system that allows the maintenance of a limited amount of information and its concurrent processing (Baddeley and Hitch, 1974). WM has limited capacity and can only maintain a certain amount of information in an activated state (Cowan, 2005). This constraint requires an updating mechanism to continuously activate information relevant to the goals of the task. WM plays a crucial role in the performance of numerous laboratory and everyday cognitive tasks. Indeed, individual differences in WM capacity are in turn related to individual differences in different cognitive domains: reading ability (Cain, 2006; Peng et al., 2018), math performance (Friso-van Den Bos et al., 2013; Lee and Bull, 2016; Peng et al., 2016), and intelligence (Cornoldi and Giofrè, 2014; Friedman et al., 2006), as well as learning ability and academic performance (Alloway and Alloway, 2010).

1.1. *N-back task*

There are a wide array of tasks available for measuring and investigating WM. Among them, the *n*-back task (Kirchner, 1958) has become a widely used paradigm. According to Kane et al. (2016), Gevins et al. (1990) introduced the *n*-back task into the field of neuroscience to investigate event-related potentials (ERPs) under different loads. Since then, it has been widely used, probably because it has certain advantages over other WM tasks. It has lower response requirements, allows for easy manipulation of difficulty, and enables the collection of response latency and accuracy data (Conway et al., 2005). The *n*-back is a continuous recognition task in which a sequence of stimuli (consisting of words, letters, numbers, symbols, locations, etc.) is presented. The participant has to decide whether or not the current item is the same as the one presented *n* positions back. In the present study, only the 0- and 1-back levels are used. In the 0-back level, the participant must determine whether each item in the sequence is initially designated as a target or a

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* Corresponding author at: Department of Psychology, University of Jaen, Paraje Las Lagunillas s/n., 23071 Jaen, Spain.
E-mail address: spelegri@ujaen.es (S. Pelegrina).

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distractor, whereas in the 1-back level, the subject has to decide whether the presented item matches (target) or does not match (non-target) the one that immediately preceded it. Both levels require maintaining an item in memory, but while in the 0-back, the item in memory remains the same, in the 1-back it changes continuously so that the information about the target has to be continuously updated. As *n* increases (e.g., 2-back and above) the task becomes more difficult, because the items to be compared are not adjacent in the sequence and additional processes may be involved (e.g., reordering, counteracting proactive interference). Increases in difficulty have a detrimental effect on performance, as reflected in a drop in accuracy and slower responses times (RTs).

Behavioral studies have documented a rapid increase in WM ability through childhood and adolescence (Gathercole et al., 2004), and specifically in the ability to update information in WM (Lendínez et al., 2015; Linares et al., 2016). These age-related changes in WM functioning are reflected in *n*-back performance. Studies using this task have consistently observed a gradual improvement during childhood that continues into adolescence, especially at more demanding levels of the task (Kwon et al., 2002; López-Vicente et al., 2016; Pelegrina et al., 2015; Schleepen and Jonkman, 2009; Vuontela et al., 2003). These age-related changes are reflected in increased accuracy, driven by higher hit and lower false alarms rates, along with decreasing RTs.

N-back consistently activates various brain regions (Mencarelli et al., 2019; Rottschy et al., 2012; Yaple et al., 2019), particularly bilateral frontal and parietal cortical areas, which are considered essential for working memory (Owen et al., 2005; Rottschy et al., 2012). Brain processing varies with the difficulty of the *n*-back task, as evidenced by increased amplitudes of evoked fMRI BOLD responses in frontal and parietal cortical regions as load (i.e., *n*) increases from 1 to 3 back (e.g., Braver et al., 1997), whereas a plateau has been found from 3 to 6 back (Lamichhane et al., 2020). Maturation of frontoparietal systems contributes to WM improvements during childhood and adolescence (e.g., Casey et al., 2005; Kwon et al., 2002; Tamnes et al., 2013; Rosenberg et al., 2020). Indeed, increases in activation in frontoparietal regions during *n*-back tasks mediate the relationship between age and performance (e.g., Satterthwaite et al., 2013; see also Kwon et al., 2002).

Electrophysiological responses in the *n*-back task include P300, which may reflect attentional processing and updating. Typically, P300 amplitude decreases with *n*, suggesting greater resource allocation and higher effort as load increases (Daffner et al., 2011). However, 0-back shows a lower P300 amplitude than 1-back, probably due to differences in attentional demands and updating requirements (Chen et al., 2008; López Zunini et al., 2016). Additionally, P300 amplitude is greater for targets than for non-targets, possibly reflecting recognition (Chen et al., 2008; Gevins et al., 1996; Vilà-Balló et al., 2018; Watter et al., 2001). In children and adolescents, a decrease in P300 amplitude with age has been observed, along with a longer duration of the load effect in young children, indicating that WM updating during the *n*-back requires a greater allocation of resources at younger ages (see Pelegrina et al., 2020 for a review of ERPs on *n*-back tasks in children and adolescents).

1.2. Brain oscillations

As outlined above, neural substrates of *n*-back performance and its development have been explored through ERPs and fMRI studies, yet investigations of brain oscillations in the context of this task are limited. Our objective is to help fill this gap, given that brain oscillations are a crucial aspect of neural activity related to basic sensorimotor processing, but also to complex cognitive processing (Baghdadi et al., 2023; Başar, 1999; Schmidt et al., 2018). Brain oscillation power changes with respect to baseline appear as an event-related synchronization (ERS) or event-related desynchronization (ERD), as a brain response to new stimulation. Please notice that increases in ERS or ERD, implies increase of synchronization or desynchronization, respectively. Now we will review different studies that have addressed the dynamic changes in brain oscillation power using the *n*-back task, excluding studies that did not consider a time-frequency approach (i.e., studies using power spectral density in predefined time windows), given the fast changes observed in ERS and ERD in a variety of tasks (e.g., Gómez et al., 2023).

1.2.1. Theta

Theta oscillations (around 5–7 Hz) may play a variety of roles in WM processes. They are thought to be involved in organizing sequentially ordered items in WM (Chen and Huang, 2016; Costers et al., 2020). They have also been associated with central executive functioning and cognitive control in WM (Costers et al., 2020; Dong et al., 2015; Sauseng et al., 2009). Moreover, theta power has been linked to the manipulation of information in WM (Costers et al., 2020), supporting the continuous cognitive processing necessary for tasks like the *n*-back (Dai et al., 2017). It has been proposed that theta activity regulates the activation of relevant information in WM (Dong et al., 2015; Missonnier et al., 2013) and suppresses competing memories (Dong et al., 2015). Finally, theta oscillations contribute to the coordination of different sub-functions of WM through interregional synchronization, and to the integration of various cognitive processes during WM tasks.

A number of studies in adults suggest that theta oscillations, particularly in the frontal and fronto-central electrodes, are sensitive to variations in WM load. Increases in memory load in *n*-back tasks are associated with higher theta power (Scharinger et al., 2015). For instance, differences in theta activity have been reported between 0-back and 1-back (Brookes et al., 2011; Zhao et al., 2023), 1-back and 2-back (Brookes et al., 2011; Grissmann et al., 2017; Scharinger et al., 2017), and 0-back and 2-back (Costers et al., 2020), with an increase of theta power with load. Although there are a few studies that have failed to observe differences (Chen and Huang, 2016; Kao et al., 2020; Krause et al., 2010; Missonnier et al., 2013; Scharinger et al., 2023; Semprini et al., 2021), or found a decrease of theta with load (Dong et al., 2015), in general it is reasonable to assume that theta power may serve as an index of variations in memory load during WM tasks (Grunwald et al., 2014; Langer et al., 2013; Sauseng et al., 2005), and specifically during *n*-back tasks (Dai et al., 2017), although as indicated before some doubts remain.

Theta activity may dissociate between targets and non-targets in the *n*-back task. Higher theta ERS has been reported for target than for non-target items (Gajewski and Falkenstein, 2014; Palomäki et al., 2012; Pesonen et al., 2007); although Krause et al. (2010) did not find such enhancement of theta ERS in association with target presentation.

Individual and age-related differences in theta oscillations have been reported during WM tasks. For example, Klimesch (2012) found that increased theta oscillations during the memory retention period were linked to improved memory performance. Higher frontal theta ERS has been associated with higher WM capacity and better cognitive abilities (Dong et al., 2015). Finally, Missonnier et al. (2013) noted reduced-amplitude of early frontal theta activity in subjects with attention deficit hyperactivity disorder (ADHD) compared to controls. However, studies of children or adolescents using WM tasks are very scarce (Krause et al., 2010; Zhao et al., 2023), and those that are available are restricted in terms of age range and do not provide a developmental trajectory of brain oscillations during *n*-back tasks, as seen in the delayed match-to-sample test (Gómez et al., 2023). Krause et al. (2010) showed a higher theta ERS in the target condition in adolescents, but no differences according to task load; however, Zhao et al. (2023), who recruited a population aged between 9 and 17 years and focused on differences between control and clinical groups, found an increase in theta ERS with load.

1.2.2. Alpha

Modulation of the dominant alpha rhythm (around 8–12 Hz) has a dual role: it must be enhanced for suppressing interference of an ongoing processing (ERS) (Klimesch, 2012) but also at some point must be suppressed to permit processing of the current stimulus (ERD) (Vázquez Marrufo et al., 2001). In the case of the *n*-back task, the sequencing of an early ERS theta followed by a late and long standing alpha ERD has been often reported (Krause et al., 2010; Missonnier et al., 2013; Scharinger et al., 2015).

The post-stimulus alpha oscillation has been shown to be modulated by load and type of target in *n*-back tasks. For the load effect, an increase of ERD amplitude and/or duration with load has been the most frequently reported result (Chen and Huang, 2016; Haegens et al., 2014; Kao et al., 2020; Krause et al., 2010; Palomäki et al., 2012; Pesonen et al., 2007; Scharinger et al., 2015, 2017, 2023). However, a decrease of alpha ERD with increasing load, at least in the early period of the post stimulus alpha ERD (Costers et al., 2020), as well as no load effect, have been reported (Dong et al., 2015; Semprini et al., 2021; Zhao et al., 2023). With respect to the type of target, the most typical result is an increase of ERD in target trials relative to non-target (Krause et al., 2010; Missonnier et al., 2013; Palomäki et al., 2012; Pesonen et al., 2007). Therefore, regarding the processing of targets and load increase, the most commonly reported effect, namely ERD increase, suggests the need for enhanced processing of the presented stimulus, which requires suppression of alpha (Klimesch, 2012). In fact, during the expectancy period in cueing paradigms, and during the processing of targets in visual search paradigms, a reduction of alpha in the contralateral hemisphere for the cue location and the presented target is obtained as an index of active processing (Worden et al., 2000; Bacigalupo and Luck, 2019). Similarly to theta, the information for alpha during development in *n*-back tasks is very limited, and no age-related changes have been described (Krause et al., 2010; Zhao et al., 2023). Krause et al. (2010) found an increase in alpha ERD for targets, and with load, whereas Zhao et al. (2023) did not report load effects for alpha.

1.2.3. *Beta*

The frontal beta rhythm has traditionally been linked to active processing of information (Vázquez Marrufo et al., 2001). However, a posterior beta in the low frequency range (around 15 Hz) has been frequently recorded and related to active information processing (Arnal et al., 2011; Bastiaansen et al., 2010).

Beta rhythm has been found to be modulated during *n*-back tasks. An increased duration of beta ERD with load increase has been described (Missonnier et al., 2013; Palomäki et al., 2012; Pesonen et al., 2007), and a lower beta ERD was seen in a high-load condition relative to a low-load condition (Chen and Huang, 2016; Costers et al., 2020), although an increase of beta ERD with load has also been described (Brookes et al., 2011; Scharinger et al., 2017). The longer duration and/or increased beta ERD was more strongly associated with target conditions than non-target conditions (Krause et al., 2010; Palomäki et al., 2012). In this vein, an increase of beta ERD in attentional experiments is related to the number of items attended to (load) (Rouhinen et al., 2013). As for theta and alpha, age-related changes have been reported for beta in the context of *n*-back tasks. An increase of beta ERD amplitude has been described in adolescents with increasing load and in target conditions (Krause et al., 2010).

For an accurate interpretation of posterior ERD and ERS beta, it must be taken in account that the beta rhythm during the resting state shows a simultaneous anterior and posterior topography in children up to young adults (Rodríguez-Martínez et al., 2017), and the posterior low beta should be considered as a high frequency alpha rhythm that would show similar reactivity to the alpha rhythm (Gómez et al., 2006). This interpretation is supported by Costers et al. (2020), who consider alpha and posterior beta as a continuum of oscillations related to stimulus processing in posterior sites.

Although the high frequency gamma rhythm has frequently been related to WM (Miller et al., 2018), in EEG studies there is always the possibility of contamination from muscle activity and rapid retino-corneal dipole changes produced by microsaccades (Yuval-Greenberg et al., 2008). Therefore, this important WM-related band is not considered in the present report.

1.3. *The present study*

The current study sought to investigate potential age-related changes in EEG brain oscillations during an *n*-back task. While there is a growing body of research on this task in adults, no study has comprehensively covered a wide age range from childhood to adulthood. The objectives of the present study were to determine possible age-related differences in absolute and relative event-related spectral perturbation (ERSP) during the encoding and updating phase of an *n*-back task. While a general decrease of absolute ERSP with age is expected in both ERS and ERD, due to the known decrease of EEG power with age (e.g., Segalowitz et al., 2010), a more complex pattern is predicted for relative ERSP. The possible mediating role of brain oscillation amplitudes between age and behavior was explored.

We are also interested in studying the main effects of load and type of target in different frequency bands in young adults and across age groups. As reviewed above, there are some inconsistencies among studies in adults, with some reporting effects in certain bands not found in other studies. For example, while some studies have reported increases in theta associated with load (Grissmann et al., 2017; Scharinger et al., 2017), others have not observed the same patterns (e.g., Chen and Huang, 2016; Dong et al., 2015). Similarly, previous research has reported some inconsistencies regarding load effects in alpha. Some studies reported an increase in alpha ERD amplitude with load (e.g., Pesonen et al., 2007), but other studies did not observe such an increase (e.g., Zhao et al., 2023). Thus, we will conduct complementary analyses focused on a young adult group.

In the present study, both absolute and relative power were investigated. Although relative power is a more common way to analyze time-frequency data than absolute power, it must be taken in account that relative power emphasizes amplitude changes over baseline, but it loses the possible influence that current EEG bands energy might have on stimuli processing. Therefore, the analysis of both, relative and absolute power, would be complementary. For instance, it is expected that absolute ERD and ERS will decrease with increased age due to synaptic pruning, although some exceptions have been observed to this rule such as the increased beta with increased age, as well as the inversion from ERS to ERD in theta; those results were obtained in a delayed match-to-sample test (Gómez et al., 2023). On the other hand, the relative ERD and ERS would be expected to overcome this general effect and mainly reflect age-related changes related to task processing. Although absolute power would potentially be influenced by the age-related changes of skull thickness and mineralization (Hoekema et al., 2003; Pant et al., 2011), it has been shown that magnetoencephalography (MEG) recordings, which are much less influenced by the physical properties of the skull, mirror the reduction of power with age over a broad frequency range. This suggests that the age-related absolute power reduction is a genuine process observable not only through MEG but also in EEG. The latter results indicate that although some effects on EEG power would be due to physical changes in the skull, the basic property of reduction of amplitude with age would still be due to physiological age-related processes, such as synaptic pruning (Gómez et al., 2017). Therefore, measuring absolute power remains a valid method to capture neural maturation processes.

2. Method

2.1. *Participants*

The study involved 168 participants aged 6–20 years. In total, 37 participants were excluded from the initial sample (36 participants due to EEG artifacts and 1 participant who did not understand the task), leaving a final sample of 131 participants. The sample consisted of 56 males and 75 females. Participants were assigned to five groups according to their age. The first group consisted of 11 boys and 7 girls in middle childhood (aged 6–8 years). The second group comprised 10 boys and 10 girls in late childhood (aged 9–11 years). The third group was composed of 14 males and 17 females in early adolescence (aged 12–14 years). The fourth group was made up 15 males and 16 females in middle adolescence (aged 15–16 years), and finally, the fifth group consisted of 6 males and 25 females in late adolescence (aged 18–20 years). A power analysis performed using G*Power (Faul et al., 2009) suggested that, for the design used in the present study, which involved a mixed ANOVA with four repeated measures (target, non-target, 0-back and 1-back) and five age groups, 100 participants are sufficient to detect a small/medium effect size ($f = 0.15$) with a power ($1-\beta$) = 0.80, and $\alpha < 0.05$. Our final sample exceeded this minimum.

All children and adolescents were recruited from local schools in a middle socio-economic area of a medium-sized city. Written informed consent was obtained from a parent or legal guardian, and children and adolescents were asked for their assent before the study began. Participants in the oldest group were undergraduate students at a university. They gave written informed consent before the first session and received course credit for their participation. The subjects and families did not report any neurological or psychological impairments. This study was approved by the Research Ethics Committee of the University of Jaén, and it was carried out in accordance with the Declaration of Helsinki.

2.2. Experimental task

Participants performed a visual *n*-back with two levels of complexity: 0-back and 1-back. Each trial began with the presentation of a fixation cross (+) in the center of the screen for 2000 ms. Then, a stimulus pair consisting of a letter of the alphabet (B, C, D, F, G, H, J, K, L, M, N, P, Q, R, S, T, V, W, X, Y, Z) and a symbol (!, #, $, %, (, /,?, @,}, ¦, ¿, ¤, <, =, >, ±, §, ©, ¶, æ) was presented. Both stimuli appeared side by side, with an eccentricity of 4.8 deg. on the horizontal plane. In all trials, the location of each stimulus (i.e., right or left) was determined pseudorandomly. Stimuli were presented for 2000 ms because this response window allows the assessment of ERPs related to selection, matching and updating processes. The interstimulus interval was set to 1500 ms (Fig. 1).

In the 0-back task, participants had to indicate whether the letter appearing on the screen was the letter X, whereas in the 1-back task, participants had to determine whether the current stimulus matched (by pressing the "yes" key on a serial response box) or did not match (by pressing the "no" key) the previous one. Participants were instructed to respond using two fingers of their dominant hand.

The experiment consisted of four blocks, each comprised of two lists: one for the 0-back level and one for the 1-back level. Thus, there were eight lists, four for each of the n-back levels. Each list consisted of 60 trials, 20 requiring a "yes" response (33.3 % target) and 40 requiring a "no" response (66.7 % non-target), making a total of 480 trials. To prevent fatigue, a short break was allowed after each block.

The tasks were administered to the oldest group in a laboratory at the university, while the rest of the groups were tested in a quiet room in their school or high school. For the latter groups, especially the younger ones, parents were given the opportunity to accompany their children during the experiment, as long as they remained silent and out of sight of the participants. Participants were seated in a chair about 70 cm from the computer screen and were instructed to maintain a comfortable posture and to avoid eye movements and blinking during the experimental trials.

2.3. Recording and pre-processing of the EEG data

In an extended version of the International 10–20 system, an electrode cap with 32 scalp sites (Fz, Cz, Pz y Oz, Fp2, F4, F8, Fc2, Fc6, C4, Cp2, Cp6, Tp10, P4, P8 y O2, Fp1, F7, F3, Ft9, Fc5, Fc1, C3, Cp5, Cp1, P7, P3, O1) was fitted to the participant's head, with the ground electrode at the mid-anterior frontal electrode and the reference electrode at the left mastoid (Tp9). Three additional electrodes were placed around the eyes to record vertical and horizontal eye movements, and the Fp2 electrode was also used to record vertical eye movements. EEG data were recorded and digitized using a BrainVision ActiChamp amplifier and the BrainVision Recorder software (Brain Products, Munich, Germany). The EEG was recorded at a sampling rate of 500 Hz, and the impedance was kept below 10 kΩ. EEG data pre-processing was performed with the BrainVision Analyzer v.2.1 (Brain Products, Munich, Germany), EEGlab v2020.0 (Delorme and Makeig, 2004) and FieldTrip v20220104 (Oostenveld et al., 2011) software packages using Matlab R2016a (MathWorks Inc., Natick, MA, USA).

A band-pass filter (low cutoff: 0.1 Hz, high cutoff: 40 Hz, time

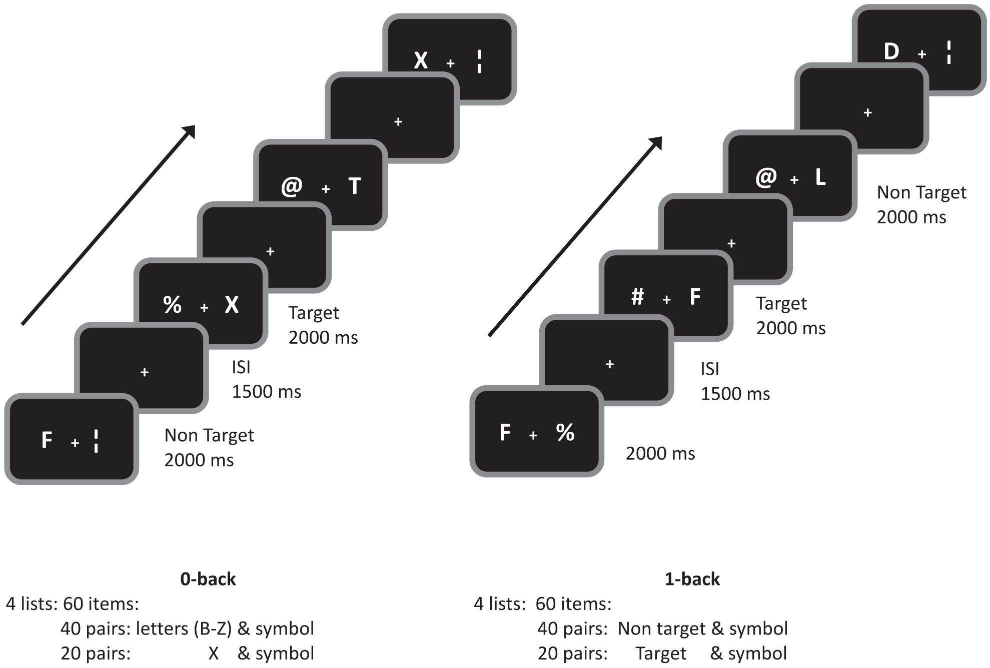

Fig. 1. Display of 0-back and 1-back Trials. *Note.* Examples of item sequence for 0-back (on the left) and 1-back (on the right) lists. A response was required each time a stimulus was presented, affirmative if it matched the target and negative if it did not. There were four lists consisting of 60 trials (33.3 % targets) for each level.

constant: 0.3, order 2) was applied using a Butterworth digital filter to obtain a well-filtered signal with zero phase shift. Then, independent components (ICAs) related to eye movements or blinks were eliminated using the restricted infomax algorithm (Makeig et al., 1997), as implemented in Brain Vision Analyzer 2.

Data were referenced to the average of the left and right mastoid (TP9 and TP10, respectively). Epochs were extracted from raw EEG, with a total duration of 4500 ms, 1000 ms before stimulus presentation and 3500 ms after stimulus presentation. These long epochs permitted the exclusion of edge artifacts at baseline (from −500 to −100 ms before stimuli presentation) and post-stimuli ERSP. The baseline was set before the arrival of stimuli, to minimize power spread at baseline due to the convolution of Morlet wavelets with the EEG signal (Cohen, 2014). These epochs permitted us to observe the ERSP related to the processes of encoding and updating (Pesonen et al., 2007; Krause et al., 2010). Epochs with codes associated with trials with omissions or commission errors were excluded from the subsequent analysis.

Finally, an artifact rejection procedure was implemented with a rejection threshold ±100 μV for adolescents and young adults (12 years and older), and a threshold ±150 μV was used for participants in middle and late childhood (from 6 to 11 years). The decision to use different voltage thresholds according to age was based on previous findings indicating differences in EEG spectral power between children and adults. Specifically, children were found to have higher spectral power compared to adults (Barriga-Paulino et al., 2011), such that applying the same criterion to children would result in a disproportionately large amount of rejected data. Consequently, a higher artifact rejection threshold was used for children under 12 years of age to account for age-related changes in spectral power. For one subject to be admitted for subsequent analysis, a minimum of 15 trials in each condition was requested. Table 1 reports the number of participants per age group and the mean number of trials included per condition.

2.4. Time frequency analyses

The FieldTrip toolbox (version 20,220,104) was used for time-frequency analyses (Oostenveld, et al., 2011). The time-frequency representation (TFR) for each participant and condition (type of target and load) was calculated using a Morlet wavelet (width = 6) for EEG frequencies ranging from 2 to 30 Hz in steps of 0.5 Hz. The pre-stimulus time interval (−500 ms to −100 ms) was used as the spectral baseline. For the first set of analyses, log10 transform of the quotient between the power in each trial relative to its baseline (expressed in dB) was executed. In a second set of analyses, the absolute change with respect to the baseline was calculated.

The present study focused on the following oscillatory EEG bands, which have previously been investigated in *n*-back research and presented an amplitude modulation in theta (4–6 Hz), alpha (8–13 Hz), and beta (16–22 Hz) (e.g., Chen and Huang, 2016; Gevins et al., 1998; Gevins and Smith, 2000; Haegens et al., 2014; Krause et al., 2010; Pesonen et al., 2007; Scharinger et al., 2017). In order to identify the time range of interest, the maximum and 50 % power values, prior to and after the maximum, were obtained for each EEG band after collapsing ERSP data across subjects and conditions (Fig. 2). For the selection of electrodes, a topographical representation of the ERSP for the selected frequencies and time windows was displayed, and the electrodes with maximum ERSP values were selected. Please note the non-biased method used for the selection of electrodes and time windows, where ERSPs for experimental conditions and subjects were averaged together. The different time frequency windows and electrodes identified for subsequent statistical analyses are presented in Table 2.

There are several reasons for choosing the above described time-frequency analysis method instead of cluster-mass permutation (Maris and Oostenveld, 2007): (i) the number of electrodes (30), age groups (5), relative and absolute power (2), would have produced 600 time-frequency panels statistical comparisons, (ii) the high number of time-frequency points would reduce the possibility to obtain significant results, (iii) the computed ANOVAs (see below) imply three factors (type of target, load and age groups), resulting in a number of interactions of the factor effects that cannot be analyzed in a straightforward manner with cluster-mass permutation, and (iv), the age evolution of power would not be so graphically expressed as it is now in the displayed figures.

2.5. Statistical analyses

RTs and *d*-prime (d') were used as dependent variables in the behavioral analyses. RTs were computed separately for each load condition (0-back and 1-back). RTs from incorrect trials and practice lists were discarded, as well as those RTs below 200 ms and those exceeding 3.5 standard deviations from the mean RTs of each participant and condition. As a result, 0.72 % of the RTs were excluded from further analysis. As a measure of sensitivity to discriminate between targets and non-targets, we used the d' parameter, which was calculated using the formula $d' = Z_{\text{Hits}} - Z_{\text{FalseAlarms}}$, and following the fourth method suggested by Stanislaw and Todorov (1999), to avoid indeterminate d' values.

The data (RTs and d' values) were subjected to two mixed-model ANOVAs with load (0-back, 1-back) as the within-subject variable and age group as the between-subject variable. Follow-up ANOVAs were conducted when there were significant interactions. Post-hoc pairwise tests with Bonferroni correction for multiple comparisons were performed to examine main effects (e.g., age group differences). Alpha was set at 0.05.

For the statistical analyses of TFR, the EEG processing was repeated to focus on the time window of interest (using an epoch of −1000 to 2000 ms) in order to decrease the number of rejected trials following the same protocol defined previously. Once the ERSPs were obtained, a baseline from −500 to −100 was applied. We conducted a series of mixed-model ANOVAs on mean ERSP values for each frequency band (theta, alpha and beta) and measure of power (dB and absolute). Relative power was computed as $dB = 10 * LOG_{10}(\mu V^2 \text{ poststimulus}/\mu V^2 \text{ at baseline})$. Absolute power was computed by subtracting the value at baseline from the power in the analyzed time-frequency window.

These ANOVAs included load (0-back, 1-back) and type of target (target, non-target) as within-subject variables and age group as a between-subject variable. Follow-up ANOVAs were conducted in case of interactions, and post-hoc pairwise tests with Bonferroni correction were performed to test the main effects.

Given the scarcity of studies including children and adolescents on

Table 1
Characteristics of participants included in the analysis after artifact rejection and mean number of trials per condition.

Age	*n*	Gender (male/female)	Handedness (left/right)	Age Mean (SD)	Mean (SD) number of trials included			
					0-back-T	0-back-nT	1-back-T	1-back-nT
6–8	18	11/7	1/17	7.7 (0.93)	43.8 (15.9)	81.7 (30.1)	27.6 (11.0)	65.8 (28.8)
9–11	20	10/10	1/19	10.5 (0.77)	47.5 (18.8)	93.0 (39.3)	40.7 (17.8)	87.3 (35.8)
12–14	31	14/17	4/27	13.6 (0.88)	50.7 (15.2)	97.2 (32.8)	44.9 (19.1)	92.9 (37.6)
15–17	31	15/16	6/25	16.5 (0.91)	58.1 (17.4)	114.4 (34.9)	55.6 (16.4)	119.0 (33.5)
18–20	31	6/25	0/31	19.6 (0.83)	57.0 (16.1)	110.9 (35.4)	56.7 (18.2)	111.4 (38.2)

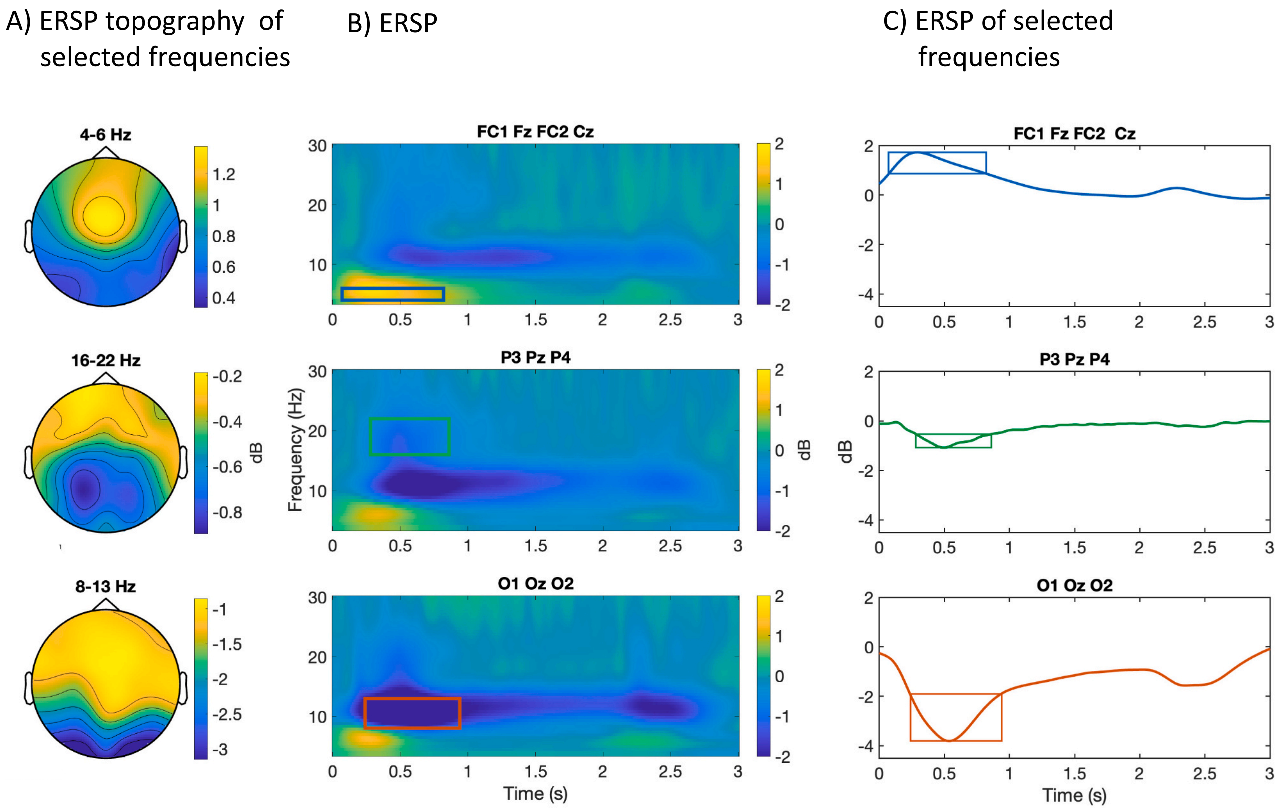

Fig. 2. Average relative event-related spectral perturbation (ERSP) panels and topography for theta, alpha and beta during the *n*-back task collapsed across subjects and conditions. *Note*. Panel 2A: Relative ERSP topographies of selected frequencies. Panel 2B: Time-frequency display collapsed across subject and conditions for selected electrodes in the different regions. The squares in 2B represent the time interval and the frequency windows selected for subsequent analyses. Panel 2C: Relative ERSP (collapsed across subjects and conditions) over time of the selected frequency windows. The squares in 2C represent the time windows selected for subsequent analyses, which were defined by the time points before and after the maximum power value at which 50 % of the power value was reached.

Table 2
Time frequency windows identified for statistical analyses.

Frequency band	Electrodes	Frequencies	Time interval dB	Time interval absolute
Alpha	O1 Oz O2	8.0–13	0.24 to 0.94 s	0.21 to 1.15 s
Beta	P3 Pz P4	16.0–22	0.28 to 0.86 s	0.27 to 0.88 s
Theta	FC1 FC2 Fz Cz	4.0–6.0	0.07 to 0.82 s	0.08 to 0.78 s

oscillatory behavior in *n*-back tasks, and because most of the research has been conducted in adults, an additional and preliminary set of analyses was conducted specifically on the young adults group. This was done to allow us to compare the present results with previous findings reported in other adult studies.

Finally, a set of analyses examined the possible mediating role of ERSP in the relationship between age and behavioral measures. Fig. 3 represents the general model. The coefficient *a* refers to the relationship between age and power. The coefficient *b* is the relationship between power and behavioral measures. The term $a \times b$ quantifies the indirect effect of age on behavioral measures through the mediator. The coefficient *c* represents the total effect of age on behavioral measures. The coefficient c' indicates the effect of age on behavioral measures independent of the mediator. Variables were standardized in the mediation analyses. False discovery rate (FDR) was used for correcting the alpha level after multiple comparisons. These analyses were performed using the lavaan package (Rosseel, 2012) in R (version 4.2.0; R Core Team, 2022).

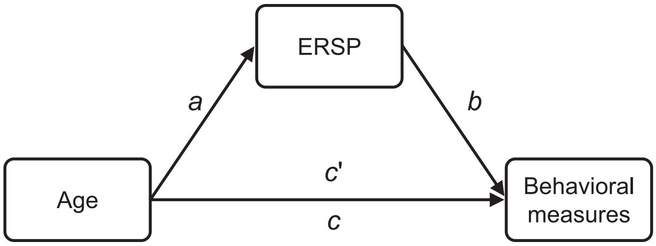

Fig. 3. Path diagram of the mediation model.

3. Results

3.1. Behavioral data

3.1.1. Response times

A mixed ANOVA model with age group (G-6-8, G-9-11, G-12-14, G-15-17, and G-18-20), load level (0-back, 1-back) and type of target (target, non-target) as independent variables and reaction time as the dependent variable was computed. For RTs, the results showed significant main effects of age group, $F(4, 126) = 65.14, p < .001; \eta p2 = 0.674$, due to a reduction of RTs with age; of load level, $F(1, 126) = 179.39, p < .001; \eta p2 = 0.587$; 0-back ($M = 791$) < 1-back ($M = 879$); and of type of target, $F(1, 126) = 26.31$, $p < .001$; $\eta p2 = 0.173$; target ($M = 821$) < non-target ($M = 849$); as well as interaction effects of load and type of target $F(1, 126) = 12.85$, $p < .001$; $\eta p2 = 0.093$; and of age, load, and type of target, $F(4, 126) = 2.97$, $p = .022$; $\eta p2 = 0.86$ (Fig. 4A). To decompose the higher-order interaction, we examined the effects of age and type of target separately for each level of load.

The analysis of the 0-back condition showed significant effects of age group, $F(4, 126) = 71.73, p < .001, \eta p2 = 0.695$; and type of target, $F(1,$

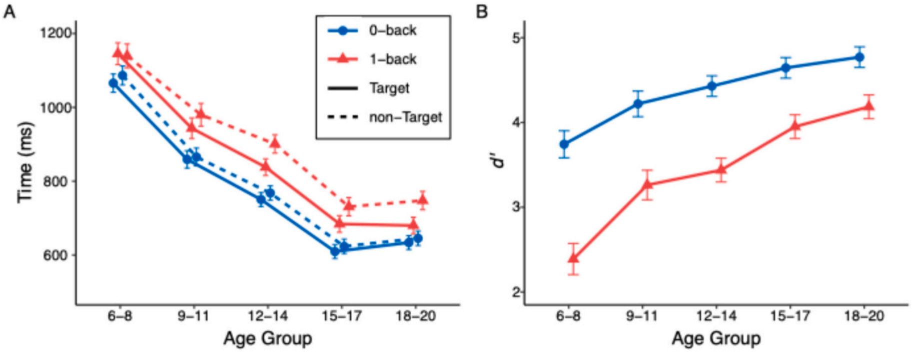

Fig. 4. Means response times and d' as a function of age group, type of target, and load. *Note.* Please note the decrease in RTs (Panel A) and the increase in d' (Panel B) with age; the load effect: 0-back showed shorter RTs and higher performance accuracy than 1-back; and the type of target effect: non-targets resulted in longer RTs than targets. Panel A represents RTs, and Panel B represents d'. Error bars represent 2 standard errors.

126) = 9.72, $p = .002$, $\eta p2 = 0.072$, due to longer times for non-targets ($M = 798$) than for targets ($M = 784$). The Bonferroni post-hoc analysis of group is described in Supplementary Table 1, and it shows a significant difference among all groups except between the oldest groups (G-15-17 and G-18-20). The analysis of the 1-back condition showed analogous results to those described for the 0-back condition. There were significant effects of age group, $F(4, 126) = 49.28$, $p < .001$, $\eta p2 = 0.610$; and type of target, $F(1, 126) = 25.53$, $p < .001$, $\eta p2 = 0.168$, due to longer RTs for non-targets ($M = 900$) than for targets ($M = 858$). Bonferroni post-hoc t-tests (Supplementary Table 1) of RTs showed differences among all age groups except between the G-9-11 and G-12-14 groups, and between the G-15-17 and G-18-20 groups.

In summary, three main results were found for RTs: shorter times with age, longer times in 1-back than in 0-back, and longer times in non-targets than in targets.

3.1.2. *d-Prime (d')*

An ANOVA was computed with d' as the dependent variable and age and load as independent variables. Type of target was not included in this analysis, given that d' is calculated from the performance in target and non-target conditions. The results showed significant effects of age, $F(4, 126) = 17.70$, $p < .001$; $\eta p2 = 0.360$ due to an increase of d' with age, and of load level, $F(1, 126) = 170.55$, $p < .001$; $\eta p2 = 0.575$; 0-back ($M = 4.36$) > 1-back ($M = 3.45$); there was also a significant interaction between age and load level, $F(4, 126) = 3.41$, $p = .01$; $\eta p2 = 0.098$ (Fig. 4B). Separate post-hoc analyses were conducted for each level of memory load. For 0-back, the post-hoc tests showed significant differences of the G-6-8 group with the G-12-14, G-15-17 and G-18-20 groups (Supplementary Table 2). For the 1-back condition, there were significant differences between group G-6-8 and all of the other four age groups; between the G9-11 group and the G-15-17 and G-18-20 groups; and between the G-12-14 and the G-18-20 group. This suggests that an asymptotic level of d' is reached earlier in the 0-back than in the 1-back. (Supplementary Table 3).

3.2. *Event-related spectral perturbation*

In our sample, there was an age difference between the gender groups (girls were older than boys: $Mgirls = 15.22$, $Mboys = 13.36$; $p = .01$). In a set of preliminary analyses, the possible effect of gender and the interaction age group × gender on all TFR dependent variables were tested for by two-way ANOVAs. Gender was found to be significant only for absolute beta ERD, $F(1, 121) = 4.21$, $p = .04$; $\eta p2 = 0.03$, indicating somewhat greater beta desynchronization among female ($M = -105.2$) compared to male participants ($M = -67.4$). No other gender-related effects or gender interactions with age group reached significance ($ps > .17$). Therefore, possible age-related differences were not confounded by gender effects. In order to simplify the ANOVA design and enhance statistical power, gender was not included in subsequent ANOVAs.

3.2.1. *Theta*

3.2.1.1. Initial analysis for the adult group. The ANOVA (load × target) for the adult group showed that, for the relative ERSP, there was a significant interaction between type of target and load, $F(1, 30) = 7.66$, $p < .010$; $\eta p2 = 0.203$. This interaction was driven by a significant load effect in the target condition, $t(30) = 2.59$, $p = .015$, with 0-back ($M = 1.98$) > 1-back ($M = 1.85$). The load effect did not reach significance in the non-target condition, $t(30) < 1$. The means are displayed in Fig. 5.

For the absolute theta ERSP in the adult group, the effect of type of target presents a trend for significance, $F(1, 30) = 4.00$, $p = .055$; $\eta p2 = 0.118$, as well the interaction between type of target and load, $F(1, 30) = 7.02$, $p = .013$; $\eta p2 = 0.190$, reached significance. The interaction was due to a load effect for targets, $t(30) = 2.147$, $p = .04$, with 0-back ($M = 1092$) > 1-back ($M = 1009$), which was not observed for non-targets ($p < 1$) (see Fig. 5).

3.2.1.2. Analysis across age groups. For the relative theta ERSP, there were significant effects of the age group, $F(4, 126) = 8.81$, $p < .001$; $\eta p2 = 0.219$; load, $F(1, 126) = 9.31$, $p = .003$; $\eta p2 = 0.060$, with more theta synchronization in 0-back ($M = 1.52$) than in 1-back ($M = 1.35$), and of type of target, $F(1, 126) = 5.4$, $p = .022$; $\eta p2 = 0.041$, with more theta synchronization in the target ($M = 1.50$) than non-target ($M = 1.36$) condition. There was also a significant interaction effect of age group, type of target and load, $F(4, 126) = 2.77$, $p = .03$; $\eta p2 = 0.081$ (Fig. 6A). The Bonferroni post-hoc analysis, which is described in Supplementary Table 4, showed a significant difference between G-6-8 and groups G-12-14, G-15-17 and G-18-20; and between G-9-11 and G-18-20. Subsequent t-test analysis revealed that the significant difference between target and non-target occurred only in the 0-back in the G-15-17 and G-18-20 groups ($p = .007$ and $p = .008$, respectively).

For the absolute theta ERSP, there was a significant effect of age group, $F(4, 126) = 6.39$, $p < .001$; $\eta p2 = 0.169$; load, $F(1, 126) = 6.69$, $p = .011$; $\eta p2 = 0.05$, with more theta synchronization in 0-back ($M = 1505$) than in 1-back ($M = 1308$), and of type of target, $F(1, 126) = 6.58$, $p = .012$; $\eta p2 = 0.05$, with more theta synchronization in the target ($M = 1518$) than non-target ($M = 1296$) condition (Fig. 6B). The Bonferroni post-hoc analysis is described in Supplementary Table 5 and shows significant differences between the G-9-11 group with G-15-14, the G-15-17 and G-18-20 groups.

3.2.2. *Alpha*

3.2.2.1. Initial analysis for the adult group. The ANOVA (load × target) of the relative alpha ERSP in the group of young adults showed a main effect only of type of target, $F(1, 30) = 12.31$, $p = .001$, $\eta p2 = 0.291$,

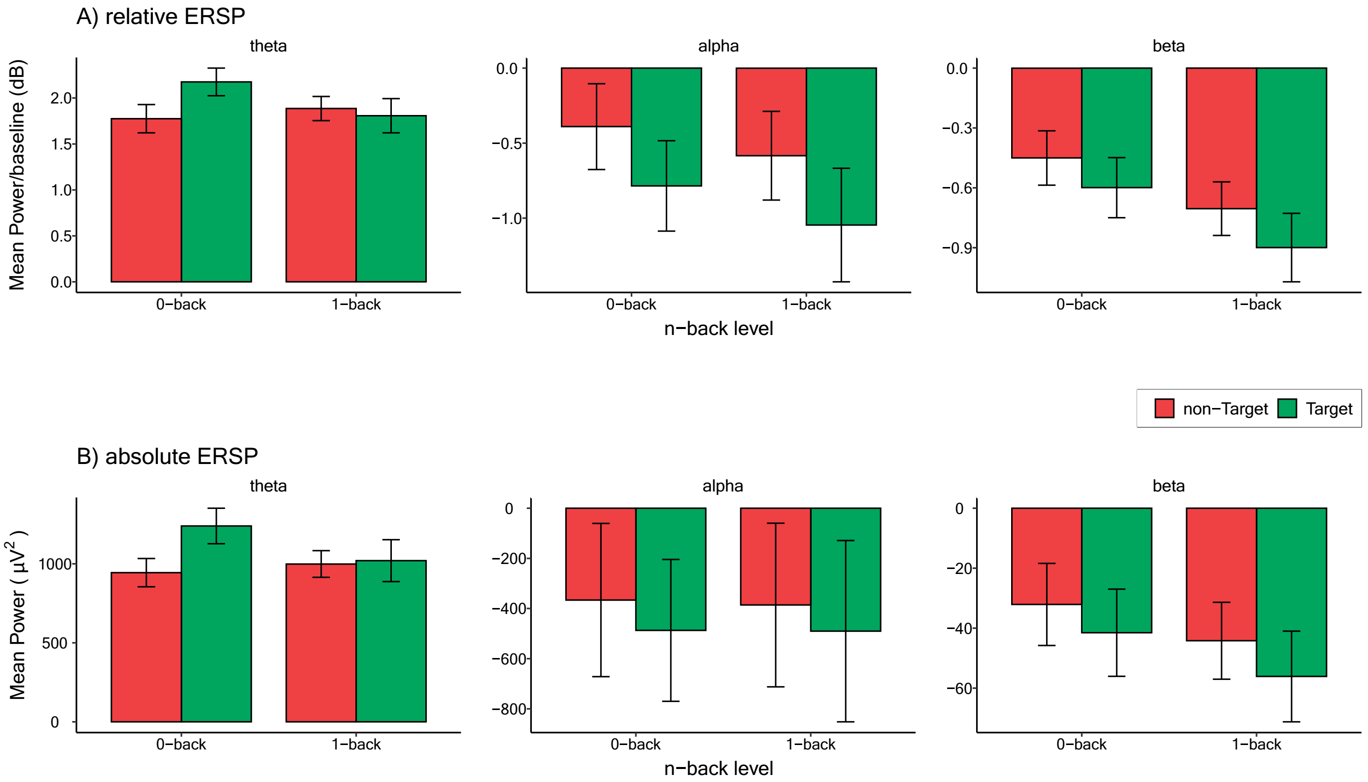

Fig. 5. ERSPs for the group of young adults for each frequency band, as a function of memory load and type of target. *Note*. Error bars represent 2 standard errors.

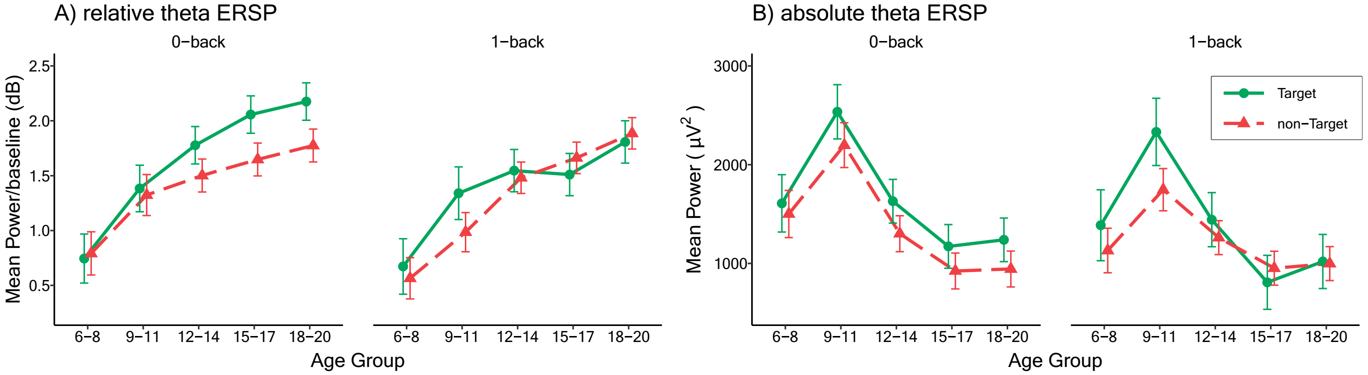

Fig. 6. Relative (panel A) and absolute (panel B) ERSP theta as a function of age group, memory load and type of target. *Note.* Please note the increase in relative theta ERS with age and the decrease in absolute ERS theta with age. Error bars represent 2 standard errors.

with a somewhat higher ERD in targets (*M* = −0.92) than in non-targets (*M* = −0.49) (Table 3). Means are displayed in Fig. 5. The analogous ANOVA of the absolute alpha ERSP values showed a main effect of type of target, *F*(1, 30) = 4.68, *p* = .039, *ηp2* = 0.135. Absolute alpha presented a higher ERD in the target (*M* = −489) than in the non-target (*M* = −376) condition.

Table 3
Summary of the ANOVA (type of target × load) results for the adults group.

	Load	Target	Load × target
Relative theta			(0-b > 1-b) in T
Absolute theta		T > nT	(0-b > 1-b) in T
Relative alpha		T > nT	
Absolute alpha		T > nT	
Relative beta	1-b > 0-b	T > nT	
Absolute beta	1-b > 0-b		

Note. T: Target, nT: non-Target; 0-b: 0-back; 1-b: 1-back. Theta comparisons are of ERS, and alpha and beta corresponds to ERD comparisons. Higher ERS means higher theta synchronization. Higher alpha or beta ERD means higher desynchronization.

3.2.2.2. Analysis across age groups. For the relative alpha ERSP, there was a significant effect of age group, *F*(4, 126) = 3.57, *p* = .009; *ηp2* = 0.102; load, *F*(1, 126) = 10.32, *p* = .002; *ηp2* = 0.076, with more alpha desynchronization in 1-back (*M* = −1.97) than in 0-back (*M* = −1.73), and of type of target, *F*(1, 126) = 48.71, *p* < .001; *ηp2* = 0.279, with more alpha ERD in the target (*M* = −2.06) than in the non-target (*M* = −1.63) condition (Fig. 7A) (Table 4). The Bonferroni post-hoc analysis is described in Supplementary Table 6, and shows differences between G-6-8 with G-18-20, and between G-15-17 with G-18-20.

For the absolute alpha ERSP, there were significant effects of age group, *F*(4, 126) = 2.78, *p* = .030, *ηp2* = 0.081, and type of target, *F*(1, 126) = 6.93, *p* = .01, *ηp2* = 0.052, due to a higher ERD in targets (*M* = −2243) than in non-targets (*M* = −1902). The interaction of load and

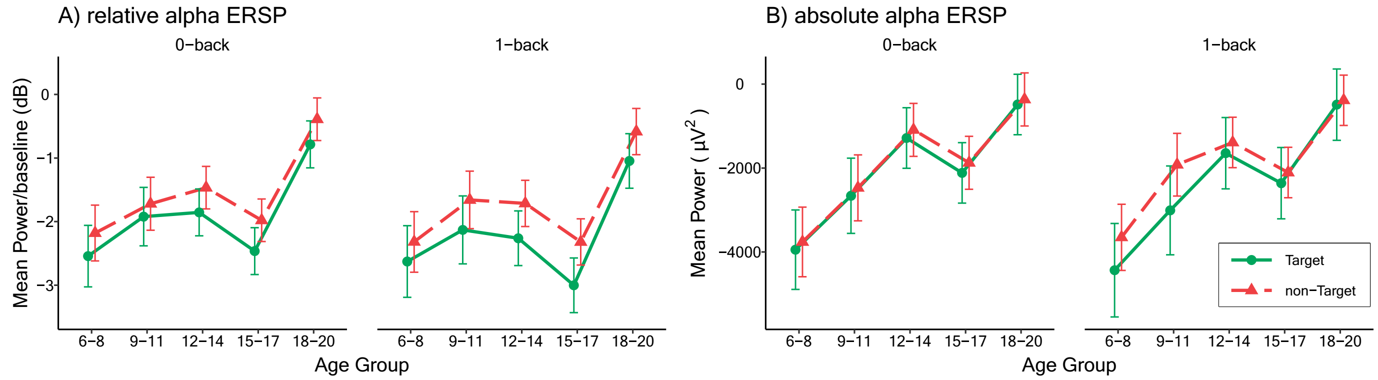

Fig. 7. Relative (panel A) and absolute (panel B) ERSP alpha as a function of age group, memory load and type of target. *Note.* Please note the decrease of relative and absolute alpha ERD with age. Error bars represent 2 standard errors.

Table 4
Summary of the ANOVA (age group × type of target × load) results.

	Load	Target	Age	Load × target	Load × target × age
Relative theta	0-b > 1-b	T > nT	G-6-8 < All; G-9-10 < G18–20		[(0-b > 1-b) in T] in G-15-17 & G-18-20 groups
Absolute theta	0-b > 1-b	T > nT	G-9-11 > (G-15-17 & G-18-20)		
Relative alpha	1-b > 0-b	T > nT	G-6-8 > G-18-20; G-15-17 > G-18-20		
Absolute alpha		T > nT	G-6-8 > G-18-20	(T > nT) in 1-b	
Relative beta	1-b > 0-b	T > nT			
Absolute beta	1-b > 0-b	T > nT	G-9-11 > G-18-20		

Note. T: Target, nT: non-Target; 0-b: 0-back; 1-b: 1-back. Theta comparisons are of ERS, and alpha and beta corresponds to ERD comparisons. Higher ERS means higher theta synchronization. Higher alpha or beta ERD means higher desynchronization.

type of target was also significant, $F(1, 126) = 4.42$, $p = .037$; $\eta p2 = 0.034$ (Fig. 7B). The Bonferroni post-hoc analysis of group appears is described Supplementary Table 7, and shows a significant difference between the G-6-8 with G-18-20 groups. The interaction of load and type of target was due to a significant higher alpha ERD for target ($M = -2133$) than for non-target ($M = -1714$) only in 1-back ($p = .019$).

3.2.3. Beta

3.2.3.1. Initial analysis for the adult group. When considering relative beta ERD in the adult group, the ANOVA (load × type of target) revealed a main effect of load, $F(1, 30) = 14.4$, $p < .001$; $\eta p2 = 0.325$, with more negative values in 1-back ($M = -0.80$) than in 0-back ($M = -0.52$), and a main effect of type of target, $F(1, 30) = 8.00$, p = .008; $\eta p2 = 0.211$, with targets showing more negative values ($M = -0.75$) than non-targets ($M = -0.58$) (see Fig. 6).

For absolute beta in the adult group, the analogous analysis revealed only a main effect of load, $F(1, 30) = 9.42$, $p = .005$; $\eta p2 = 0.239$, with more negative values in the 1-back ($M = -50.6$) than in the 0-back load condition ($M = -37.0$). Neither the effect of type of target ($p > .07$) nor the interaction effect ($F < 1$) was significant. Means are represented in Fig. 6.

3.2.3.2. Analysis across age groups. For relative beta ERD, there was a significant effect of load, $F(1, 126) = 32.67$, $p < .001$; $\eta p2 = 0.206$, with more beta desynchronization in 1-back ($M = -0.96$) than in 0-back ($M = -0.73$), and of type of target, $F(1, 126) = 39.69$, $p < .001$; $\eta p2 = 0.240$, with more beta desynchronization in the target ($M = -0.96$) than non-target ($M = -0.72$) condition (Fig. 8A).

For absolute beta ERD, there was a significant effect of age group, $F(4, 126) = 3.00$, $p = .02$; $\eta p2 = 0.087$; load, $F(1, 126) = 6.48$, $p = .012$, $\eta p2 = 0.049$, with more beta desynchronization in 1-back ($M = -91.95$) than in 0-back ($M = -78.24$), and of type of target, $F(1, 126) = 23.27$, $p < .001$; $\eta p2 = 0.156$, with more beta desynchronization in the target ($M = -96.63$) than non-target ($M = -73.55$) condition (Fig. 8B). The Bonferroni post-hoc analysis of group is described in Supplementary Table 8, and shows a significant difference between the G-9-11 and G-18-20 groups in absolute beta ERD.

Tables 3 and 4 show a summary of the ANOVA results of the ERD and ERS of theta, alpha and beta, for adults and across ages respectively.

3.3. Mediation analyses

The results of the mediation models with age as a predictor are presented in Table 5. Age was a significant predictor of most ERSP amplitudes (coefficients a). As for the mediation effect of ERSP in the relationship between age and behavioral measures (coefficients a × b), only relative theta emerged as a significant mediator. Specifically, the increase of relative theta had a mediation effect between age and d' in the 1-back level ($a \times b = 0.032$, $p = .003$). Further, relative theta was also a mediator of the effect of age on RTs in both levels of the n-back, indicating that the increase of ERS theta contributed to the decrease of RTs with age ($a \times b = -0.021$, $p = .006$; $a \times b = -0.024$, $p = .004$, respectively for 0 and 1-back).

4. Discussion

The behavioral results of this study showed the expected decrease in RTs and increase in d' with age, where the RTs increased and d' decreased with load. Posterior alpha and beta ERD, and frontocentral theta ERS, were generated as brain responses to the task. Age-related differences in absolute and relative ERS and ERD during n-back performance were investigated. The results showed that while relative theta ERS increased with age, absolute theta ERS, absolute and relative alpha, and absolute beta ERD, decreased. There was a general trend of higher amplitude of theta ERS, alpha and beta ERD in the target than in the non-target condition. Further, alpha and beta showed higher ERD amplitude in the in the 1-back, while ERS theta presented a higher amplitude in the 0-back condition. The mediation analyses showed that relative theta was the brain oscillation that mediated the relationship between age and behavior. When the young adult group was considered independently, the theta ERS amplitude increased in the target condition for the 0-back, while absolute theta ERS, relative and absolute alpha and relative beta

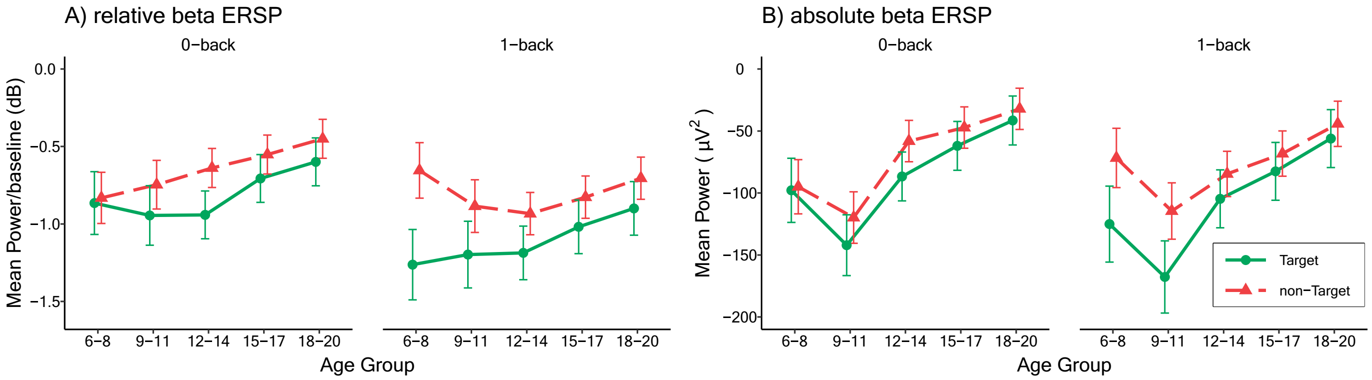

Fig. 8. Relative (panel A) and absolute (panel B) beta ERSP as a function of age group, memory load and type of target. *Note.* Observe the higher relative and absolute beta ERD in the target than in the non-target condition, and in 1-back than in 0-back. Error bars represent 2 standard errors.

Table 5
Mediation analyses: standardized direct and indirect effects of age on behavioral measures through ERSP amplitudes.

Outcome	Load	Mediator	*a*	*b*	*a* × *b*	95 % *CI*	*c*′	*c*
Absolute								
d′	0-back	Alpha	0.056*	−0.094	−0.005	[−0.015, 0.004]	0.111**	0.105**
	0-back	Beta	0.069*	0.020	0.001	[−0.01, 0.013]	0.104**	0.105**
	0-back	Theta	−0.068*	0.002	0.000	[−0.011, 0.011]	0.105**	0.105**
	1-back	Alpha	0.053*	−0.057	−0.003	[−0.011, 0.005]	0.152**	0.149**
	1-back	Beta	0.057*	0.191*	0.011	[0, 0.022]	0.138**	0.149**
	1-back	Theta	−0.049*	0.239*	−0.012	[−0.023, 0]	0.161**	0.149**
RT	0-back	Alpha	0.056*	0.068	0.004	[−0.003, 0.01]	−0.198**	−0.194**
	0-back	Beta	0.069*	−0.026	−0.002	[−0.009, 0.006]	−0.192**	−0.194**
	0-back	Theta	−0.068*	−0.076	0.005	[−0.003, 0.013]	−0.199**	−0.194**
	1-back	Alpha	0.053*	0.055	0.003	[−0.004, 0.01]	−0.182**	−0.179**
	1-back	Beta	0.057*	−0.061	−0.004	[−0.011, 0.004]	−0.176**	−0.179**
	1-back	Theta	−0.049*	−0.120	0.006	[−0.002, 0.013]	−0.185**	−0.179**
Relative (dB)								
d′	0-back	Alpha	0.055*	−0.038	−0.002	[−0.011, 0.007]	0.107**	0.105**
	0-back	Beta	0.045	0.000	0.000	[−0.007, 0.007]	0.105**	0.105**
	0-back	Theta	0.119**	−0.003	0.000	[−0.022, 0.021]	0.106**	0.105**
	1-back	Alpha	0.042	−0.014	−0.001	[−0.006, 0.005]	0.150**	0.149**
	1-back	Beta	0.030	0.187*	0.006	[−0.003, 0.014]	0.144**	0.149**
	1-back	Theta	0.114**	0.281**	0.032*	[0.012, 0.052]	0.117**	0.149**
RT	0-back	Alpha	0.055*	0.041	0.002	[−0.004, 0.008]	−0.196**	−0.194**
	0-back	Beta	0.045*	−0.047	−0.002	[−0.007, 0.003]	−0.192**	−0.194**
	0-back	Theta	0.119**	−0.178*	−0.021*	[−0.036, −0.006]	−0.173**	−0.194**
	1-back	Alpha	0.042	−0.028	−0.001	[−0.006, 0.004]	−0.178**	−0.179**
	1-back	Beta	0.030	−0.103	−0.003	[−0.009, 0.002]	−0.176**	−0.179**
	1-back	Theta	0.114**	−0.211*	−0.024*	[−0.041, −0.008]	−0.155**	−0.179**

Note: *p*-Values were adjusted using FDR; *a*: coefficients for the path from age to ERSP amplitudes; *b*: coefficients for the path from ERSP amplitudes to behavioral measures; *a* × *b*: indirect effects of age on behavioral measures through ERSP amplitudes; *c*′: direct effects of age on behavioral measures; *c*: total effects of age on behavioral measures; *CI*: confidence interval for the coefficients *a* × *b*.

** $p < .001$.

* $p < .05$.

ERD increased with the presentation of targets, and beta ERD increased in the 1-back condition. This developmental study suggests that theta ERS maturation is a crucial developmental step for improving WM performance during *n*-back tasks, while posterior alpha and beta are also maturing but are less important determinants of behavioral performance improvement with age, probably because the alpha-beta suppression level in young children is already sufficient to permit task focusing.

4.1. N-back performance

The behavioral results showed a general trend toward a decrease in RTs and improvement in accuracy with age (Kwon et al., 2002; López-Vicente et al., 2016; Pelegrina et al., 2015; Schleepen and Jonkman, 2009; Vuontela et al., 2003). The improvement of RTs with age independent from the type of task should be attributed to general developmental changes in processing speed (Fry and Hale, 2000; Kail and Miller, 2006) which could be due to age-related changes in white matter microstructure (Peters et al., 2014). Task effects independent of age would reflect the higher difficulty of 1-back compared to 0-back tasks due to the different substitution requirements (Pelegrina et al., 2020). The improvement in accuracy with age may result from increased distance in terms of the neural representation of presented items, as suggested by signal detection theory (Macmillan and Creelman, 2004), due to a sharpening of these representations with age. This process could also operate in the 0-back task due to repetition suppression of the 0-back target (Barron et al., 2016). However, to substantiate this latter interpretation, the neural activity of individual neurons, or the minimal morphological differences between standard and deviants needed for generating a reliable visual mismatch negativity, should be ascertained in a developmental context.

4.2. Brain oscillations

After collapsing the TFR results of all the conditions and age groups, three different brain oscillations appeared: an early and short-duration fronto-central ERS theta, a long-standing posterior alpha ERD and, a short-duration posterior beta ERD. Regarding the beta posterior ERD, it is difficult to disentangle it from posterior alpha in terms of frequency, given that Loreta studies localizing posterior oscillations have shown that posterior low beta rhythms would form a continuous pattern with posterior alpha rhythms, interpretable as the high frequency tail of the alpha rhythm (Gómez et al., 2006; Costers et al., 2020). However, the present results showed a more parietal topography for beta ERD when compared with alpha ERD, therefore it is possible that beta ERD reflects not only the high frequency tail of posterior alpha, but also beta ERD related to motor responses (McFarland et al., 2000). This set of theta, alpha and beta oscillatory patterns has been broadly described in previous results of *n*-back tasks in children, adolescents and adults (Costers et al., 2020; Pesonen et al., 2007; Scharinger et al., 2015, 2017, 2023). As indicated before, there is controversy in the literature regarding how the type of target and load impact the brain oscillations generated during the *n*-back task in adult subjects. Therefore, we analyzed young adults in terms of brain oscillations related to WM operation.

In our young adult group, the observed increase of theta ERS under the lower load (0-back > 1-back) only for the target condition, and the lack of a load effect in the non-target condition, is consistent with previous results that failed to find load effects in theta (Chen and Huang, 2016; Dong et al., 2015; Kao et al., 2020; Krause et al., 2010; Missonnier et al., 2013; Scharinger et al., 2023; Semprini et al., 2021), and those that found an increase of theta for the target condition (Gajewski and Falkenstein, 2014; Palomäki et al., 2012; Pesonen et al., 2007). With respect to alpha and beta ERD, the general trend was of increasing ERD with greater task difficulty and with targets; this was seen in a more restricted manner for alpha (target > non-target), relative to beta, where the effect of task difficulty was more evident with a higher ERD in 1-back and target conditions. This trend of higher ERD with more difficult tasks and targets has been extensively described in previous studies (Brookes et al., 2011; Chen and Huang, 2016; Haegens et al., 2014; Kao et al., 2020; Krause et al., 2010; Palomäki et al., 2012; Pesonen et al., 2007; Scharinger et al., 2015, 2017, 2023). Taken together, the results suggest that an increase in alpha and beta ERD for the more engaging conditions would help the networks processing the received stimuli to accomplish the intended goal. The most consistent involvement of alpha and beta for processing the most difficult conditions (1-back and target), suggests that the increased cortical disinhibition indexed by alpha and beta ERD is more crucial than theta ERS activity for processing the most difficult and engaging conditions.

4.3. Developmental trajectories in brain oscillations

From a developmental point of view, the most important questions that arise from the present report in relation to WM operation are: (i) how the different brain rhythms evolve with age, (ii) which brain oscillations are most related to behavioral performance across development, and (iii) whether it is possible to unequivocally define the relationships of some of the obtained brain oscillations with the encoding and updating processes during development. These points should be addressed from a transversal perspective.

With respect to how the different brain rhythms evolve with age, there was an increase of relative theta ERS, and a reduction of absolute theta ERS, absolute and relative alpha and absolute beta ERD. Other authors (Krause et al., 2010; Zhao et al., 2023) reported the same brain oscillatory patterns of theta, alpha and beta obtained in the present study, but they did not describe age dependence or developmental trajectories.

In the present report, the absolute ERS theta and absolute ERD alpha and beta decreased with age, a result that could be related to the general reduction in power for brain rhythms with age due to synaptic pruning (Barriga-Paulino et al., 2011; Segalowitz et al., 2010). More interesting is the increase in relative power obtained in theta, which implies that the relative strength of theta with respect to baseline increases with age. The mediational analysis also showed that maturation of relative (increase with age) were critical for improving WM performance with age. In a developmental study of TFR in another WM task, the DMTS, in which developmental trajectories of absolute brain oscillations were obtained (Gómez et al., 2023), a decrease of absolute power with age was also observed for most brain oscillations and in particular for an early posterior theta. Interestingly, theta also exhibited a mediational role with respect to behavioral performance. The present report and Gómez et al. (2023) indicate that theta maturation is crucial for behavioral performance improvement with age, in terms of both accuracy and RTs. Up to a point, it is possible that the ERSP in the theta range presented here could be in part due to the presence of a P300 ERP component, which has been shown to decrease with age in terms of absolute values (Pelegrina et al., 2020; Polich, 2011; Van Dinteren et al., 2014). Given the long-standing proposal that P300 is related to the process of memory encoding (Polich, 2007), it is possible that the increase in theta relative power observed in the present report is related to an improvement of memory encoding with age. Therefore, the observed reduction in P300 amplitude with age would be associated to the decrease in absolute theta. However, to support this conclusion a topographic similarity, and a significant correlation between P300 and theta should be obtained. The influential role of theta in encoding is supported by the observed differences between the target and non-target conditions, given that the latter condition requires new encoding while the former needs only reinforcement of the currently encoded item in memory.

Absolute alpha and beta ERD showed a decrease in amplitude with age, as has been described previously for spontaneous and stimuli-linked brain oscillations (Barriga-Paulino et al., 2011; Gómez et al., 2023; Segalowitz et al., 2010); this result is likely due to synaptic pruning with age. However, the observed reduction of relative alpha ERD with age, covarying with (although not mediating) developmental behavioral trends, implies a general phenomenon, given the broadly accepted dual role for alpha: (i) would reflect inhibition of the visual cortices to control for interferences (alpha ERS), and (ii) would facilitate the processing of visual stimuli by disinhibiting the cortical networks needed for current stimulus processing (alpha ERD). Therefore, the reduction of relative alpha ERD with age would reflect a lower dependency of cortical disinhibition for effective visual processing as brain matures (Gratton, 2018; Heinrichs-Graham and Wilson, 2015; Lenartowicz et al., 2014) . Moreover, the very low alpha ERD obtained in the adult group would possibly be related to the easy nature of the task, which would require a very low cortical disinhibition for further target processing. The higher relative alpha and beta ERD in the 1-back condition suggests that more cortical disinhibition is needed for more difficult tasks (1-back > 0-back), with a higher level of focused attention required for processing the stimuli (Gratton, 2018). The higher ERD obtained for targets also suggests a greater focus on targets than non-targets, probably due to the target shape validation needed in the presence of a target. In contrast, non-targets can be recognized simply based on discordance between the features of the stimulus stored in memory and the new stimuli being processed.

The general trend of increased alpha and beta ERD for the 1-back and target conditions seen in the young adults in this study is similar to the results obtained regarding load and type of target in the developmental analysis, indicating a degree of consistency in brain processing strategies across developmental stages. The non-significant results for some comparisons in the adult group, are probably due to a lack of statistical power due to the relatively lower number of recorded subjects when compared to the whole sample.

Given that the 0-back and 1-back conditions differ in their updating requirements, the load effect on brain oscillations, particularly relative theta, could also be attributed to this process. It is noteworthy that there were no clear interactions of load with age, suggesting that the basic mechanism appears to be in place at all ages studied.

The developmental trajectory of brain oscillations for the *n*-back task showed some similarities with the results obtained in the DMTS during the encoding and maintenance phases, with the former showing a more simple TFR structure than the DMTS (Gómez et al., 2023). In the DMTS, a theta ERS during encoding, followed by a Parieto-central theta ERS during maintenance and a long-lasting alpha ERD during the encoding and maintenance phases, were observed (Gómez et al., 2023). Although the developmental trajectories are very similar in both experiments, the different TFR signatures of the two tasks suggest a somewhat different processing strategy. For instance, early theta was more prominent in posterior sites and a fronto-central theta subsequently developed in the DMTS, while in *n*-back theta ERS was already present in the early post-stimulus period, suggesting greater involvement of the frontal cortex for the *n*-back with respect to the DMTS.

4.4. Conclusions

In general, present results showed statistically effects primarily in terms of the main factors, suggesting a dominant independent processing of load and type of target. This independence maintained along the developmental stages of childhood, adolescence and emergent adulthood.

During the encoding and updating phases in an *n*-back task, posterior alpha and beta, and frontocentral theta brain activity, are observable from childhood through early adulthood. Alpha and beta ERD were more pronounced for the most difficult task (1-back) compared to the easier 0-back task, and also for the target than for the non-target condition. The effects of type of target and load were largely consistent across development, but age-related changes were observed for absolute and relative power in the different frequency bands. Relative theta ERS increased with age, whereas absolute theta ERS, and absolute and relative alpha and absolute beta ERD, decreased with age. The maturation of theta brain activity appears to play a role in the development of WM performance, as suggested by its mediation of the age-related improvement in *n*-back performance. In contrast, the maturation of alpha and beta brain activity could be less critical for age-related changes in behavioral performance, possibly because young children already have sufficient alpha-beta ERD, ensuring proper functioning of basic WM processes.

CRediT authorship contribution statement

Carlos M. Gómez: Writing – original draft, Validation, Methodology, Conceptualization. **Rocío Linares:** Writing – original draft, Resources, Investigation, Data curation. **Elena I. Rodríguez-Martínez:** Writing – review & editing. **Santiago Pelegrina:** Writing – original draft, Visualization, Supervision, Software, Methodology, Formal analysis, Conceptualization.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijpsycho.2024.112372.

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