Working memory and attention-related EEG oscillations and the impact of a physical exercise on the brain

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Abstract [English]

Understanding the underlying neural mechanisms between visual working memory and visual attention has been of great interest in Neuroscience. Evidence shows that neural oscillations from an electroencephalogram (EEG) have a distinct activity pattern during specific cognitive processes. This dissertation's overarching purpose was to contribute to our growing understanding of the neural basis of visual working memory (WM) and visual attention, with an emphasis on measuring the impact of physical exercise on such processes. Specifically, if an increase in aerobic fitness extends to changes in theta and alpha power, and in turn, to WM integrity and attention in the context of 4-month physical exercise training in sedentary young adults.

In Chapter 2, I examined the changes in time-frequency power and how they relate to working memory and visual attention. Forty-three participants (19 - 34 years) performed both a delayed-match-to-sample (DMS) WM task and a visual attention-search (VAS) task. The DMS task required mnemonic discrimination of similar visual stimuli, akin to pattern separation, while the VAS task required detecting the presence of a spherical object (i.e., target) in an image. Results showed an increase in frontal midline theta (fm-theta) power during the VAS task and a decrease during the DMS task. The latter correlated with behavioral performance displaying a stronger decrease in fm-theta power during the maintenance phase associated with better mnemonic discrimination and faster response time (RT) during lure trials. Alpha power, on the other hand, decreased for both tasks displaying a greater decrease during the DMS task than during the VAS task, demonstrating its sensitivity to attentional demands. Alpha power also correlated with behavioral performance, where faster response time during the VAS task exhibited a stronger decrease in alpha power. Overall, these findings provide further evidence that theta and alpha power display a unique pattern of activity during specific cognitive processes and were also proportional to behavioral performance in both the DMS task and the VAS task.

Working memory (WM) and attention have shown behavioral and structural benefits due to physical exercise (Cassilhas, Tufik, & De Mello, 2016). Quantifying the EEG neural activity in specific frequency bands from a longitudinal perspective can provide further insight into exercise-induced benefits in the brain. In Chapter 3, I investigated whether four months of physical exercise

training modulated theta and alpha power. Behavioral and EEG data were acquired during a DMS task and VAS task before and after the intervention period. The same forty-three participants from the experiment in Chapter 2 were pseudorandomly assigned to an exercise group (indoor treadmill, n = 20) or a control group (n = 23). Behaviorally, there were no exercise-related effects on behavioral performance in either task. Although, compared to the pre intervention baseline, the exercise group showed an increase in frontal alpha power (9 - 12 Hz) during the VAS task after the intervention. Also, changes in alpha power positively correlated with changes in aerobic fitness and behavioral performance (RT - VAS task). These findings substantiate that physical exercise may influence neural dynamics underlying visual attention rather than visual WM and mnemonic discrimination in sedentary young adults (Chaire, Becke, & Düzel, 2020).

In Chapter 4, I investigated the neural mechanisms of WM interference, generated from the clash between an internal (i.e., a number or color word) and an external representation (i.e., a Stroop-like distractor) presented during the maintenance phase. Specifically, I compared two dual-task paradigms that elicited different types of interference. That is, the trials could be more or less demanding (i.e., incongruent vs. congruent) and having the interference within the same or different feature domain than the memoranda (i.e., overlapping or non-overlapping features). Behavioral and neural differences were measured during retrieval as a function of prior congruency in a group of healthy young adults (n = 33). Behavioral results revealed higher accuracy and faster RT during the congruent trials of the domain-overlapping (DO) WM task, indicating a facilitation effect. Moreover, the P300 amplitude was larger on trials following a congruent distractor regardless of the task. On the other hand, theta power during WM retrieval was significantly larger for the incongruent trials during the DO WM task only, which may be reflective of the need for greater allocation of cognitive resources to tackle conflict resolution during WM retrieval. Overall, fm-theta revealed to be a more sensitive indicator of facilitating effects than the P300. Finally, in Chapter 5, I summarized the findings of the dissertation and discussed how EEG measures are used to infer the underlying mechanisms of physical exercise on visual attention, WM, and attention as a shared mechanism. I also add some recommendations for the use of EEG measures to answer future questions.

Abstract [German]

Das Verständnis der neuronalen Mechanismen, die dem visuellen Arbeitsgedächtnis und der visuellen Aufmerksamkeit zugrunde liegen, ist für die Neurowissenschaften von großem Interesse. Es gibt Hinweise darauf, dass neuronale EEG-Oszillationen während bestimmter kognitiver Prozesse ein einzigartiges Aktivitätsmuster aufweisen. Das übergreifende Ziel dieser Dissertation ist es, einen Beitrag zu unserem wachsenden Verständnis der neuronalen Grundlagen des visuellen Arbeitsgedächtnisses (WM) und der visuellen Aufmerksamkeit zu leisten, wobei der Schwerpunkt auf der Messung der Auswirkungen von körperlicher Bewegung auf entsprechende Prozesse lag. Insbesondere wird im Rahmen eines 4-monatigen körperlichen Bewegungstrainings bei sitzenden jungen Erwachsenen untersucht, ob vermehrte aerobe Fitness zu Veränderungen in Theta und Alpha Stärke führt und sich somit auf die WM-Integrität und Aufmerksamkeit auswirkt.

In Kapitel 2 untersuche ich die Veränderungen der Zeit-Frequenz-Leistung und wie sie sich auf das Arbeitsgedächtnis und die visuelle Aufmerksamkeit auswirken. Dreiundvierzig Teilnehmer (19 - 34 Jahre) führten sowohl eine delayed-match-to-sample (DMS) WM-Aufgabe als auch eine Aufgabe zur visuellen Aufmerksamkeitssuche (VAS) durch. Die DMS-Aufgabe erforderte die mnemonische Unterscheidung ähnlicher visueller Stimuli, was einer Mustertrennung ähnelt, während die VAS-Aufgabe die Erkennung eines kugelförmigen Objekts (d.h. eines Ziels) in einem Bild erforderte. Die Ergebnisse zeigten einen Anstieg der frontalen Mittellinien-Theta (fm-theta) Stärke während der VAS-Aufgabe und einen Rückgang während der DMS-Aufgabe. Letzteres korrelierte mit der Verhaltensleistung, die einen stärkeren Abfall der fm-Theta-Stärke während der Erhaltungsphase zeigte, verbunden mit einer besseren mnemonischen Unterscheidung und einer schnelleren Reaktionszeit (RT) während des Versuches. Die Alpha-Stärke hingegen nahm bei beiden Aufgaben ab, wobei sie bei der DMS-Aufgabe stärker abnahm als bei der VAS-Aufgabe, was ihre Sensibilität für Aufmerksamkeitsanforderungen beweist. Die Alpha-Stärke korrelierte auch mit der Verhaltensleistung, wobei die schnellere Reaktionszeit während der VAS-Aufgabe einen stärkeren Abfall der Alpha-Stärke zeigte. Insgesamt liefern diese Ergebnisse weitere Belege dafür, dass Theta und Alpha-Stärken ein einzigartiges Aktivitätsmuster während spezifischer kognitiver

Prozesse aufweisen und auch proportional zur Verhaltensleistung sowohl bei der DMS-Aufgabe als auch bei der VAS-Aufgabe waren. Das Arbeitsgedächtnis (WM) und die Aufmerksamkeit haben durch körperliche Betätigung verhaltensbezogene und strukturelle Verbesserungen gezeigt (Cassilhas, Tufik, & De Mello, 2016). Auch frühere Querschnittsstudien zeigten Leistungsmodulationen auf mehreren Frequenzbändern, die mit kognitiven Verbesserungen bei jungen Erwachsenen zusammenhingen (Chang, Chu, Wang, Song, & Wei, 2015; Wang et al., 2015). Die Quantifizierung der neuronalen EEG-Aktivität in bestimmten Frequenzbändern aus einer Längsschnittperspektive kann weitere Einblicke in belastungsinduzierte Vorteile im Gehirn liefern.

In Kapitel 3 untersuche ich, ob vier Monate körperlichen Trainings Theta- und Alpha-Stärke modulieren. Es wurden Verhaltens- und EEG- Daten während einer DMS-Aufgabe und einer VAS-Aufgabe vor und nach der Interventionsperiode erfasst. Dieselben dreiundvierzig Teilnehmer aus dem Experiment in Kapitel 2 wurden pseudozufällig einer Übungsgruppe (Indoor-Laufband, n = 20) oder einer Kontrollgruppe (n = 23) zugeordnet. Verhaltensmäßig gab es bei keiner der beiden Aufgaben bewegungsbedingte Effekte auf die Verhaltensleistung. Obwohl die Übungsgruppe im Vergleich zur Basislinie vor der Intervention einen Anstieg der frontalen Alpha-Stärke (9-12 Hz) während der VAS-Aufgabe nach der Intervention zeigte. Außerdem korrelierten Veränderungen der Alpha-Stärke positiv mit Veränderungen der aeroben Fitness und der Verhaltensleistung (RT - VAS-Aufgabe). Diese Ergebnisse belegen, dass körperliche Bewegung die neuronale Dynamik, die der visuellen Aufmerksamkeit zugrunde liegt, eher beeinflussen kann als das WM und die mnemonische Unterscheidung bei sitzenden jungen Erwachsenen (Chaire, Becke, & Düzel, 2020).

In Kapitel 4 untersuche ich die neuronalen Mechanismen der Arbeitsgedächtnisinterferenz, die aus dem Aufeinandertreffen zwischen einer internen (d.h. einer Zahl oder einem Farbwort) und einer externen Repräsentation (d.h. einem Stroop-ähnlichen Distraktor) entsteht, die während der Erhaltungsphase präsentiert werden. Konkret vergleiche ich zwei Dual-Task-Paradigmen, die unterschiedliche Arten von Interferenzen hervorrufen. Das heißt, die Versuche können mehr oder weniger anspruchsvoll sein (d.h. inkongruent vs. kongruent) und die Interferenz innerhalb desselben oder eines

anderen Merkmalsbereichs als die Memoranden haben (d.h. überlappende oder nicht überlappende Merkmale). Verhaltens- und neuronale Unterschiede wurden während des Abrufs als Funktion der früheren Kongruenz in einer Gruppe gesunder junger Erwachsener (n = 33) gemessen. Die Verhaltensergebnisse zeigten eine höhere Genauigkeit und schnellere RT während der kongruenten Versuche der domänenübergreifenden (DO) WM-Aufgabe, was auf einen Erleichterungseffekt hinweist. Außerdem war die P300-Amplitude in den Studien nach einem kongruenten Distraktor unabhängig von der Aufgabe größer. Andererseits war die Theta-Stärke während des WM-Abrufs nur bei den inkongruenten Versuchen während der DO-WM-Aufgabe signifikant größer, was auf die Notwendigkeit einer stärkeren Allokation kognitiver Ressourcen zur Konfliktlösung während des WM-Abrufs hindeuten könnte. Insgesamt erwies sich fm-Theta als ein empfindlicherer Indikator für erleichternde Wirkungen als die P300.

Schließlich fasse ich in Kapitel 5 die Ergebnisse der Dissertation zusammen und erörtere, wie EEG-Messungen verwendet werden, um auf die zugrunde liegenden Mechanismen der körperlichen Betätigung auf die visuelle Aufmerksamkeit, das WM und die Aufmerksamkeit als gemeinsamen Mechanismus zu schließen. Ich füge auch einige Empfehlungen für den Einsatz von EEG-Messungen zur Beantwortung künftiger Fragen hinzu.

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Abbreviation List

AF	Aerobic fitness
AD	Alzheimer’s disease
ACC	Anterior cingulate cortex
BDNF	Brain-derived neurotrophic factor
BMI	Body-mass-index
BOLD	Blood-oxygen-level-dependent
Cong	Congruent
dB	Decibel
DLPC	Dorsolateral prefrontal cortex
DMS	Delayed-matched to sample
DO	Domain overlapping
nonDO	Non-domain overlapping
EEG	Electroencephalogram
EOG	Electrooculography
ERD	Event-related desynchronization
ERP	Event-related potentials

ERSP	Event-related spectral perturbation
fMRI	Functional magnetic resonance imaging
fm-theta	Frontal midline theta
fNIRS	Functional near-infrared spectroscopy
GM	Grey matter
iAPF	Individual alpha peak frequency
iEEG	intracranial electroencephalogram
Inc	Incongruent
LFP	Local field potential
LTM	Long-term memory
LPC	Late positive component
PA	Physical Activity
PE	Physical exercise
PFC	Prefrontal cortex
ROI	Region of interest
RT	Response time

TFA	Time-frequency analysis
TFR	Time-frequency representation
VAS	Visual-attention search
vEOG	Vertical electrooculogram
VO_2 max	Maximum oxygen consumption
VO_2 VAT	Oxygen consumption at ventilatory anaerobic threshold
VT	Ventilatory threshold
WM	Working memory

1. General Introduction

1.1 Investigating the impact of physical exercise on brain-related changes

Physical exercise (PE) is a subcategory of physical activity characterized by being planned, structured, and repetitive to improve or maintain aerobic fitness. In our modern society, physical activity, generally continues to lose importance in the list of priorities compared to past generations (Guthold, Stevens, Riley, & Bull, 2018), even though the amount of evidence on the negative consequences of adapting to a sedentary lifestyle is substantial (Levine et al., 2005). Globally, more than a quarter (27.5%) of adults are not getting enough physical activity, and more than 80% of young adults do not engage in the recommended 30-min moderate-to-vigorous daily exercise (Guthold et al., 2018). These levels of physical activity only seem to decrease with age (Troiano et al., 2008), despite the fact that engaging in physical exercise has been shown to improve a range of different physiological and more recently cognitive aspects. Studies have shown that PE reduces the risk of numerous metabolic and cardiovascular diseases (Barry et al. 2014; Peurala et al. 2014, for meta-analysis), it increases mental well-being (Galper, Trivedi, Barlow, Dunn, & Kampert, 2006), and to a less extent, PE has been shown to improve cognitive function over one's lifespan (Falck, Davis, & Liu-Ambrose, 2017). Hence, it is crucial to continue to systematically study the impact of physical exercise, especially on brain functions in a controlled longitudinal exercise intervention setting.

An increasing amount of evidence exists measuring the impact of physical exercise on the structure of the brain (Chaddock et al., 2010; Kirk I Erickson et al., 2011; Thomas, Dennis, Bandettini, & Johansen-Berg, 2012) and cognitive functions, such as working memory (Voss et al., 2013), selective attention (Sousa, Medeiros, Rosso, Stults-kolehmainen, & Boullosa, 2018a), and attentional control (Kirk I. Erickson, Hillman, & Kramer, 2015; Sibley & Beilock, 2007a) (for reviews see Cotman and Berchtold, 2002; Roig et al. 2016; Sousa et al. 2018b). These exercise-related cognitive benefits are possible given the brain's remarkable ability to modify its molecular structure due to external factors (e.g., physical exercise), improving the efficiency of synaptic pathways (Marmeleira, De Melo, Tlemcani, & Godinho, 2011). However, the changes in the brain's structure and neural network due to physical exercise are extraordinarily complex. Despite the positive outcomes of the cited studies, there exists a large outcome variability, where studies fail to show changes in behavioral performance or structural brain differences between populations that exercise regularly versus sedentary people (Rigdon & Loprinzi, 2019; Verburgh, Königs, Scherder, & Oosterlaan, 2014a). Yet, there is still a consensus that physical exercise benefits cardiovascular functions, which in turn has been linked to seemingly preserving brain health and even serving as a protecting agent against cognitive decline and neurodegenerative diseases (Cassilhas et al., 2016; Lin, Tsai, & Kuo, 2018).

Furthermore, numerous functional neuroimaging techniques have been implemented to quantify physiological and functional changes associated with changes due to engaging in physical exercise. For instance, electro/magnetoencephalography (EEG/MEG), functional magnetic resonance (fMRI), and functional near-infrared spectroscopy (fNIRS) have provided insight into how exercise affects neural activity. With these techniques, changes in brain volume (hippocampus), modulations in specific frequency-band activity (alpha-band power), and neurotropic levels (plasma level) can be measured and compared between participants that engage in exercise to those who are sedentary. Additionally, those changes can be correlated to cognitive performances, expressing the functional neural efficiency gained from a particular intervention. The following two sections further expand on these studies.

1.1.1 Exercise-induced cognitive changes

The majority of exercise-related cognitive studies in young adults are cross-sectional (i.e., independent of physical exercise) (Sousa et al., 2018a). Typically during these studies, researchers rely on measuring a person's aerobic fitness (AF), which is a person's VO_2max (mL/Kg/min) – the body's maximal amount of oxygen uptake during exercise. Greater VO_2max values correspond to higher AF, that is, enhanced transport of oxygenated blood and enhanced extraction of oxygen at the muscle cell level. Many studies have related higher aerobic fitness to better performance during WM (Moriya, Aoki, & Sakatani, 2016), spatial memory (Kirk I Erickson et al., 2009, 2011), and attentional control (i.e., the flanker task Verstynen et al. 2012; Westfall et al. 2018). In a study by Westfall et al., (2018), the associations of aerobic fitness and attentional control in adolescents was investigated. Their tasks consisted of a flanker task, which measures attentional inhibition and a switch-task that tested cognitive flexibility. They found that adolescents with higher aerobic fitness levels had shorter response times (RT) and higher accuracy in the flanker task, indicating better control performance. Results from the switch task associated greater fitness to greater drift rate (i.e., the speed and quality of stimulus information processing, the higher the drift rate the better the performance). A different study divided 38 older adults (26 females; 77 ± 5 years) into a low fitness group and a moderate fit group. They assessed attention with a Stroop test and found that the moderately fit group achieved significantly better accuracy. Also, there was a correlation between VO_2max and attention scores (i.e., mean response times for the Go-NoGo test and the Stroop test), where participants with higher aerobic fitness had higher selective attention (Netz, Dwolatzky, Zinker, Argov, & Agmon, 2011).

A recent review by Rigdon and colleagues (2019) reviewed seventeen studies, fifteen of which were cross-sectional, and two were prospective cohorts. This review highlights the potential effects of AF on attentional and memory function among adults (Rigdon & Loprinzi, 2019). A study mentioned in the review by Scott et al. (2016) found a positive association between aerobic fitness and a batch of executive functions in 120 women (18 – 29 years; avg. age = 22.7 ± 0.4). Specifically, they found a positive association between AF and accuracy in the Sternberg's WM search task and another with the modified flanker task (Scott, De Souza, Koehler, Petkus, & Murray-Kolb, 2016). A different mentioned study, however, failed to find an association between AF and memory complaints in young adults (Loprinzi & Wade, 2019), while another demonstrated a positive association between AF and memory only in one out of their two cohorts (Oberlin et al., 2016). Overall, 88.2% of the review's studies demonstrated evidence of a positive association of AF and memory function (Rigdon & Loprinzi, 2019). This review confirms that having greater aerobic fitness might improve working memory and attentional functions. However, it remains uncertain as to whether this association is mediated via physical activity behavior.

Remarkably, very few human intervention trials have examined the neural correlates behind changes in exercise-related cognitive functions, and the few that exist mainly focuses on developing population (i.e., children or teenagers) or on older adults. Hillman and colleagues (2014) investigated the effects of a 9-month exercise activity program among preadolescent children (8 to 9 years). They aimed to investigate the effects of PA on executive functions and its neural underpinnings by comparing the before and after changes in VO_2max, behavioral performance, and the amplitude and latency of the P3 component. Specifically, they measured cognitive flexibility with a task-switching test and attentional control with a flanker task from two groups of preadolescents; one group participated in an extracurricular program, while the other was waitlisted (control group). Their program consisted of two approximately 40-minute periods of moderate exercise with a snack break in between sessions. They found that preadolescents registered in the extracurricular program had significantly increased their aerobic fitness, behavioral indices during the executive control tasks (i.e., accuracy), neural indices of attention (i.e., larger P3 amplitude), and processing speed (i.e., shorter P3 latency). Additionally, changes in neural and behavioral indices positively correlated with intervention attendance (Hillman et al., 2014). Relatedly, other randomized control trials in older adults (age= 65-70) yielded similar results. Voelcker-Rehage et al. (2011) demonstrated that a 6 months aerobic training resulted in better performance and more efficient brain functioning during an executive control task compared to members of the control group who received nonaerobic stretching and toning exercises (Voelcker-Rehage, Godde, & Staudinger, 2011). Hence, routinely engaging in physical exercise might alter the allocation of attentional resources and potentially increase speed processing.

A fewer number of studies have relied on computing changes in oscillating power while performing a specific cognitive task. For instance, Wang et al. (2015) were one of the first cross-sectional studies to investigate the relationship between aerobic fitness and neural oscillations during visuospatial attention in young adults. They observed relatively lower beta but higher theta activity during their modified Posner task, a task which allows for the measurement of visuospatial attention and motor preparation (Wang et al., 2015). Importantly, changes in theta power were negatively correlated with the overall mean RTs; that is, those participants who showed higher theta activity might perform better with regard to visual spatial attention. Additionally, others have relied on individual alpha peak frequency (iAPF) because of the positive relationship between iAPF and cognitive functioning. For instance, individuals with higher iAPF have shown shorter RT (Jin et al. 2006), better WM scores (Grandy et al., 2013), and superior memory performance (W. Klimesch, Schimke, & Pfurtscheller, 1993). Gutmann et al., (2015) were the first to associate AF to iAPF in physically active young adults (>30 min/day on >3 days/week for at least two consecutive years before the study). Their work aimed to detect changes on iAPF after a short bout of exhaustive exercise and after a 4-week training on the iAPF (Gutmann et al., 2015). They did not find any changes in iAPF after 4-weeks of steady state exercise training. However, they found that an acute bout of strenuous physical exercise increases iAPF, which might activate mechanisms in the brain, facilitating information processing. These studies reveal the nuances of the time-frequency domain as a technique to measure the neural correlates associated with aerobic fitness and cognitive functions.

1.1.2 Exercise-induced molecular changes

Animal models have been essential for the understanding of the behavioral, molecular, and neurobiological benefits that physical exercise entail (Cassilhas et al., 2016). It allowed for the discovery of a protein called brain-derived neurotrophic factor (BDNF), a member of the neurotrophin family of growth factors, and one of the strongest candidates for bridging the gap between exercise and neurogenesis (i.e., the generation of new neurons) (Cotman and Berchtold 2002; for review see Hillman, Erickson, and Kramer 2008). Along with other neurotrophins, BDNF brings about a cascade of biochemical interactions that not only preserve neurons but also are essential for neurogenesis, specifically in the hippocampus – the brain region involved in learning and memory and is crucial for cognitive functioning. Many rodent studies have shown the exercise-related effects in the brain. For example, when mice were allowed to engage in wheel running voluntarily, it led to an increase in the rate of neurogenesis, specifically in the dentate gyrus after only a few days of physical exercise (Kronenberg et al., 2006; Marlatt, Potter, Lucassen, & van Praag, 2012). Such studies imply that aerobic training in mice may improve cognitive functioning due to augmented neurogenesis, which leads to enhanced learning and memory performance (P. Z. Liu & Nusslock, 2018).

Microelectrodes and local field potential (LFP) recordings can capture electrophysiological changes during exercise in rodents. Li and colleagues (2008) used a 30-minute treadmill running paradigm at 13 m/min and found an increase in theta (6 – 10 Hz) power together with a higher heart rate (R-R interval - electrocardiogram), which reversed when rodents stopped. They concluded that the cerebral cortex activates along with the autonomic system during running (Li, Kuo, Hsieh, & Yang, 2008). Other rodent studies examining the LFP patterns during PE have also found that the hippocampal theta is consistently present during wheel (involuntary PE) and treadmill (voluntary PE) running (Li, Kuo, Yen, Tsai, & Yang, 2014). Additionally, it has been demonstrated how, during theta band activity, the hippocampus is bathed in an increasing concentration of acetylcholine that is believed to facilitate plasticity (Giocomo & Hasselmo, 2007). Theta activity has also been shown to organize hippocampal neurons into sequential activity patterns that are later repeated during subsequent behaviors, reinforcing the synapses between neurons to support subsequent required memory for a particular event. These findings suggest that the exercise-induced sustained theta oscillations may specifically enhance performance on tasks that depend on hippocampal-prefrontal interactions.

Even though it is more challenging to study exercise-related neurogenesis in humans, some studies have suggested that physical exercise does lead to neurogenesis (Lin et al., 2018). This has been accomplished by associating the size of the hippocampus with behavioral performance, where larger hippocampi were associated with improvements in memory in older adults who exercise compared to those who lived a sedentary life (K. I. Erickson et al., 2011). In young adults (19 to 29 years), Hwang et al., (2017) demonstrated that higher levels of VO_2max performed better on a computerized cognitive task assessing sustained attention and WM.

Higher fit subjects had faster response times during a selective attention task as well as shorter memory retrieval and better accuracy during a working memory task (Hwang, Castelli, & Gonzalez-Lima, 2017). BDNF was a moderator of the effect of VO_2max on WM.

In conclusion, physical exercise appears to have a beneficial influence on the neural networks that support several cognitive functions, such as working memory and attention. In particular, we were interested in measuring the impact of a controlled exercise intervention in sedentary young adults to assess the relationship between improvements in cardiovascular fitness, memory performance, and changes in EEG spectral power during visual working memory and visual attention task. For the remaining part of this chapter, I will expand on working memory and attention, from definitions and the different paradigms that can be implemented to study their underlying neural mechanisms to the experiments that have already been published.

1.2 Framework for working memory

WM is defined as the ability to temporarily store and manipulate information in order to guide behavior with information that is not present in the environment (D'Esposito et al., 1995; Eriksson, Vogel, Lansner, Bergström, & Nyberg, 2015). The significance of WM to overall cognitive function has led to several different definitions and models concerning the organization of human memory. From Baddeley and Hitch's multicomponent model (A. D. Baddeley & Hitch, 1974), to more recent state-based models that assume that the allocation of attention to internal representations motivates the short-term maintenance of memory information (D'Esposito & Bradley R., 2015).

State-based models fall into two categories based on the class of stimuli that denotes the internal representations from which each had separately arisen. The activated long-term memory (LTM) models take into account stimuli already in LTM, such as letters, digits, and words. The sensorimotor level recruitment model takes into account stimuli such as visual colors and orientation, auditory pitches, and tactile vibrational sequences. Despite the differences in recruitment, both state-based theoretical models emphasize the need to allocate attention to mental representation in order to bring them into WM. A common feature of WM theoretical models is that if WM fails, so does the ability to carry out many daily life activities. Hence, it is crucial to continue to explore this particular cognitive function.

Conventionally, the delayed-match-to-sample (DMS) task has been widely used to investigate the different brain substrates of encoding, maintenance, and retrieval sections of WM (Schon, Tinaz, Somers, & Stern, 2008). During such a task, participants are instructed to encode a sample stimulus (e.g., an indoor scene, object, or a word) in WM and maintain it for later recall. The delay period usually lasts for a few seconds, and then participants are prompted to respond whether a second, “probe” stimulus matched the sample(s). There are many different manners of data analysis that can be applied to this task to isolate different aspects of WM and the consequences of attentional prioritization. For instance, one could compare behavioral performance and neural activity from accurately encoded trials vs. ones that were not, or one could add distractions during the maintenance period to measure interference. Inclusively, one could also modify the WM load to study the limiting capacity of WM.

Furthermore, electroencephalography (EEG), particularly event-related potential (ERP) analysis, have provided insight into the neural activity underlying WM by obtaining a time-locked average of the experimental events creating ERP brain waveforms known as components. These ERP components are characterized by a systematically positive or negative voltage deflection. Earlier ERP components (e.g., P1 or P100, N1 or N100, P2, N2) generally relate to exogenous processes (i.e., external factors) generated by physical attributes of the stimulus such as brightness, while later ERP components (e.g., P3 or P300, late positive component (LPC)) relate to endogenous processes associated with the interpretation of the stimulus. Notably, it is the change in amplitude and latency between the different contrasting conditions that can infer the neural processes involved. For example, the P300 is the central-parietal positive ERP component that has been associated with the allocation of attention and memory updating (Polich, 2007; Polich & Kok, 1995), WM capacity (Dong, Reder, Yao, Liu, & Chen, 2015), and has been shown to have an inverse correlation with the amount of WM load (Pratt, Willoughby, & Swick, 2011).

Moreover, work by Pinal and colleagues (2014), manipulated the WM load of a DMS task by having a high load vs. low load condition to investigate the limited capacity of WM. The paradigm consisted of encoding a single domino with either 2-3 dots versus one with 4-5 dots. This study also created a delay manipulation consisting of a short duration (3500ms) and a longer one (6000ms). The objective was to study the time course of brain activity during encoding and retrieval. They observed changes in memory load modulated task performance and yielded variations in frontal lobe activation. Specifically, the P300 amplitude was smaller in the high load condition during both encoding and retrieval, which led them to conclude that WM load might modulate resources for context updating of WM and post-categorization processes (Pinal, Zurrón, & Díaz, 2014). Others have also found this inverse relationship between P300 and WM memory load (Polich, 2007; Pratt et al., 2011).

Apart from ERP analysis, there are other ways to explore the brain's electrical activity. Measuring changes in oscillatory patterns can also give insight because engaging in a specific cognitive process produces changes in the oscillatory EEG background activity and may reflect event-related modulations (Cruz, Burgos, Kilborn, & Evans, 2017). Such oscillatory EEG modulations can be obtained by applying another method known as the time-frequency analysis (TFA), which is characterized by decomposing the EEG signal into two important pieces of information: the power (i.e., amplitude square) and the phase information for each frequency that is time-locked to the events of interest. This method of analysis is believed to shed a different, more insightful level of information about the underlying mechanisms of cognitive functions since information is not being lost in the averaging process (Lopes da Silva, 2013; Scott Makeig, Debener, Onton, & Delorme, 2004). Because EEG oscillatory activity allows stimulated short and long-range brain regions to become temporarily linked (i.e., synchronized), they are thought to carry essential information about cognitive and executive processing (Enriquez-Geppert, Huster, Figge, & Herrmann, 2014; Wolfgang Klimesch & Klimesch, 2017; G Pfurtscheller & Lopes, 1999). Hence, assessing low- and high-frequency band power provides new and dynamic insight into oscillatory brain behavior.

1.2.1 Oscillatory EEG measures associated with working memory

Berger (1930) was the first to introduce the idea that certain events can block or desynchronize the ongoing EEG patterns of 8 – 12Hz rhythm (i.e., alpha waves). He measured alpha oscillatory patterns during eyes-closed resting state compared to eyes-opened condition and noticed an increase in power when eyes were open. This observation led him to suggest that the alpha wave becomes suppressed with visual stimulation reflecting cortical idling. However, its role has since shifted with different studies now suggesting that alpha-band power represents active inhibition processes for task-irrelevant information (for a review see Klimesch, 2012), cortical deactivation (G. Pfurtscheller, Stancák, & Neuper, 1996), and might also be involved in working memory (Roberts, Hsieh, & Ranganath, 2013) and attention (Y. Liu, Bengson, Huang, Mangun, & Ding, 2016). Berger's findings gave rise to many clinical and basic research, which led to the discovery of other slower wave such as, delta (1 – 3Hz), and theta (4 – 8Hz), and faster ones such as beta (13 – 30Hz) and gamma (> 30Hz). Importantly, it was later discovered that the spatial extent of synchrony is dependent on frequency, that is, fast oscillations are destined for local information processing due to their shorter time window for communication. In contrast, slow oscillating neurons (e.g., theta and alpha-band) tend to communicate to broader areas of the brain and can involve many neural groups across widely distributed brain areas (Draguhn & Buzsaki, 2004), such as the frontoparietal network (Wang et al., 2015).

Converging evidence has observed increases in theta-band power and decreases in alpha-band power when memory demands are higher (Wolfgang Klimesch, 1999). Specifically, the magnitude of increased theta-band power is typically proportional to the amount of information maintained in memory, with greater loads and cognitive efforts resulting in higher theta band-power, specifically at frontal sites (Zakrzewska & Brzezicka, 2014). This frontal theta band power is known as the frontal midline theta (fm-theta) and was first introduced by Ishihara and Yoshi (1972). They reported an increased occurrence of EEG fluctuations centering around 6.5 Hz that was maximal over frontal electrodes during 15 different subtests, including simple arithmetic and mental memory. Since then, many studies have related frontal midline theta power increases to successful memory performance (S Hanslmayr et al., 2011), WM load (Jensen, Gelfand, Kounios, & Lisman, 2002), and control processing of WM function (Liang, Hu, & Liu, 2017; Sauseng et al., 2009). Such studies have helped infer about the brain's organization and the coordination of information it processes through synchronized oscillatory activity. However, understanding the specific neural mechanisms that underlie how the brain executes cognitive functions is still unknown.

A study conducted by Roberts and colleges (2013) assessed the neural mechanisms of WM for temporal order (i.e., four items) and spatial information, intending to characterize the neural implementation of WM maintenance processes between temporal and spatial information and how processing of such information might differ. They presented two different tasks, one during temporal trials, where participants maintained the order in which stimuli were presented on the screen, and another during spatial trials, where participants maintained the quadrant of the screen in which each stimulus was presented. They hypothesized that neural oscillations in the theta and alpha range might uniquely contribute to temporal and spatial WM. They found an enhanced left frontal theta power and a greater decrease in posterior alpha power during the maintenance of correct temporal trials compared to correct spatial trials (Roberts et al., 2013). Previous research found similar findings between temporal and visual objects where they demonstrate that theta oscillations are a crucial substrate for temporal organization of information in WM (L.T. Hsieh, Ekstrom, & Ranganath, 2011). Together, these studies demonstrate that oscillatory neural activity provides distinct mechanisms for temporal vs. spatial information in WM.

Additionally, theta band power has shown to be crucial for the control process of WM functions (Liang et al., 2017). Previous studies have found greater frontal midline theta power in conditions with higher needs of cognitive control (Eschmann, Bader, & Mecklinger, 2018; Scharinger, Soutschek, Schubert, & Gerjets, 2017). For instance, a study conducted by Staudigl and colleagues (2010) used a retrieval practice-paradigm, which consisted of 3 blocks (i.e., phases). The study phase consisted of participants memorizing words of either fruit or insects for later retrieval during the test phase (Staudigl, Hanslmayr, & Bäuml, 2010). In between those blocks was the intermediate phase, which consisted of two conditions, (1) in the selective retrieval block, a subset of the previously studied items was presented, while (2) in the reexposure block, the same subset of items was revealed entirely, making it easier for later retrieval at the test phase. They measured and analyzed EEG during the intermediate phase. Their results showed that higher levels of interference from related WM items are indexed by more theta band activity and that successful interference resolution via inhibition causes a reduction in theta amplitude. Thus, theta band activity can serve as a neural marker of the dynamics of interference in selective episodic retrieval. Still, the question remains whether people can filter the irrelevant information with the same capacity if the irrelevant information were in the same or in a different feature domain (i.e., fruits vs. insects or color vs. words).

Moreover, the brain regions associated the most with WM is the prefrontal cortex (PFC). Specifically, sustained activity in the prefrontal neurons during the delay period has been regarded as the neural correlate of memory maintenance. Additionally, it has been proposed that the PFC is crucial in carrying mnemonic information (Fuster & Alexander, 1971). Miller et al. (1996), indicated that detecting a mismatch in the context of WM could also activate the frontal region, particularly the right dorsolateral prefrontal cortex (Miller, Erickson, & Desimone, 1996; Rypma & D'Esposito, 1999). In the next section, I will elaborate on another crucial mechanism that is needed to carry out everyday life activities. Lastly, I will elaborate on how WM and attention might interact.

1.3 Framework for attention

Given the sheer complexity of our internal and external worlds, and the fact that as humans we are constantly flooded by an overload of sensory information, we need a mechanism to help us prioritize and process everything that surrounds us. Attention is that process; it maintains the focus while filtering out extra information to achieve a particular goal. For example, finding a friend at a festival involves: searching for the correct signs and landmarks, navigating through crowds, keeping track of your group, scanning the panorama for their unique colorful outfit – all of which require distinguishing relevant from irrelevant information. Additionally, the attentional system can be perceived as an evolved adaptation due to the limited computing power of the brain necessary to select specific streams of information for further processes.

Formally, it is the fundamental cognitive process needed to successfully navigate our complex and dynamic environment (Broadbent, 1958). Several attention models have compared attention to a filtering system that only permits particular information to get through, acting as a “bottleneck” of information processing in cognition.

Attention has discrete modes of operations. It can be directed exogenously by salient stimuli such as dazzlingly colored or fast-moving items, also known as the “bottom-up” process. Alternatively, it can be engaged endogenously biasing our neural processing to accomplish our objective (i.e., when the goal-driven behavior influences the attentional processes; Luck and Vogel 2013), known as the “top-down” process. Most models of visual attention state that the modulation of visual processing is controlled by a frontoparietal attention network whose top-down influences alter the gain of signal in multiple visual areas (Y. Liu et al., 2016). Neuroimaging studies have shown how in visual attention, the frontoparietal attention control areas are thought to issue a signal to selectively bias sensory neurons to both facilitate behavior relevant information and suppress distractions.

A classic paradigm used to study the underlying brain mechanisms of selective attention is the Stroop task (Stroop 1935). During such task, participants are presented either with a written color word (e.g., “blue”) with the same colored ink as the written word (congruent trials), or one printed with the color word written on a different colored ink (incongruent trials). Modifications of this task exist where participants must selectively attend to either the written color word or the color of the background. For example, in Kiyonaga et al. (2014) study, instead of having the word “red” in blue ink, they presented the word “red” written in white over a blue color patch. Regardless of the presentation style, the classical behavioral outcome was that participants are significantly more accurate and respond faster on congruent trials compared to incongruent ones; this is known as the “incongruency effect.” By only attending to color information and ignoring the autonomic nature of the written color words, this performance outcome is thought to be due to costly attentional filtering of the task-irrelevant color information. Measuring neural correlates, such as ERPs and time-frequency representations (TFRs) during this task, has helped gather information about the mechanisms involved in attentional processes.

Jiang et al. (2015), used a masked Stroop priming version to investigate how semantic and response conflict at different levels of conflict awareness are processed in the human brain. They dissociated semantic and response conflict in the same task by using four-color words and four colored patches with a four-to-two mapping between the target patch (i.e., colors) and the required response (i.e., left and right index fingers). Also, they presented the “prime” (i.e., color distraction) word either for a short duration (29ms) or a longer one (143ms), creating high and low conflict trials. They found that the mid-frontal theta power was enhanced during both response and semantic conflict (Jiang, Zhang, & van Gaal, 2015), and alpha power was enhanced only during the processing of semantic conflict. This midline frontal theta may be a reflection of general conflict detection and a monitoring mechanism of the medial frontal cortex, while decreases in parietal alpha power were linked to an inhibitory mechanism that gates and filters sensory information. Its decrease during attentional conflict may reflect the refocusing of attention or increase in alertness after conflict to amplify the task-related stimuli feature, potentially minimizing subsequent conflict.

Lesions studies in both humans and animals have established the involvement of the frontoparietal network in attention, where the frontal-parietal network sends control signals that modulate processing relevant sensory regions. Liu et al. (2016) correlated single-trial EEG alpha power with blood-oxygen-level-dependent (BOLD) signal to investigate the relation between activity in attention control areas and attention-related modulation of posterior alpha activity. They were interested in identifying the source responsible for the direct interaction between the frontoparietal control system and visual cortical activity during anticipatory attention. They found that alpha decreased contralateral to the cued hemifield, and was associated with BOLD decreases in the sensorimotor cortex and the default mode network. This study fits well with the "push-pull" mechanism that has been observed in past studies where they involved attention to multiple sensory modalities (Wolfgang Klimesch, Sauseng, & Hanslmayr, 2007; Y. Liu et al., 2016).

1.3.1 Working memory and attention as a shared mechanism

Traditionally, WM and attention used to be conceptualized as a separate cognitive construct. WM was explained as an internal process, whereas attention was described as selectively focusing on a limited amount of external information (Broadbent, 1958). Nowadays, it is considered that these processes are not so readily dissociated, and the demands on WM and attention reciprocally influence one another (Gazzaley & Nobre, 2012) and engage many of the same brain regions (Jerde, Merriam, Riggall, Hedges, & Curtis, 2012). Kiyonaga and Egner (2014) tested this notion in a laboratory setting. Their interest was whether holding a color-word in WM could produce an "interference effect" in a color-discrimination task, as the one observed in the classic Stroop task. In their behavioral experiments, they showed how internally maintaining a color word that was incongruent to an external color patch drastically slowed the naming of that patch, comparable to when the word was simultaneously attended externally. Such studies have supported the hypothesis that WM is internally directed attention, operating over representations of items that are no longer present in the environment (i.e., endogenously activated) in much the same way as attention to the external environment (i.e., exogenously activated) (Chen, Wang, Wang, Tang, & Zhang, 2017; Kiyonaga & Egner, 2014). Despite the decades of research investigating the interplay between working memory and attention, the precise link between them remains unknown.

Another way the interaction between WM and attention are studied in a laboratory setting is by measuring the neural correlates during a dual-task paradigm. Pratt and colleagues (2011) conducted an experiment where participants performed a flanker task either alone or in combination with a Sternberg task. A flanker task is a set of response inhibition tests used to assess the ability to suppress inappropriate responses in a particular context, and a Sternberg task provides a measure of processing speed and WM retrieval speed. Their results showed a decrease in P300 during the dual-task paradigm indicating the sensitive nature of the P300 to task demands, decreasing during incongruent trials when working memory load increased. That is, the interference from the incongruent flankers was more difficult to suppress when the dual-task taxed WM**.** (Pratt et al., 2011). Particularly, larger amplitudes and earlier latencies are observed during tasks with easy versus difficult target discrimination or during low versus high task demands. These findings show the sensitivity of the P300 component to decrease in amplitude during tasks where more cognitive resources are needed to tackle harder trials. Hence, reflecting the brain's greater need for resources to solve the task requiring both attention and WM vs. only attention for the Flanker task alone.

The DMS task, as the Stroop task, can also be modified. In this case, the DMS task can be manipulated to cause interference or to facilitate the retrieval of an item held in working memory, as we did for Experiment 3 (see Chapter 4). Similarly, Eschemann et al. (2018) measured theta power during a DMS and a Stroop task. They aimed to investigate whether different forms of fm-theta activity are recruited in two cognitive control tasks that are characterized by either proactive (DMS task) or reactive (Stroop task) control demands. In their study, both tasks had two conditions with a low and high need for control. Their findings stated that frontal midline theta acted functionally different depending on the task requirements, where greater fm-theta was observed for the conditions with a higher need for control.

Working memory and attention use similar brain regions. Ferodes et al. (2011) demonstrated the strength of the top-down input from the dorsolateral prefrontal cortex to posterior brain areas using a combined TMS-fMRI study. His findings confirmed the importance of functional connectivity between the two areas in promoting the successful maintenance of task-relevant items during the WM maintenance phase. They concluded that the dorsolateral prefrontal cortex (DLPC) ensures successful maintenance of visual WM stimuli (faces or houses) in the presence of distraction.

1.4 Aim of thesis

The primary aim of this dissertation was to investigate the exercise-induced electroencephalographic (EEG) oscillatory effects in sedentary young adults while performing a visual WM and a visual attention task. To achieve this, we explored the neural mechanisms underlying visual working memory (WM), visual attention, and how these two processes interact (e.g., attentional conflict). Examining the brain's oscillatory EEG activity in the context of specific paradigms will allow for a more global understanding of cognitive processes to infer how they might be modulated by a physical exercise regimen (i.e., Chapter 3). Accordingly, we addressed this question by deploying several different tasks, from a delayed-matched-to sample (DMS) WM and a visual attention search (VAS) task (i.e., Chapter 2 and 3) to a dual-paradigm task where both WM and attention processes are meant to interact (i.e., Chapter 4).

For decades, these two cognitive processes have been among the most studied in cognitive neuroscience. Since 1970 the number of studies published on WM and attention has dramatically increased (Ku, 2018). Despite these efforts, the neural mechanisms underlying these cognitive functions are still under debate, especially in the time-frequency domain. For instance, there is a discrepancy in the modulation of theta-band power and its association with working memory. Some researchers argue that theta-band power increases with the retrieval of an item in WM, while others associate the retrieval to a decrease in theta oscillatory activity.

The current work investigates the oscillatory EEG activity contributing to WM, visual attention, and cognitive interference by using time-frequency analysis to decompose the EEG signal into oscillatory EEG patterns. This dissertation includes three chapters; the first two are derived from a longitudinal study measuring the impact of physical exercise on WM and attention-related neural oscillations in young adults. Specifically, we investigated separate outcomes at the theta (5-7Hz) and alpha (9-12Hz) range because of their relationship with working memory and attention, respectively. Chapter 2 focuses on the modulatory effects of the oscillatory EEG activity between the DMS working memory task, which requires maintaining an item in working memory for subsequent discrimination, and our visual attention search task, where no maintenance demands were required. From previous literature, we hypothesized that frontal theta power would be associated with memory performance in the WM task, while posterior alpha power would be associated with visual attention performance. We also hypothesized that the DMS task would generate a greater increase in theta power and a greater decrease in alpha power, reflecting a larger need for cognitive resources compared to the ones needed for the VAS task. Our results highlight how different cognitive functions reflect distinct neural activity on the task being accomplished.

Previous cross-sectional studies performed in humans of various age groups have concluded that engaging in physical exercise increases one’s aerobic fitness and, in turn, improves memory ability and efficiency of attentional processes (Kirk I Erickson et al., 2011; Sousa et al., 2018b). Chapter 3 investigates whether physical exercise would affect attention, WM performance, and potential neural correlates (i.e., modulation of theta and alpha-band power) in the context of a 4-month exercise intervention. To the best of our knowledge, this is the first controlled longitudinal exercise study performed in sedentary young adults designed to report the impact of physical exercise training on cognitive functions from a time-frequency perspective (Chaire et al., 2020).

In Chapter 4, we further expand our knowledge of the mechanisms underlying WM and attention by combining the two in a novel dual-task experimental paradigm that allows studying the substantial interplay between them (i.e., attentional conflict). Specifically, we are interested in understanding how external information might interfere with the maintenance of an item being held in WM or might inclusively facilitate later retrieval (i.e., when the internal representation matches the external information, reinforcing the WM item). In a recent study, Zhao (2014) and colleagues studied how WM and attention interact. In their research, they manipulated the type and the amount of WM load and showed that greater WM load interfered with the performance on a selective attention task (Zhao et al., 2014). Other studies have compared how selective attention may bias WM (Doherty et al., 2018; van den Berg, Geib, San Martín, & Woldorff, 2018). However, to my knowledge, there is no EEG study that contrasts how different characterizing features of the distraction (i.e., color- versus number- words) might affect retrieval. We investigated the behavioral and neural correlates of distinct types of attentional resolution that WM retrieval might be affected by shifting our attention from an internal representation to an external color-discrimination task presented during the maintenance phase. We hypothesized that if the internal representation and external color-discrimination item matches, it would facilitate retrieval, which would reflect on the behavioral performance as well as an increase in frontal-midline theta.

2. Theta and alpha power related to visual working memory and visual attention mechanisms

2.1 Introduction

Electroencephalography (EEG) has become the standard tool to study electrical brain activity in humans noninvasively. This technique has helped uncover the neural correlates of behavior and cognition, particularly in the investigation of real-time cognitive processes. EEG can detect and amplify the brain's bioelectrical potentials through electrodes placed on the scalp's surface. Neural mechanisms of specific cognitive processes have been studied by measuring changes in time-frequency representation (TFRs), which are obtained by decomposing the EEG signal into two essential pieces of information: the power (i.e., amplitude squared) and the phase information for each frequency that is time-locked to the events of interest. This method is called time-frequency analysis (TFA), and it allows contrasting the frequency band power between different tasks. This information can infer the neural mechanism required to accomplish a specific task. Despite EEG's poor spatial resolution compared to other techniques, such as fMRI, EEG has high time specificity, making it an excellent method to benefit the understanding of the underlying neural mechanisms in specific cognitive processes. In particular, we are interested in linking the timing of cognitive processes to working memory and attention-related oscillations by measuring the theta- and alpha band power during delayed-matched to sample (DMS) task and a visual attention search (VAS) task.

Neural network communication is a product of the synchronized neural activity, which can be measured in the high- and low-frequency range by scalp recorded EEG. This broad range of oscillatory activity at different frequency bands have been associated with distinct physiological and cognitive functions (Draguhn & Buzsaki, 2004; Hari & Parkkonen, 2015). Recent studies suggest that frequency-specific oscillatory activity, such as theta- and alpha-band, represent distinct cortical operations for performing and maintaining information during attention (Chen et al., 2017), memory encoding (Greenberg, Burke, Haque, Kahana, & Zaghloul, 2015), maintenance and retrieval of WM items (Düzel, Penny, & Burgess, 2010). Theta oscillations have received substantial attention from researchers, including studies of hippocampal theta in rodents (for review, see Buzasaki, 2002) and cortical theta in humans (Mitchell, McNaughton, Flanagan, & Kirk, 2008). Specifically, in humans, frontal midline theta (fm-theta; typically 4 – 8Hz) has been implicated in WM processes (Yamagishi, Callan, Anderson, & Kawato, 2008), and has been shown to increase at frontal sites with increasing task difficulty (Gevins, Smith, McEvoy, & Yu, 1997; Gundel & Wilson, 1992), with higher WM load (Jensen et al., 2002), and with successful memory performance (Fuentemilla, Penny, Cashdollar, Bunzeck, & Düzel, 2010; Klimesch, W., Doppelmayer, M., Russegger, M., Pachinger, 1996). Alpha band power on the other hand generally decreases (i.e., desynchronization) in power reflecting an inverse relation to the amount of cortical resources allocated to the task at hand (Babiloni et al., 2010; Gevins et al., 1997; Haegens, Nácher, Luna, Romo, & Jensen, 2011; Wolfgang Klimesch et al., 2007).

To further understand the underlying mechanisms of WM and attention, we deployed two cognitive tasks: the delayed match-to-sample (DMS) task, which required mnemonic discrimination of similar visual stimuli, akin to pattern separation, and the visual-attention search (VAS) task, which requires detecting the presence of a specific object (i.e., target) in an image. The main difference between these tasks is that the DMS task requires maintaining an item or an indoor scene in working memory for later (5000ms) discrimination (i.e., match/non-match), while the VAS does not require any memorization or discrimination effort between trials. Importantly, the WM task was developed to asses the dentate gyrus (DG) function, a subsection of the hippocampus capable of resolving mnemonic interference by using pattern separation – the ability to independently represent and store similar experiences (Leal & Yassa, 2018).

Certain external factors, such as engaging in physical exercise, can increase the efficiency of mnemonic discrimination. A human cross-sectional study in young adults studied the relationship between aerobic fitness and mnemonic discrimination. They found that higher fitness group had better discrimination performance for moderate interference levels than the lower fit group, they called it “memory flexibility”– a selective improvement in the ability to overcome moderate levels of mnemonic interference. Also, aerobic fitness levels were positively associated with discrimination performance (Suwabe et al., 2017). Additionally, rodent exercise studies have established the importance of physical movement on the hippocampus and the characteristics of the theta activity generated during spatial navigation (Basso & Suzuki, 2017) and episodic memory (Buzsáki & Moser, 2013). Together these studies add to the growing evidence linking the benefits of physical exercise to hippocampal related memory.

Typically, working memory is associated with increases in fm-theta activity. However, other studies have measured intracranial EEG (iEEG) and have associated decreases in theta power to memory performance during encoding (Greenberg et al., 2015), and during the maintenance phase of a WM task (Brzezicka, Kamiński, & Rutishauser, 2019). Zakrzewska and colleagues (2014) recorded iEEG from13 participants performing a WM Sternberg task. They were interested in the modulation of theta in three different brain areas. They found increases in theta power for the hippocampus and dorsal ACC (dACC) and decreases in theta power at the dorsolateral prefrontal cortex (DLPFC). The decreases in theta power at the DLPFC were predictive of behavioral memory performance; that is, participants who had a relatively more significant decrease in theta power were faster at accessing WM. This finding led them to conclude that only the DLPFC has a role in the maintenance of information and that it is associated with a decrease in theta power (Brzezicka, Kamiński, Reed, et al., 2019). Such studies represent the discrepancy that exists over theta power activity during a DMS task. Hence, it is essential to measure further time-frequency representations (TFRs) such as theta power during different cognitive tasks.

To study visual attention, some researchers have relied on the modulation of alpha-band (typically 8-12 Hz) activity, typically used as an index of general and selective attention (van Den Berg, Appelbaum, Clark, Lorist, & Woldorff, 2016). Also, alpha-band power is the most prominent frequency-band found in humans, and many associates it with cortico-cortical and thalamo-cortical networks. In addition to aiding in the understanding of attentional processes (L.T. Hsieh et al., 2011; Jensen et al., 2002; Wolfgang Klimesch, 2012), alpha power has also been observed during several other cognitive functions such as perception (Benwell et al., 2017; VanRullen, 2016), and memory (Jensen, Bonnefond, & VanRullen, 2012; Wolfgang Klimesch, 1999; Wolfgang Klimesch & Klimesch, 2017). Decreases in alpha band power potentially arise by gating the communication from local to other cortical regions (Fries, 2015).

Previous research has relied on implementing different experimental paradigms to understand the neural correlates of WM and attention. However, despite the previous research mentioned, the interpretation of such processes' neural mechanisms is not entirely straightforward, mainly because the relationship between neural oscillations and cognitive processes is uncertain. Nonetheless, continuing to measure and contrast oscillatory activity during different paradigms that elicit specific cognitive demands will provide better inference about these critical cognitive processes. We aimed to investigate the modulations of fm-theta and posterior alpha activity that we recruited during paradigms that recruit distinct cognitive mechanisms, that is, either holding an item in WM or not. Based on previous findings, we predicted that theta power would associate with the DMS task, whereas alpha power would associate with the VAS task. Also, given that the DMS task requires more considerable efforts to accomplish the task then (1) theta power should present more significant effects at frontal electrodes (i.e., a greater increase in fm-theta), and (2) there should be a more prominent decrease in alpha power at posterior sites for the DMS task compared to the VAS task.

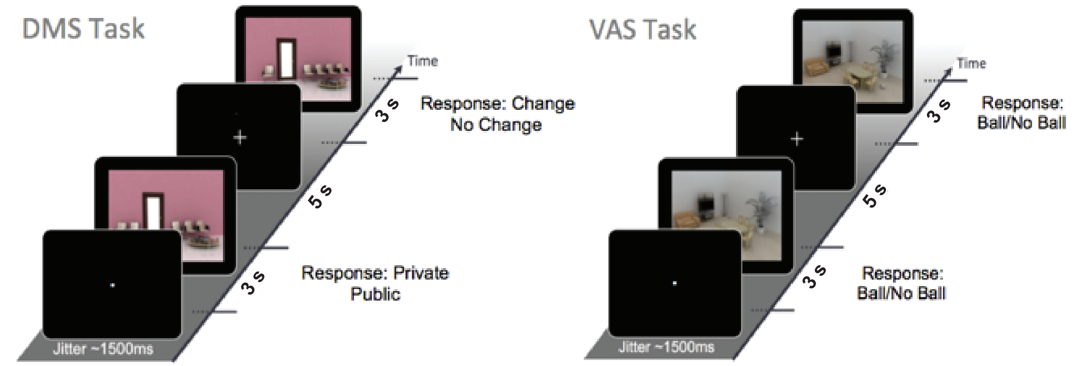
2.2 Methods

2.2.1 Participants

Forty-three healthy, sedentary young adults (age range: 19 to 34 years, mean age: 25.33 ± 3.62 years, 23 females) were recruited for the study; 3 participants were excluded because of technical issues with the EEG recording, leaving a total of 40 participants. All subjects reported no signs of neurological or psychiatric illness and had normal or corrected-to-normal vision. Subjects received monetary compensation for their participation, and the experiment was carried out in accordance with the guidelines of the ethics committee of the Faculty of Medicine from Otto von Guericke University Magdeburg.

2.2.4 Task and study design

The experimental paradigm can be shown in Figure 1. Participants performed 120 trials of a DMS WM task (Figure 1A) and 60 trials of a VAS task (Figure 1B). The trials from both tasks were divided into 4 and 2 blocks, respectively, which were presented in a random sequence. During the DMS task, a sample stimulus and a probe stimulus were presented in succession for 3 sec, separated by a 5-sec delay (i.e., the maintenance phase). Subjects were instructed to answer as quickly as possible whether the sample stimulus was a public or a private place and to spend the remaining time memorizing the image. The maintenance phase is critical for sustaining the WM item and is susceptible to interference from other external factors. Afterwards participants then had to decide whether the probe image was identical to (i.e., repeat) or a modification (i.e., lure) of the sample image. All of the DMS stimuli were computer-generated indoor scenes, including 50% lure images. During the VAS task, participants were shown a similar indoor scene and were instructed to detect whether a target (i.e., spherical object) was present. The background image for the VAS remained the same throughout the different blocks, so neither encoding nor maintenance was required for this task.



A. Delayed Match-to-Sample Task B. Visual-Attention Search Task

Figure 1 The working-memory experimental paradigm is a DMS task of 120 trials (A). A sample stimulus (encoding) and a probe stimulus (retrieval) were presented with a stimulus delay of 5 sec. Participants were instructed to respond to whether the sample stimulus was either private or public and to memorize the image. When the probe appeared, small changes in the image (lure items) needed to be detected. The attention experimental paradigm is a VAS task of 60 trials (B). During this task, subjects had to detect whether a small ball was present in the image. The background image remained the same throughout the visual-attention paradigm.

2.2.5 Data acquisition and processing

Continuous electroencephalogram (EEG) was acquired from 32 active electrodes mounted in an elastic cap (Brain Products GmbH, Germany) with a bandpass filter of 0.1–250 Hz and digitized at a rate of 500 Hz. Electrodes were placed according to the international 10–20 system. From the 32 electrodes, 2 electrodes were positioned at the external ocular canthi of each eye, and a vertical electrooculography (EOG) was placed below the left eye to measure horizontal and vertical eye movement, respectively. The left mastoid was used as the online reference, and all electrode impedances were kept below 5 $k\Omega$. The skin under the electrodes was slightly abraded with a blunt needle, which was used to fill each electrode with electrolyte gel. MATLAB (MATLAB and Statistics Toolbox Release, 2012b, The MathWorks, Inc., Natick, Massachusetts, United States) and its EEGLAB toolbox (Delorme & Makeig, 2004) were used for offline EEG data processing. The continuous EEG data were high-pass filtered at 0.1 Hz, low-pass filtered at 50 Hz, and rereferenced to the right mastoid. The data were segmented into 13-sec epochs, including 1-sec pre stimulus as the baseline and 1-sec post trial. Next, independent component analysis (ICA) was performed to correct for eye-related artifacts and excessive muscle activity. In addition, all trials were visually inspected, and those containing additional artifacts were excluded from further analysis. Participants included in the data analysis had fewer than 80% of their trials excluded after artifact correction.

2.2.6 Time-Frequency Analysis (TFA)

Event-related spectral perturbation (ERSP) was computed using algorithms from EEGLAB (Delorme & Makeig, 2004) and custom MATLAB scripts. EEGLAB is a great MATLAB toolbox with an abundant set of built-in functions needed for EEG data analysis. Artifact-free data comprising 13-sec segments were used for TFA. Trial-by-trial event-related spectral power was calculated using Hamming window tapering with 5 cycles and 100 logarithmically spaced frequencies ranging from 3 to 20Hz. For each frequency, event-related spectrum power at each time-frequency point was divided by the average spectral power in the prestimulus baseline period at the same frequency. Subsequently, these measures were normalized by taking the log value of the percentage of baseline activity ($ERSP_{\%}$) (Grandchamp & Delorme, 2011). By definition, the unit of $ERSP_{log}$ is the decibel (dB), which is commonly used in the literature (Cohen & Donner, 2013; Jiang, Zhang, & Van Gaal, 2015; S Makeig, 1993).

The mean ERSPs were calculated for two frequency bands of interest: theta (5 – 7Hz) and alpha (9 – 12Hz). These bands were chosen because of their involvement in working memory (Jacobs, Hwang, Curran, & Kahana, 2006) and visuospatial attention with the frontoparietal network (Wang et al., 2015). Because of frequency smearing after time-frequency decomposition, we used a width slightly different from the typically defined theta (4 – 8Hz) and alpha (8 – 12Hz) frequency bands (Wolfgang Klimesch, 1996). Narrower frequency bands were chosen to better characterize the changes in neural oscillations at those frequency bands (L.T. Hsieh et al., 2011). Additionally, electrodes were grouped into two different clusters with three electrodes each: frontal cluster (F3, Fz, F4) and posterior cluster (P3, Pz, P4). For the DMS task, the encoding, maintenance, and retrieval phases can be separated to extract important temporal information (see Figure 2A); however, our statistical analysis will only focus on the maintenance and retrieval period in order to decrease multiple comparison problems. Power estimates from the frontal and posterior clusters were averaged across a section spanning the frequency band (see Figure 2A & 2B) and the time periods of interest: maintenance (4500ms to 7500ms) and retrieval (8000ms to 11000ms). Then, they were subjected to statistical analysis.

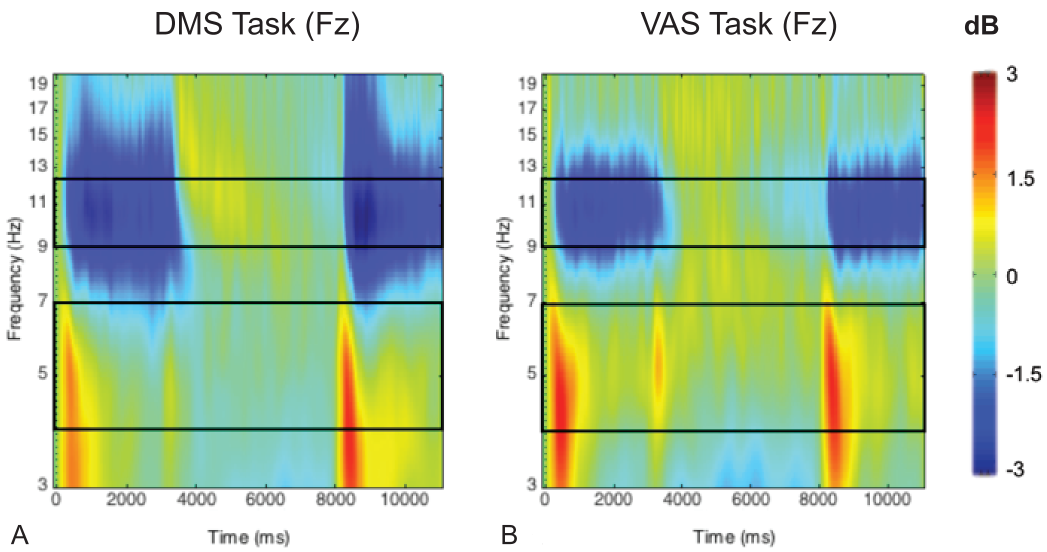


Figure 2 Group-averaged time-frequency 2D spectra (in dB) during a DMS task (A) and a VAS task (B) for the Fz electrode. Time (in ms) is indicated on the x-axis, with 0ms defined as the onset of the sample stimuli and 8000ms for the onset of the probe stimuli. Frequency (in Hz) is shown on the y-axis and is logarithmically scaled from 3 to 20 Hz. The event-related desynchronization (ERD) corresponds to negative values and is shown in blue, while the event-related synchronization (ERS) is shown in red.

2.2.7 Statistical analysis and Correlations

To examine the behavioral effects of the DMS and VAS task, we first calculated the mean accuracy (correct trials divided by the total amount of trials), the response times (RT), and the variability (SD) for each task separately (see Table 1). A paired t-test was performed for accuracy and RT between the tasks to establish the difficulty level. In addition, for the DMS task, we obtained the corrected hit rate (CHR = hits – false alarms), which takes into account both the hits (i.e., correctly responded repeats) and the lures via the false alarm values (i.e., false alarm = 1 – lure rate). The CHR takes into consideration any response biasing towards matched trials (i.e., hits), by compensating for those participants who tend to use the matched button (i.e., no change) at a higher rate than the non-match button. As for the VAS task, we averaged both target-present and target-absent trials into one condition. We considered performance values that were higher than 2.2 SDs from the mean as outliers, and these were excluded from the statistical analysis. All statistical analyses were performed using the statistical software SPSS (IBM Corps., IBM SPSS Statistics, V24, Armonk, NY, USA., 2016).

To assess the neuronal processing behind WM and attention, we explicitly focused our statistical analyses on oscillatory power data that was time-locked to the probe sample (i.e., retrieval). Further, we extracted the mean theta-band (4 – 7Hz) power and the alpha-band power (9 – 12Hz) from midline-frontal and parietal electrodes, separately. Power estimates from the midline regions were then averaged across a section spanning the theta and alpha band from a time window of interest (8000 – 11000ms) and then subjected to statistical analysis (Nigbur et al., 2012). Two rmANOVAs were performed for each frequency band separately by *task* (DMS, VAS) and *cluster* (frontal including F3/4, Fz, and posterior including P3/4, Pz) as within-subject factors. When significant interactions were found with rmANOVA, post hoc independent t-tests were conducted. All alpha levels for significance were set as .05.

To examine how different cognitive process engages, we estimated bivariate (Pearson) correlations between behavioral performance and theta and alpha-band power separately. These correlations were estimated during the maintenance phase of the DMS task to corroborate that theta power is associated with memory performance. Correlations for alpha-band power were estimated during the VAS task and behavioral performance.

2.3 Results

2.3.1 Behavior data

Behavioral performance data shows that the response time (ms) for the DMS task was 1507 for Hits and 1319 for Lures. For the VAS task, the response time was 1204 for target and 1237 when the target was absent (Table 1). The mean accuracy for the DMS was 0.86 for hit and 0.82 for lure. For the VAS task, the mean accuracy was 0.93 for target and 0.90 when the target was absent (Table 1). RmANOVA was performed for response time with 2 within factors: task (DMS, VAS) and condition (2 levels – DMS: hits, lures and VAS: target-present, target-absent), and revealed a main effect of *task* (F (1,36) = 34.055, *p* = .000), a main effect of *condition* (F (1,36) = 14.362, *p* = .001), and in interaction (F (1,36) = 28.153, *p* = .000). Further post hoc analysis showed a significant RT difference between Hits and Lures (t (1,38) = 4.774, *p* = .000) and between Target-present and Target-absent (t (1,37) = -3.308, *p* = .002). As for accuracy there was a significant difference between hits and lures (t (1,38) = 2.056, *p* = .042) and between target-present and target-absent (t (1,37) = 4.167, *p* = .002).

Table 1 Behavioral performance data. Mean accuracy and response times (± standard deviation) for the DMS (i.e., hits and lures) and the VAS (i.e., target-present and target-absent) task. Included are the p-values for the difference in performance within the two different tasks.

	DMS Task			**VAS Task**		
	Hit	Lure	*p*-value	Target	No Target	*p* -value
RT (ms)	1507 (292)	1319 (225)	.000	1204 (229)	1237 (243)	.000
Accuracy	.86 (.07)	.82 (.09)	.042	.93 (.03)	.90 (.04)	.002

For accuracy, we took into consideration the CHR (hits – false alarms) for the DMS task and the mean accuracy rate for both target-present and absent trials for the VAS task. A t-test was performed between the accuracy of the two tasks and revealed a significant difference (t (1,35) = -11.955, *p* = .000), corroborating that the working memory was, in fact, the harder task (CHR = 0.67 vs. Avg.: 0.92).

2.3.3 Theta and alpha power dynamics during a DMS and a VAS task

Changes in frequency-specific EEG power have been found to underlie changes in neuronal synchrony. For theta band, we found a main effect for task (F (1,39) = 6.166, *p* = .017) and a main effect for cluster (F (1,39) = 14.089, *p* = .416), but no interaction (F (1,39) = 0.016, *p* = .899). This suggests that a decrease in power was produced for the DMS task (frontal: -.12 dB and posterior: -.24 dB), and an increase in theta-band power was observed for the VAS task (frontal: .32 dB and posterior: .19 dB). Our main effect for task goes along with Greenberg's (2015) research stating that a broad decrease in theta power associates with memory formation and that it could be related to encoding mechanisms that benefit later retrieval (Greenberg et al., 2015; Simon Hanslmayr & Staudigl, 2014).

As for alpha-band activity, there was a main effect for task (F (1,39) = 6.084, *p* = .005) and a main effect for cluster (F (1,39) = 56.130, *p* = .000), but no interaction effect (F (1,39) = 0.042, *p* = .733). This indicates that both tasks had similar alpha-band power distributions, hence the lack of interaction. Although, we observed a greater decrease in power for the DMS task (i.e., the more demanding task), indicative of the general attentional demands, filtering out unnecessary information, and determining the brain’s capacity to process information (Fuentemilla *et al.*, 2010; Klimesch, 2012). There was a difference in distribution between the anterior and posterior clusters. We found a greater decrease in alpha-band power compared to the frontal electrodes, which agrees with the literature stating that alpha activity is more prominent at posterior electrodes. This can be better appreciated in Figure 3, which shows a topography plot indicating similarity in the activity pattern of alpha, although with a different intensity. That is, greater alpha power predominated at posterior electrodes during different types of cognitive processes, whether mnemonic discrimination takes place or not.

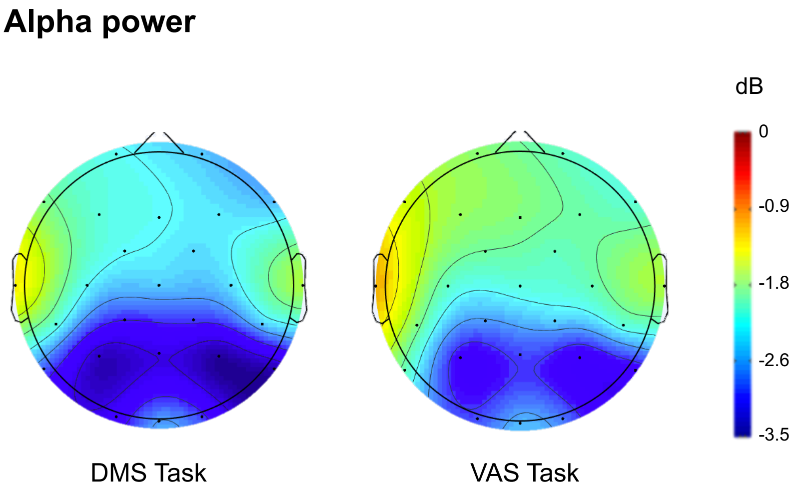


Figure 3 Topographical plots are showing similar patterns of distribution spanning from 8000ms to 11000ms. Specifically, it shows the alpha band power distribution during the retrieval section of the DMS task (left panel) and the VAS task (right panel).

2.3.4 Frontal midline theta, posterior alpha power, and behavioral performance

To test WM and the internal brain processes, we decided to estimate the correlation between fm-theta and behavioral performance during the maintenance phase, during which items are being internally held for later retrieval. We wanted to compare whether holding a representation in WM relates to theta-band power, specifically for the fm-theta. Pearson's correlation analysis was performed on the CHR and fm-theta, given its association with memory performance (*r* = 0.343; *p* = .040; see Figure 4). Figure 4A shows a negative correlation, where better performance was associated with a greater decrease in theta power relative to the baseline. Furthermore, fm-theta also correlated positively with response time, where faster detection of a lure was also associated with a more significant decrease in theta power during the maintenance phase (*r* = 0.431; *p* = .006; see Figure 4B). We did not observe correlations between behavioral performance and theta power at parietal sites or central electrodes (r < 0.094; *p* > .870). As expected, only the frontal theta power associated with cognitive performance.

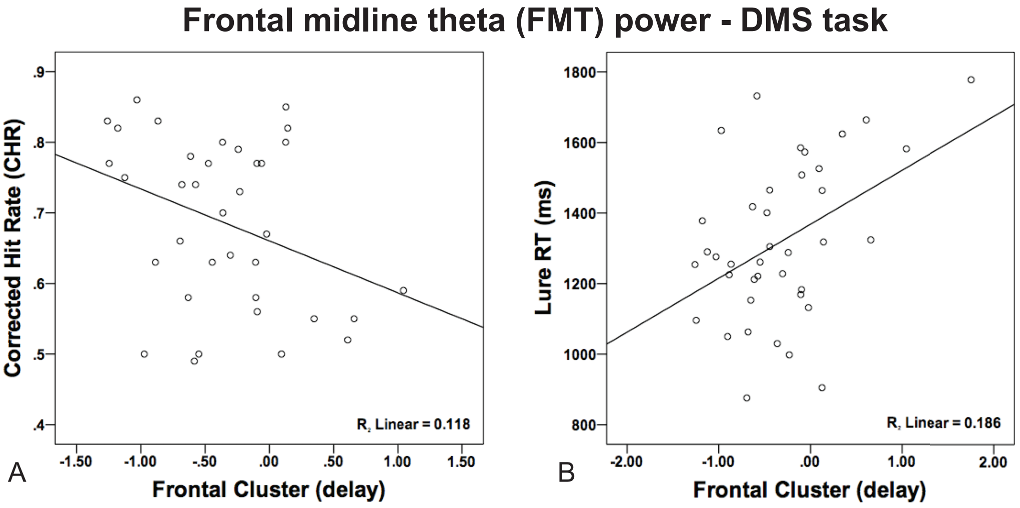


Figure 4 Correlation between frontal midline theta (fm-theta) power and accuracy performance (corrected hit rate) during the maintenance phase (A). Correlation between frontal midline theta and response time (lure stimuli) during the maintenance phase (B). These correlations show that a decrease in fm-theta led to better accuracy and RT during the delay phase.

To test attention (i.e., the external brain processes), we focused on obtaining the estimate of the VAS task during the target search performance. We found a positive correlation between alpha power and the target-absent condition (r = .333, *p* = .041; Figure 5 B) and marginal between alpha-band power and for the target-present conditions (r = .284, *p* = .084; Figure 5A), where the greater the decrease in alpha power the faster participants performed during the VAS task. We did not find, however, a correlation with accuracy performance (r = 0.019, *p* = .906).

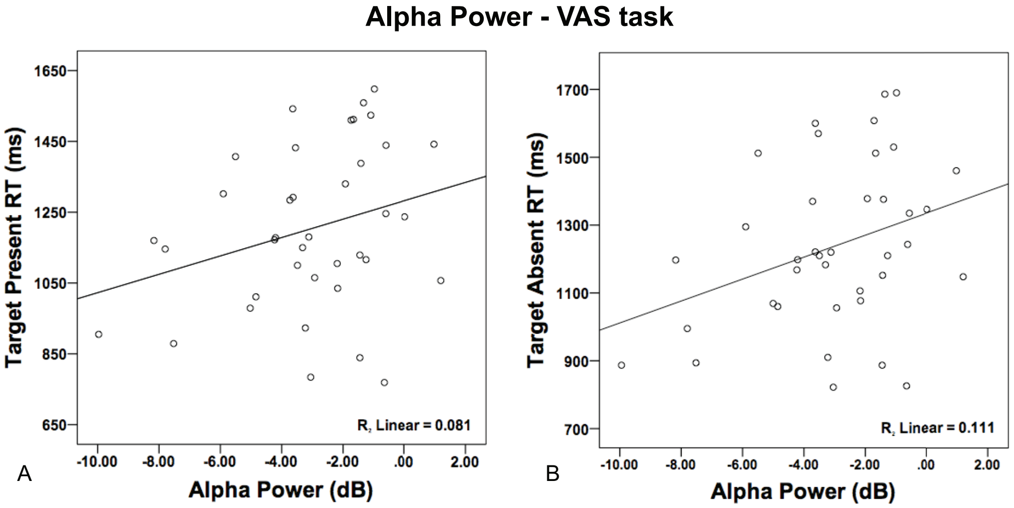


Figure 5 Correlation between posterior alpha power and response time (RT) during the retrieval section (8000 to 11000ms) of the VAS task, specifically during target-present trials (A) and target-absent trials (B).

2.4 Discussion

The goal of this study was to further expand on the understanding of neural correlates during visual working memory and visual attention. We investigated the theta- and alpha-band activity in the frontoparietal network during the performance of a delayed-match to sample (DMS) task and a visual attention search (VAS) task. Our study found a decrease in fm-theta power during the retrieval period and an increase in theta power in the VAS task. Additionally, we found an overall decrease in alpha power most prominent at posterior sites, which goes in line with the idea that the reduction of alpha power happens when there is cortical activation (Gert Pfurtscheller, 2006). Correlation analysis revealed that theta rather than alpha power was negatively correlated with memory performance during the maintenance phase (in the DMS task; Figure 5). Thus, a greater decrease in theta power during the maintenance phase associated with better mnemonic discrimination and faster RT (in lure trials), which is in line with previous findings in the literature (Greenberg et al., 2015). This relationship suggests that the patterns concerning theta relate to the behavioral effect of memory performance. Posterior alpha also correlated positively with the target-absent and showed a trend with target-present condition demonstrating its association to attention.

2.4.1 Behavioral data

As expected, our behavioral results revealed significantly worse performance for the DMS task compared to the VAS task. This finding suggests that performing a mnemonic discrimination task was generally harder to complete compared to only searching for an object without needing to encode a WM item (see Table 1). Although, the question remains on whether these behavioral differences reflect distinct neuronal mechanisms. Would holding a WM item (i.e., indoor scene) require a different theta- and alpha band activity? If so, do the oscillatory activity correlate with the behavioral performance?

2.4.2 EEG spectral power

Our results showed an overall increase in theta power relative to the baseline for the VAS task, which was prominent in frontal electrodes (Ishii et al., 2014). On the other hand, the DMS task displayed a decrease in theta power relative to baseline during the maintenance phase and even a more substantial decrease during the encoding and retrieval periods. The latter finding goes along with Greenberg's (2015) research, where a decrease in theta power was correlated to memory formation and that it could be related to encoding mechanisms. Even though others have observed a decrease in theta power (Burke et al., 2013; Guderian, Schott, Richardson-Klavehn, & Duzel, 2009), it is in disagreement with a more established view, where an increase in theta power is observed during memory retrieval (Klimesch 1996; Sederberg et al. 2003; Hanslmayr et al. 2011; Klimesch, W., Doppelmayer, M., Russegger, M., Pachinger 1996; Klimesch 1999). Burke et al. (2013) helped reconcile this discrepancy by studying the changes in spectral power reflected during episodic memory formation. They stated that encoding involves both theta-synchrony increases and decreases occurring very near to each other in time and space, which we observed for theta band during the DMS task only. Hence, increased theta power may reflect a more general process of attention, while an interplay between increase and decrease in theta may reflect a process that marks memory formation (Burke et al., 2013; Greenberg et al., 2015).

In addition, we observed that alpha activity elicited a strong decrease in power during the presentation of the sample and probe stimulus, which was most prominent in the posterior region. As anticipated, this decrease was sustained throughout the 3-second period, and then gradually returned near the baseline during the maintenance period, before abruptly decreasing again during the probe stimuli presentation, as depicted in Figure 2. This distribution was similar for both tasks, although a greater decrease was observed during the more demanding task (Klimesch et al. 2007). These results go in line with the notion that a decrease in power at the alpha band (9

– 12Hz) is known to reflect cortical activation concerning cognitive functions such as general attentional demands.

The alpha band plays an important role in stimulus processing. Our findings also revealed a positive correlation between alpha power and RT during target-absent trials, where faster RT had greater ERD, further illustrating the importance of alpha desynchronization in attention processing. Even though alpha power is most prominent in posterior electrodes, alpha ERD has also been observed in the frontal cortex during the performance of a selective attention task (i.e., Stroop task; Chang et al., 2015), indicating that alpha ERD reflects a top-down process.

In conclusion, these findings provide further evidence that theta and alpha band power display a unique pattern of activity that happen during WM and attentional processes in healthy young adults. Such theta- and alpha-band power was proportional to behavioral performance in the DMS task and the VAS task, respectively.

3. Effects of physical exercise on working memory and attention-related neural oscillations

3.1 Introduction

The beneficial effects of exercise on brain function are of widespread interest but remain elusive. Human aging research has demonstrated that physical exercise training in older adults has the most significant impact on spatial memory, working memory (WM), and executive attention (Cassilhas et al., 2016; Sousa et al., 2018b). Particularly, older adults with higher aerobic fitness had a better performance during visual figure recognition (Maass et al., 2015), spatial memory (Erickson et al., 2009, 2011), and attentional control (i.e., the flanker task; Verstynen et al. 2012). Similar studies are lacking in representation for the healthy young adult population. It seems that age is an important factor influencing the impact of exercise-induced cognitive benefits, with those considered in the prime stages of their lives to cognitively benefit the least from exercising (Sousa et al., 2018a). Nonetheless, it is essential to continue studying the cognitive benefits and neural mechanisms associated with exercise, which, to date, has been quite inconsistent (Verburgh, Königs, Scherder, & Oosterlaan, 2014b). Notably, very few studies obtained measures of neural function in a controlled exercise intervention in addition to the commonly obtained behavioral and structural measures.

One of the less applied methods to study the exercise-related effects on the brain's cognitive functions is quantifying the changes in time-frequency representations (TFRs) during a specific cognitive task. TFRs are computed from electroencephalogram (EEG) data and correlate with rhythmically modulated firing patterns on a cellular level (M. J. Hogan et al., 2015). Also, the brain emits oscillating signals throughout neuronal networks that are frequency-band specific and are known to give insight into how the brain processes a particular cognitive task. Hence, quantifying the changes in frequency-band power after a physical exercise intervention, whether short-term (acute) or long-term (chronic), will help us understand the beneficial impact of the exercise regimen on cognitive functioning.

A recent cross-sectional study showed a relationship between aerobic fitness and neural rhythms during a Posner visuospatial attention task in high- and low-fitness young adults (Wang et al., 2015). Interestingly, high-fitness participants had faster response times as well as greater beta- and theta-band power during target processing. These findings indicated that aerobic fitness could be positively related to visuospatial attention capacity through the modulation of attentional processes. Some researchers have argued that already an acute bout of physical exercise (i.e., 30 to 50 minutes) may be sufficient to improve memory performance (Roig et al., 2016) and attentional processes (M. Hogan et al., 2013). However, it remains unclear whether these exercise-induced improvements in WM and attention relate to changes in neural oscillations.

A longitudinal neuroimaging study by Nishiguchi et al. (2015) consisted of a 12-week multimodal exercise intervention. They were interested in quantifying the benefits of physical exercise by measuring behavioral performance during several tasks, including a 0- and 1-back working memory task. Additionally, they acquired a functional magnetic resonance image (fMRI) of the whole brain. The exercise group (n

= 24; avg. age = 73.0 ± 4.8) performed three different group exercise categories, while the control group (n = 24; avg. age = 73.5 ± 5.6) had to continue with their daily activities as usual during the intervention phase. The first exercise category involved performing a verbal fluency task during short- and fast-step exercises. In the second exercise participants had to perform a seated or standing step exercise at a tempo of the accompanying music (60 – 120 beats/minute) while pointing at different parts of their bodies when requested (e.g., 1 = right shoulder, 2 = left shoulder). Finally, in the third exercise consisted of stepping in one of the four directions (right, forward, back, left) depending on the direction the instructor said out loud. The intensity and difficulty of the three exercises were gradually increased over time, where each participant had to increase their steps every month. At the end of the twelve weeks, their steps would have increased a total of 50% relative to baseline. This study revealed that older adults benefit from the exercise intervention as shown by an improved memory and executive functions. It also led to a decrease in prefrontal brain activation, which associated with short-term memory (0- and 1-back task). They concluded that aerobic and cognitive exercises may improve the efficiency of the brain function and thereby cognitive performance (Nishiguchi et al., 2015). Other studies have found similar findings, which can be interpreted as a marker for improved neural efficiency, that is, the decreased activation at comparable performance levels (Babiloni et al., 2010; Consortium, 2017).

In rodents, voluntary wheel running has been associated with hippocampal neurogenesis and has positively correlated with synaptic plasticity (Vivar, Potter, & van Praag, 2012) and spatial pattern separation (Creer, Romberg, Saksida, van

Praag, & Bussey, 2010). In elderly humans, Erickson et al. (2009) found a triple association between aerobic fitness levels, hippocampal volume, and memory functions, where higher aerobic fitness levels were associated with the preservation of left and right hippocampal volume and better performance on their spatial memory task. Together, these studies supported the idea that exercise-induced hippocampal plasticity may improve learning and memory (Erickson et al., 2009).

Here, we sought to examine how theta and alpha-band oscillations are modulated by a 4-month physical training regimen and aimed to determine the exercise-induced effects on brain dynamics in the frontoparietal network. To that end, we acquired EEG data from sedentary young adults during a delayed match-to-sample (DMS) WM task, which measured mnemonic discrimination of visual stimuli, akin to pattern separation, and a visual-attention search (VAS) task that did not require any recognition memory. We focused on theta (5 – 7Hz) and alpha (9-12 Hz) oscillatory activity due to their association with WM and attention, respectively. Based on previous findings, we expected that our training intervention would increase aerobic fitness, enhance mnemonic discrimination, and increase theta-band power, as an indication of hippocampal activity change. Particularly, for the exercise group, we expected faster response times (RTs) and/or higher accuracy. Concerning EEG power, we expected the exercise group to have changes in EEG spectral power, specifically a more significant increase in theta power during the DMS task as a reflection of neural efficiency.

3.2 Methods

3.2.1 Participants

Forty-three healthy, sedentary young adults (age range: 19 to 34 years, mean age: 25.33 ± 3.62 years, 23 females) were recruited for the study; one participant dropped out of the study, and 2 participants were excluded because of technical issues with the EEG recording. All subjects reported no signs of neurological or psychiatric illness and had a normal or corrected-to-normal vision. After providing informed consent, participants were pseudo randomly assigned either to an aerobic exercise group (n = 18) or a control group (n = 22), which were balanced in terms of age, sex, and fitness level (Table 2). Subjects received monetary compensation for their participation, and the experiment was carried out in accordance with the guidelines of the ethics committee of the Faculty of Medicine from Otto von Guericke University Magdeburg.

3.2.2 Intervention protocol

Cardiovascular training (exercise group). The exercise group ran on a stationary treadmill ergometer three times per week for 16 weeks. Each participant received an individually optimized 45 to a 75-minute set, including a 5-minute warm-up and 5-minute cool-down. Under the supervision of sports scientists, participants monitored their heart rates during their workouts and exercised at intervals with an intensity range of 70 – 90% of maximum heart rate (HRmax). Individual training intensities were determined by target heart rates, as estimated by the Karvonen method (Karvonen, Kentala, & Mustala, 1957), and verified to heart rate levels at the individual anaerobic threshold, as indicated by lactate measures.

Walking and stretching (control group). The control group walked on the treadmill only twice a week. This protocol kept variables, such as social interaction, scheduling, and motivation similar to the exercise group, while not affecting their aerobic fitness. The control group walked for 10 to 12 min, with breaks in between, and maintained a maximum heart rate of around 50 – 60% HRmax. All settings and HR monitoring procedures were kept constant between groups. Due to the low HR training zone, the maximum incline of the treadmill was 3% at a maximum walking speed of 4.5 km/h.

3.2.3 Fitness assessment

We assessed the consumption of oxygen (CPET Quark, COSMED, Italy) at the respiratory compensation point (VO_2-RC) by graded maximal exercise testing on a treadmill ergometer. The initial speed of 3 km/h was increased every 2 min to a maximum of 6.5 km/h. During this time, the slope of the treadmill also increased from 0% to 18%. This testing occurred until a respiratory exchange ratio (RER) of 1.1 was reached, indicating exhaustion near the cardiorespiratory system’s limit. Here, the oxygen exhaustion criterion was defined by the uptake at respiratory compensation (VO_2-RC) to better control for volitional effects. To assess lactate levels (Biosen C-Line, EKF DIAGNOSTIC, Magdeburg, Germany), capillary blood samples were taken from the earlobe during the resting state, at 2-min intervals during the fitness test, and 2 min after the maximum intensity. This fitness assessment was repeated after 4 weeks and again after 16 weeks when the intervention ended.

3.2.4 Experimental procedure and experimental paradigm

The task performed in Experiment 2 consisted of a delayed-matched-to-sample task and a visual attention search task that are similar to the experimental paradigm from the preintervention shown in Experiment 1 (Figure 1A & 1B). The experimental paradigms have the same structure but with a complete set of new images for the delayed matched-to-sample task to avoid any recollection from 4-month prior (i.e., preintervention measure). Also, the background image for the VAS task was different from the preintervention, but it remained the same throughout the experiment.

3.2.5 Data acquisition, processing, and time-frequency analysis

Continuous electroencephalogram (EEG) for our post intervention measure exactly acquired as in Experiment 1 (i.e., preintervention). Also, the same protocol was followed for the decomposition of the EEG data into frequency-band powers (i.e., time-frequency analysis) so we could compare the data from the two different time points.

3.2.6 Statistical analysis and Correlations

All statistical analyses were performed using the statistical software SPSS (IBM Corps., IBM SPSS Statistics, V24, Armonk, NY, USA., 2016). First, we ran independent-samples t-tests to assess whether there were any differences between the groups at baseline (preintervention). To compare differences in categorical variables such as sex and age, we used the chi-square test. There were no differences observed between the groups at baseline (Table 2).

Furthermore, to examine the possible effect of training on cognition, the data were then submitted to two separate repeated-measures ANOVAs (one rmANOVA per frequency band of interest). The factors in the rmANOVAs included *task* (DMS, VAS), *cluster* (frontal, posterior), and *time* (pre, post intervention) as within-subject factors and *group* (exercise, control) as a between-subjects factor. We did not include any variables as covariates since groups did not differ in demographics. The Greenhouse-Geisser correction was used to adjust the degrees of freedom when the sphericity assumption was violated when appropriate. Levels for significance were set as .05. When significant interactions were found with rmANOVA, post hoc independent t-tests were conducted.

To assess the possible relationship between exercise and cognition, we first calculated the intervention-related changes in performance, spectral power values and fitness. In particular, accuracy, response time, and EEG spectral power differences were obtained by subtracting pre from post measures of EEG power (Tp2–Tp1). For a better estimation of aerobic fitness increase, a composite fitness score was calculated separately for pre- and post intervention fitness test data as a mean of the inverse z-scores of blood lactate level changes (%) and the z-score of VO_2-RC changes (%). The bivariate (Pearson) correlations were calculated between changes in ERSP values, fitness scores, and behavioral performance to examine how fitness changes affect cognitive functioning after 4 months of exercise training.

3.3 Results

3.3.1 Participant's description & aerobic fitness assessment

Demographics and fitness levels for the exercise and control groups are reported below. As shown in Table 2, the groups were matched for age and sex and did not differ at baseline in body mass index (BMI), average blood lactate, and VO_2-RC (F (1,38) < 1.345; p > .198).

Table 2 Group description at baseline

Variables	Exercise group	Control group	One-way ANOVA
Age	26.1 (4.0)	24.7 (3.3)	F (1,38) = 1.345; p = .253
Sex (f/m)	10 / 8	13 / 9	F (1,38) = 1.345; p = .827
BMI	25.33 (5.71)	23.44 (3.29)	F (1,38) = 1.345; p = .198
VO_2-RC	28.12 (4.93)	29.26 (4.02)	F (1,38) = 0.656; p = .423
$[La^-]_b$	4.77 (1.34)	5.12 (1.43)	F (1,38) = 0.647; p = .426

Blood lactate ([La-]b in g/mol); oxygen uptake at respiratory compensation (VO2-RC in ml/min/kg); body mass index (BMI in kg/m2).

To measure exercise-induced changes in fitness, we performed rmANOVAs with *time* (pre- and post intervention measures) as the within-subject factor and *group* (exercise and control) as the between-subjects factor. As seen in Table 3, rmANOVA revealed a time x group interaction for lactate (F (1,38) = 36.926; *p* < .001) as well as for VO_2-RC (F (1,38) = 86.496; *p* < .001). Post hoc paired t-tests showed an increase in fitness represented as a decrease in lactate (t (17) = -9.936; *p* < .001) and an increase in VO_2-RC (t (17) = 2.270; *p* < .001) for the exercise group but not the control group (t (21) = -.245; *p* = .809 and t (21) = -1.616; *p* = .121, respectively).

Table 3 Aerobic fitness measures pre and post intervention by Group.

Variables	**Exercise**		**Control**		
	pre M (SD)	**post** M (SD)	**pre** M (SD)	**post** M (SD)	**rmANOVA**
$[La^-]_b$	4.77 (1.34)	3.05 (1.32)	5.13 (1.43)	5.50 (1.38)	F (1,38) = 36.926; p < .001*
VO_2-RC	28.12 (4.93)	32.60 (5.07)	29.26 (4.02)	29.32 (4.12)	F (1,38) = 86.496; p < .001*

Fitness measure: blood lactate ($[La^-]_b$ in g/mol); oxygen uptake at respiratory compensation **(**VO_2-RC in ml/min/kg).

3.3.2 Behavioral data

Table 4 illustrates the pre and post intervention measures for accuracy and RT for each group. We considered performance values that were greater than 2.2 SDs from the mean as outliers, and these values were excluded from the statistical analysis. RmANOVAs revealed a main effect of time for all behavioral performance measures, for the exception of the correct response (F (1,36) = 2.00; *p* = 0.166). Although, the time x group interactions were all not significant (F (1,36) < 1.959; *p* > .170), meaning that the difference in behavioral performance between the pre and post measures was not due to our intervention. The Figure 6 (A–D) further illustrates this point by showing the before and after response time during each experimental trial separated by the exercise and the control group.

Table 4 Group mean (SD) for behavioral performance values pre and post intervention.

	Exercise		**Control**		
	Pre M (SD)	**Post** M (SD)	**Pre** M (SD)	**Post** M (SD)	**rmANOVA** (time x group interaction)
DMS					
CHR	0.65 (0.12)	0.60 (0.12)	0.72 (0.11)	0.64 (0.17)	F (1,32) = 0.305; p = .585
Hit RT	1576 (320)	1688 (321)	1448 (259)	1562 (306)	F (1,37) = 0.000; p = .990
Lure RT	1335 (221)	1517 (321)	1306 (234)	1394 (258)	F (1,37) = 0.000; p = .172
VAS					
CR	0.92 (0.04)	0.93 (0.02)	0.91 (0.03)	0.92 (0.03)	F (1,35) = 0.022; p = .883
Ball RT	1288 (216)	1349 (247)	1142 (223)	1266 (214)	F (1,35) = 0.744; p = .394
No Ball RT	1328 (233)	1397 (260)	1171 (234)	1328 (231)	F (1,36) = 1.959; p = .170

Included are the results for the DMS task, in which accuracy was measured using hits minus false alarms, known as the corrected hit rate (CHR). For the VAS task, accuracy was measured by averaging the correct responses (CR) for both conditions (target-present and absent).

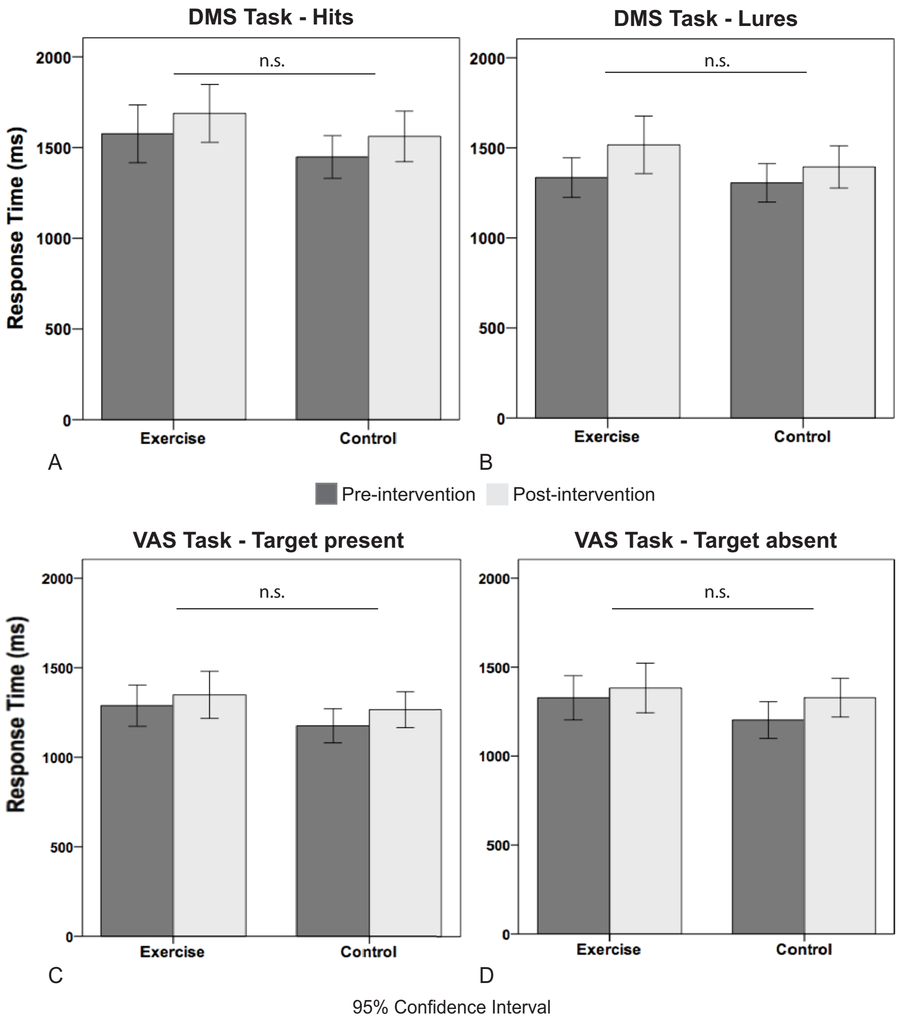


Figure 6 Illustrates the response time measures for pre and post intervention separated by group and condition. Specifically (A) shows the RT pre and post intervention measures for hits, (B) for lures, (C) for target present, and (D) for target absent trials.

3.3.3 Exercise-induced spectral power changes

RmANOVAs performed for the sample stimuli presentations (0 – 3sec) for theta power revealed a main effect of task (F (1,38) = 18.867; *p* < .001) but no task x cluster x time x group interaction (F (1,38) = 0.216; *p* = .645). During the probe stimuli presentations (8 – 11sec), theta power showed a main effect of task (F (1,38) = 10.68; *p* = .002) but no interaction (F (1,38) = 0.617; *p* = .437). For the alpha band during the sample stimuli presentations (0 – 3 sec), there was a main effect of *task* (F (1,38) =

25.090; *p* < .001), a main effect of *cluster* (F (1,38) = 17.763; *p* = .000), and a significant *task x cluster x time x group* interaction (F (1,38) = 4.255; *p* = .046). Post hoc independent t-tests showed no group difference for the posterior cluster (t (38) = 319; *p* = .751), while the frontal cluster showed a significant group difference (t (38) = 2.338; *p* = .025) during the VAS task, with increased alpha power after the intervention (see Table 5). This effect was specific to attention, as it appeared during the VAS task but not the DMS task (t (38) = 1.522; *p* = .136 and t (38) = .227; *p* = .795, respectively). This finding is further illustrated in Figure 7.

Table 5 Group mean (SD) values for theta and alpha power for frontal and posterior sites pre and post intervention.

	Exercise		**Control**		
	Pre	**Post**	**Pre**	**Post**	
Theta	M (SD)	M (SD)	M (SD)	M (SD)	Independent t -test
DMS (frontal)	-0.46 (0.83)	-0.34 (1.19)	-0.13 (0.76)	-0.08 (0.96)	F (1,38) = 0.068; p = .795
DMS (posterior)	-0.56 (1.44)	-0.33 (1.39)	-0.17 (1.46)	-0.39 (1.51)	F (1,38) = 2.315; p = .136
VAS (frontal)	0.20 (0.60)	0.14 (1.04)	0.33 (0.86)	0.28 (0.95)	F (1,38) = 0.000; p = .988
VAS (posterior)	-0.04 (1.38)	-0.03 (1.41)	0.21 (1.34)	0.01 (1.34)	F (1,38) = 0.253; p = .618
Alpha					
DMS (frontal)	-1.85 (1.63)	-1.89 (1.52)	-2.38 (1.79)	-2.39 (1.75)	F (1,38) = 0.005; p = .945
DMS (posterior)	-2.74 (2.73)	-2.46 (1.92)	-3.86 (2.29)	-3.62 (2.37)	F (1,38) = 0.013; p = .910
VAS (frontal)	-1.77 (1.62)	-1.10 (1.39)	-1.80 (2.16)	-2.04 (1.59)	F (1,38) = 5.465; p = .025*
VAS (posterior)	-2.30 (2.66)	-1.81 (2.03)	-3.45 (2.33)	-3.11 (2.01)	F (1,38) = 0.102; p = .751

Table 5 shows the frontal and posterior mean (SD) ERSP values for frontal and posterior theta- and alpha-band power. Both frequency-band power values are separated by group and further separated by task and time (pre- and post intervention measures). Independent t-tests were conducted on differences in theta and alpha power (pre minus post intervention) between groups.

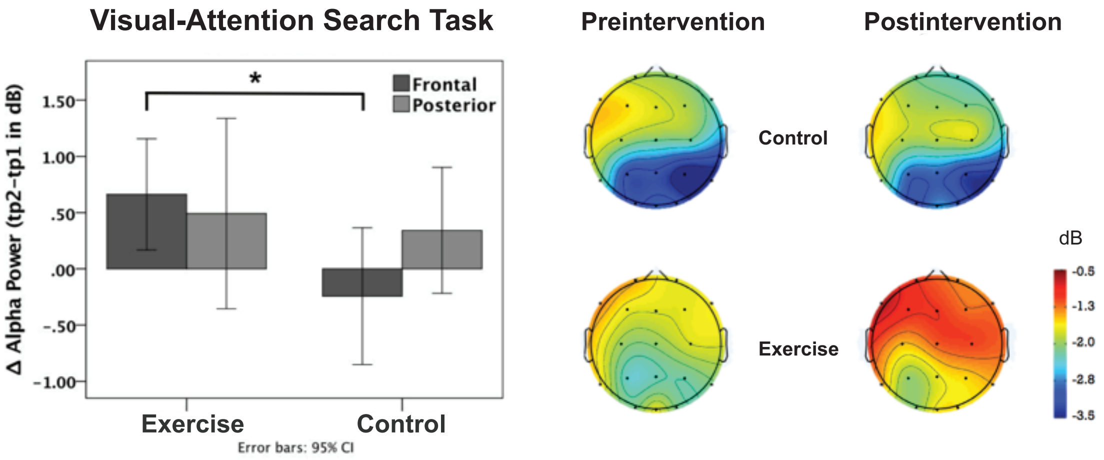


Figure 7 Bar graph shows the intervention-induced alpha power change during the VAS task at frontal and posterior clusters for each group. * Indicates $p < 0.05$ (uncorrected, 2-tailed t-test). Topographical distribution of ERSP values for alpha activity, including the first 3 sec of the sample stimuli presentation in both the pre- and post-intervention groups.

Furthermore, given the significant post hoc results, we sought to examine a direct link between anterior alpha power changes with aerobic fitness changes and behavior performance changes (during the VAS task). Such correlations were performed irrespective of the group (i.e., across all subjects). Specifically, there was a positive correlation between changes in frontal alpha power and changes in accuracy (VAS task - target-absent; Figure 8A). In addition, changes in aerobic fitness were also positively correlated with changes in alpha power at the anterior electrodes (R^2 = .145; p = .016; see Figure 8B).

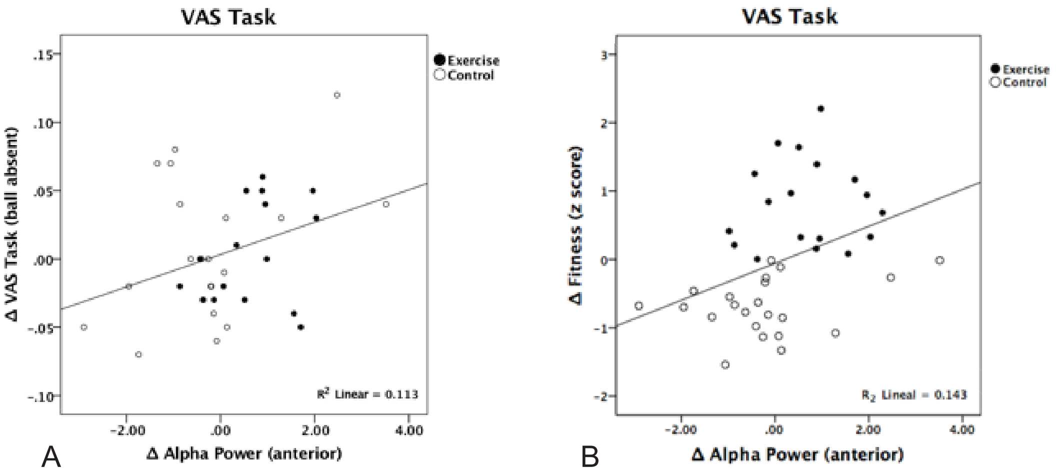


Figure 8 Correlation between change in alpha power in frontal regions and with correct response in the VAS task (target-absent). Better performance after the intervention was related to a greater increase in alpha power. (B) Correlation between changes in alpha power in frontal regions and fitness score. A higher fitness score was related to a greater increase in alpha power.

3.4 Discussion

The aim of this study was to investigate the effects of physical exercise on neuronal oscillations during two different cognitive paradigms that tap into mnemonic discrimination and attentional processes. Specifically, we quantified changes in theta and alpha power for the anterior-parietal network. As anticipated, we observed an increase in aerobic fitness after a 4-month exercise intervention, demonstrated by an increase in oxygen consumption at a ventilatory anaerobic threshold and a decrease in blood lactate threshold at maximum intensities. Contrary to our expectations, we did not observe intervention-related improvements in mnemonic discrimination or visual attention over time. Additionally, there were no effects of the exercise intervention on theta oscillations. However, the time-frequency analysis (TFA) revealed an increase in amplitude for frontal alpha power in the exercise group compared to that in the control group during the VAS task. This overall change in alpha power positively correlated with aerobic fitness changes across all participants. Changes in fitness were further associated with behavioral performance (RT) in the VAS task as well.

3.4.1 Exercise-induced changes

We observed an exercise-related increase in alpha power (i.e., weaker ERD), predominantly in the frontal sites during the VAS task. Note that an increase in alpha power stems from a reduction in alpha ERD in the post intervention session. Overall subjects had similar performance levels, but the exercise group was characterized by reduced alpha desynchronization (i.e., less cortical activity) to accomplish the same task. Tentatively, we attribute this increase in alpha power to neural efficiency, specifically to an enhanced capacity for resource allocation involving visual attention. Our findings are compatible with the Ludyga et al. (2016) study in which they measured activity before and after a month of a cycling intervention, and also observed improvements in fitness performance and decreased cortical activity during exercise (Ludyga, Gronwald, & Hottenrott, 2016).

Neuroimaging studies have demonstrated that subjects with higher WM and spatial skills have weaker frontoparietal activation during cognitive tasks (Rypma & D’Esposito, 1999). Relatedly, EEG results have indicated that elite athletes (e.g., shooters, karatekas, gymnasts) require "less" cortical activation (weaker ERD) in task-relevant brain areas than novices during sport-specific tasks (Ludyga et al., 2016) and a judgment-allocating task (Babiloni et al., 2010; Del Percio et al., 2009). This observation has been coined “neural efficiency” (Babiloni et al., 2010; Del Percio et al., 2009). Studies that have considered aerobic fitness have reached similar conclusions (M. J. Hogan et al., 2015; Ludyga et al., 2016). For instance, a cross-sectional study performed by Hogan et al. (2013) found that preadolescents with lower fitness require more neuronal resources for a given task, which was reflected by an increased EEG coherence in comparison to the fit subjects. Together, these findings suggest that aerobic fitness is linked to visual attention not only in older adults but also in young adults.

Moreover, our results showed that participants with higher fitness improvements had a more considerable increase in alpha power in the anterior regions (Figure 8B). Other cross-sectional studies have found comparable correlations (Chu et al., 2016; Hyodo et al., 2016). An exercise intervention study in older adults found that higher aerobic fitness derived from the walking program was associated with more significant changes in white matter integrity in the frontal and temporal lobes (Voss et al., 2013). Given these previous findings, it is congruent that we observed an increase in alpha power reflected in the anterior electrodes, which also correlated with changes in accuracy (Figure 8A). Notably, such correlations (alpha-fitness and alpha-performance) were existent across groups, implying that alpha power modulations may also be sensitive to other physiological changes. Fitness changes, for instance, might not only be driven by the intervention, but also other parameters such as daily routine activities, adaptability in training (Bonafiglia et al., 2016), and a genetic disposition to physical activity could also be playing a role (Bouchard, 2012). Nonetheless, only our exercise group showed less cortical activation to performed the VAS task compared to the control group, as shown by the increased alpha power after the intervention, which we attribute to neural efficiency.

Our study has limitations. First, we had a limited sample size of eighteen subjects comprising the exercise group. Further intervention studies will have to confirm our findings in larger samples, and it would be beneficial to lengthen the intervention duration to determine whether the training benefits transfer to hippocampal-dependent tasks and oscillations in young adults. On the other hand, our sedentary group matched in age, sex, and baseline fitness level. The sedentary group of young adults who underwent our vigorous training showed improvements from our 4-month exercise intervention, which we measured with not one but two fitness markers providing a more precise indication of the aerobic fitness change. Hence, the negative findings that we observed here were not due to an ineffective intervention.

Conclusively, our study provides tentative evidence in support of cardiovascular exercise modulating oscillatory brain activity. Our findings support the possibility that aerobic training of sedentary young adults may influence neural dynamics underlying visual attention. However, we did not confirm our hypothesis that aerobic exercise would enhance theta oscillations and improve WM performance in a mnemonic discrimination task.

4. Experiment 3 – Neural mechanisms behind conflict resolution from prior interference in working memory

4.1 Introduction

Working memory (WM) is the ability to temporarily store and manipulate information that is no longer present in the environment and to operate effectively, it must be undeterred by attentional distractions (A. D. Baddeley & Hitch, 1974; D'Esposito et al., 1995). These attentional distractions can interfere with working memory by redirecting resources to the external environment that the internal attention requires for successful working memory. Such a switch therefore also instigates cognitive control (Kyionaga et a., 2017), a multifaceted mental process that allows behavior to adaptively vary and focus on information that is relevant while ignoring irrelevant information to the current set of goals (Miller & Cohen, 2001; Morton, Ezekiel, & Wilk, 2011). An example of these two processes interacting would be trying to remember someone's phone number (i.e., a WM item) while a friend nearby counts aloud, which would typically interfere with one's ability to recall that phone number. Some recent behavioral studies are investigating WM and cognitive control in several different settings. Previous studies either explore how attention may bias WM (Foerster & Schneider, 2018), or how WM processing-load affects attentional performance (Scharinger et al., 2017) or they focus on how holding a WM item affects attention (Mallett & Lewis-Peacock, 2018; Zhao et al., 2014). However, it remains unclear what the underlying neural underpinnings might be when there is the need for conflict resolution at retrieval when the maintained internal information and the external distraction are in a similar or a different feature category.

Here, we deployed two different dual-tasks paradigms to investigate how the retrieval of a WM item was affected by prior conflict processing. Both dual-tasks consisted of a delayed-match-to-sample (DMS) WM task with an embedded color-discrimination (Stroop) task during the maintenance phase. The idea behind these two paradigms was that it is demanding to maintain information when asked to perform a task while holding an item in WM for later retrieval. This demand is more prominent if both the WM item and the color-distraction information are in the same characterizing category or feature domain than having a different one. Subjects were either asked to hold a color- or a number word (i.e., “red” or “five”) in working memory, followed by a 5sec delay period (i.e., the maintenance phase) where subjects had to perform a color-discrimination task as quickly and accurately as possible. Finally, subjects were prompt to select whether the sample probe (i.e., color- or number-word) was the same or different as the sample stimuli held in WM. The main difference between our two dual-task paradigms was the nature of the memoranda (i.e., WM item), which can be either domain overlapping (DO) (i.e., color word – color) or non-domain-overlapping (nonDO) (i.e., number word – color) based on whether the memoranda’s and the Stroop-like discrimination task’s features overlap.

Kyionaga and Egner (2014) were the first to implement the DO WM task, which together with a single task paradigm (i.e., modified Stroop task) were used to assess the degree in which WM and selective attention draw on the same attentional resources. Our second WM dual-task, the nonDO WM task, was created as a control for the DO WM task to assess the difference in successful conflict resolution during retrieval with conflict processing occurring at the maintenance phase (see Figure 9A &

9B). The incongruent (Inc) trials produced interference while the congruent (Cong) ones could serve as reinforcement (i.e., facilitation) if given the right circumstances. Such circumstances occur when participants are prompted to hold, for example, “red” in WM followed by a red patch, which would reinforce the WM item, thereby facilitating a match/non-match decision at retrieval. Hence, together these two particular dual-tasks could help further understand the behavior and the neural mechanisms behind cognitive-control resources that WM retrieval might entail.

Previous research has relied on non-invasive methods such as electrophysiological (EEG) measures to make inferences about the neural activity during specific cognitive tasks. These have shown reliable associations between distinct cognitive functions and neural correlates like event-related potentials (ERPs) and frequency-specific EEG activity (Darriba & Waszak, 2018; Tsoneva, Baldo, Lema, & Garcia-Molina, 2011; Yamamoto, Suh, Takeuchi, & Tonegawa, 2014). For instance, theta power has been implicated in both working memory (Jensen et al., 2002; Wolfgang Klimesch, 1999; Sauseng et al., 2009) and sustained attention processes (S Hanslmayr et al., 2008; Ko, Komarov, Hairston, Jung, & Lin, 2017). More recent studies have also associated theta power to cognitive control mechanisms in WM (Eschmann et al., 2018; Scharinger et al., 2017). Eschmann et al. (2018) manipulated the cognitive load of a DMS task by prompting participants to remember 1 versus 4 squares in a 6 by 6 panel. Their findings showed an increase in theta power for the condition that needed higher cognitive control. Similarly, Scharinger et al. (2017) measured the changes in WM-load-related activity during an N-back task and found that as the N-back levels increased (from 1-back to 3-back), theta power also increased in frontal sites, suggesting that frontal theta power might mediate cognitive control in the WM system. Taken together, theta band frequency power has proven to be sensitive to WM processing and might reflect the resource allocation necessary for conflict resolution. This leads to **Hypothesis 1:** If the increase in frontal-midline theta (fm-theta) power specifically reflects cognitive resource allocation, this difference should occur during the incongruent trials relative to the congruent ones. Moreover, we expect the DO task to require a greater cognitive control than the nonDO task given the overlapping features of the internal representation and the external distraction. This effect may be reflected by a more significant difference in fm-theta power. Hence, understanding the pattern and distribution of fm-theta may indicate how the need for successful conflict resolution during retrieval is achieved.

Event-related potential analysis has also been utilized to provide insight into different WM retrieval processes. The P300 component, for instance, is a central-parietal positive component occurring around 300 – 500ms after stimulus onset and has been related to shifts in attention that update representations in WM (Polich & Kok, 1995). Recent research has shown that both the amplitude and the latency are modulated by task demands (Pergher, Wittevrongel, Tournoy, Schoenmakers, & van Hulle, 2018; Scharinger et al., 2017). Specifically, larger amplitudes and earlier latencies are observed during tasks with easy versus difficult target discrimination or during low versus high task demands (Pratt et al., 2011), suggesting that higher demands lead to a later and smaller P300. In a study conducted by Pratt et al. (2011), participants performed a flanker task either alone or in combination with a Sternberg task. The Flanker task is used to assess the ability to suppress inappropriate responses in a particular context. On this task, participants selected the direction of an arrow while ignoring the flanking arrows surrounding it. The Sternberg task provides a measure of processing speed and WM retrieval speed. Their results showed a decrease in P300 amplitude as a function of task difficulty, decreasing on incongruent trials when working memory increased (Pergher et al., 2018; Pratt et al., 2011). That is, the interference from the incongruent flankers was more difficult to suppress when WM was taxed by the dual-task**. Hypothesis 2:** If the P300 amplitude reflects the diminished availability of resources to selectively focus attention and resolve response conflict, then our Inc trials should have the smallest P300 amplitude.

The present study aimed to investigate the behavior and neural mechanisms underlying successful conflict resolution during WM retrieval from previous maintenance interference. The specific goal was to understand the interactions between cognitive control better, entailing conflict resolution while maintaining an item in WM, and then needing to retrieve that item. Our hypotheses stem from the idea that the amount of conflict or facilitation that arises during the dual-task will be more prominent if the distraction event (i.e., prior incongruent trial) or facilitating event (i.e., prior congruent trial) is in the same feature domain (i.e., color – color – color) than if it is in a different one (i.e., number – color – number). Behaviorally, based on previous findings, we expected slower response times (RTs) and lower accuracy for trials with greater conflict during the maintenance phase of the WM task (Kiyonaga & Egner, 2014).

4.2 Methods

4.2.1 Participants

Thirty-three healthy young adults (20 female; age range 18 – 30 years) provided informed consent to participate in our experiment in accordance with the policies of the Duke University Institutional Review Board. All participants had English as their first language, normal or corrected-to-normal vision, no color-vision deficiency according to the Ishihara test for color blindness, and denied taking attention-enhancing drugs. Three participants were excluded from our analysis, one due to chance-level performance accuracy and two due to noisy EEG data, leaving 30 participants for the analysis. Participants were compensated $15 per hour for their time.

4.2.2 Experimental tasks

Domain-overlapping Working Memory Task

As previously mentioned, the DO WM task consisted of a color-discrimination task embedded in the maintenance phase of a delayed-match-to-sample WM task. More specifically, participants had to encode a color-word sample item – either “red,” ‘blue,” “green,” or “purple” – and then performed a color-discrimination Stroop-like color task by reporting the color of a rectangular swatch using the designated response keys on a gamepad (Figure 9C). Finally, participants were presented with a color-word probe, now underlined, and needed to respond as to whether it was the same or different from the cue sample being held in WM (Figure 9D). Congruent trials had the color of the color swatch in agreement with the color-word being held in WM, whereas it differed in the incongruent trials (Figure 9A). For instance, a congruent trial would consist of encoding the word “red” and then being shown a red color swatch. Additionally, if the color probe word were “red,” then that would be a matched trial. Hence, in addition to being congruent/incongruent, trials could also be matching or non-matching. There were an equal number of congruent and incongruent trials, as well as matched and non-matched trials, which were presented in randomized order.

Non-domain-overlapping (nonDO) MW Task

For this second dual-task, the WM item was a number word, *not* a color word, and thus it was of a different feature domain than the color-discrimination task embedded in the WM task. Specifically, participants were asked to encode and maintain a number word – either “four”, “five”, “six”, “seven” – in WM, while performing a Stroop-like task during the WM maintenance phase, which consisted of responding to the color box while ignoring an overlaid color-word written in white. Congruent trials had the written color-word and the color-box in agreement, while the incongruent trials had the color box in disagreement with the written color word (Figure 9B). Participants were instructed to ignore the autonomic nature of reading and select the color of the color-box. As in the DO WM task, equal numbers of congruent and incongruent Stroop stimuli, as well as matching and non-matching WM trials were presented in random order.

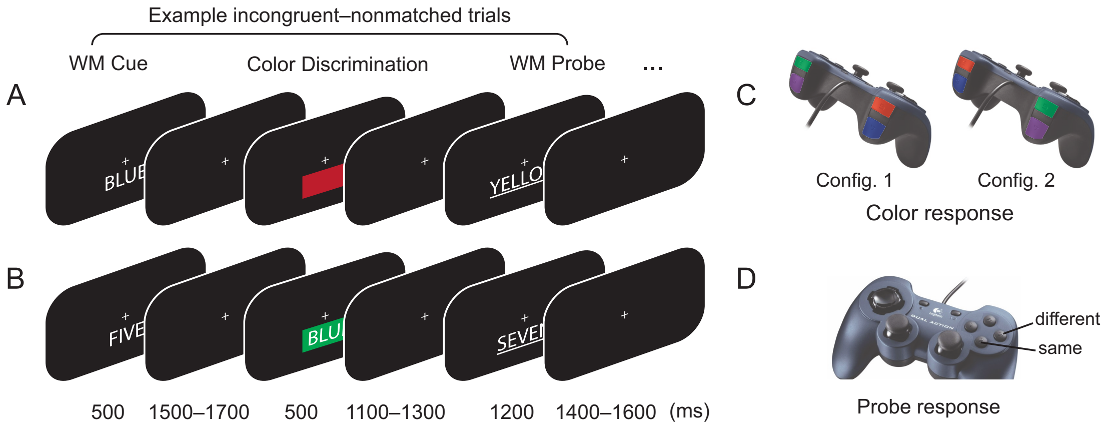


Figure 9 Dual-task experimental paradigm. (A) Shows an example of an incongruent and non-matching trial sequence for a delay match-to-sample (DMS) working memory (WM) task. On each trial of the domain overlapping (DO) WM task, participants were asked to remember a color word, then indicate the color of the swatch in a Stroop-like task, and finally, report whether the underlined WM probe matched the cue. On congruent trials, the cue and the swatch agreed, and on matching trials, the sample cue and the WM probe were the same. Similarly, on each trial of the non-domain overlapping (nonDO) WM task (B), participants were asked to remember a number word, then perform a Stroop-like task during the maintenance phase, and finally report whether the WM probe matched the sample cue. Congruent trials were ones in which the Stroop color swatch and the color word were in agreement. The color-discrimination task was performed using a gamepad, where the right and left index and middle fingers (C) and the WM probe responses were made using the right thumb (D).

4.2.3 Experimental Procedure

The experiment was displayed on a 24-inch LCD monitor (1920 x 180 resolution, 120Hz refresh rate) using Presentation software package (Neurobehavioral Systems, Inc., Albany, CA). Data were collected from a dimly lit, electrically shielded chamber where subjects sat comfortably ~60cm from the screen. Participants were asked to keep their gaze on the fixation-cross placed on the center of the screen.

Each experimental session was comprised of 240 trials per task (Classic Stroop, domain overlap (DO) WM Task, non-domain overlap (nonDO) WM task) for a total of 720 trials that were randomly and equally distributed across 4 blocks per task.

For every block of 60 trials, participants were able to take breaks lasting ~30 – 120 seconds, depending on the participant's need. The order of presentation alternated between blocks of DO WM task, nonDO WM task, and classic Stroop task. Given that our study was interested in the neural mechanisms behind conflict processing during retrieval, our analysis will focus only on the first two tasks, since there was no probe response for the classic Stroop task.

Before starting the experiment, participants had a practice session allowing them to memorize the button mappings and feel comfortable using the gamepad. The color-discrimination responses in the Stroop task were collected using both hands by selecting one of the four designated response keys from a Logitech Dual Action gamepad. Each response key button was associated with a specific color, and participants used either the middle or index fingers to make a response. There were two sets of button-color mapping that were counterbalanced across participants (Figure 9C – configuration 1 & 2). Half of the participants had the finger-to-color mapping as: left-index / red, left-middle / blue, right-index / green, right-middle / purple, and the other half switched the right hand response with the left hand, and vice versa. The match-to-sample responses had only one mapping configuration in which participants used their right thumb to select one button when the sample cue (i.e., WM item) and the WM probe were the same words and another button for when they were different (see Figure 9D).

4.2.4 Data acquisition and processing

Data binning and averaging

For EEG data analysis we time-locked to the WM probe onset with two different settings: (1) collapsed across matched and non-matched trials and separating them as a function of prior color-discrimination interference, separately for each dual-task (DO WM, nonDO WM), and (2) collapsed across prior congruency interference and separating the conditions as a function of matched / non-matched. Only correct artifact-free response trials were analyzed, which resulted in an average number of trials for each subject (mean (SD)) for DO WM congruent (97(10)), DO WM incongruent (95(13)), nonDO WM congruent (95(15)), nonDO WM incongruent (91(12)), DO WM match (111(7)), DO WM non-match (110(6)), nonDO WM match (110(10)), nonDO WM non-match (110(9)).

Behavior data

Behavioral responses were monitored and recorded as participants performed both the color-discrimination and the match-to-sample tasks. Although, for the purpose of this study, the focus was on the response to the WM probe. Specifically, we measured the accuracy (percent correct) and the RT for the WM probe response (i.e., retrieval section) as a function of the preceding congruency effect. Also, we measured the accuracy and RT of the WM probe as a function of matched / non-matched regardless of prior interference (see Table 6). We only included correct response trials and excluded ones with anticipatory responses (< 200ms) or outliers (RT greater than 1000ms for the color-discrimination task and 1200ms for the DMS task).

EEG data

We recorded EEG from a 64-channel, custom-designed, extended-coverage cap (Woldorff et al., 2002) using actiCAP active electrodes (Brain Products GmbH, Gilching, Germany) and a sampling rate of 500 Hz (low-pass anti-aliasing filter with a cutoff of 130 Hz). We kept all electrode impedances under 10kΩ, used the right mastoid as an online reference, and placed one vertical electrooculogram (EOG) channel below the left eye to monitor blinks.

The EEG data were processed using custom scripts in MATLAB [MATLAB and Statistics Toolbox Release 2016b, The MathWorks, Inc., Natick, Massachusetts, United States] and fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). The continuous EEG data was high-pass filtered at 0.05Hz, low-pass filtered at 30Hz, re-referenced to the algebraic average of the left and right mastoid electrodes, and down-sampled to 250Hz. The trials were then segmented into 3-second epochs, including a 1-second of pre-stimulus onset. The epoched data was baselined corrected from -100 to 0ms, and an independent component analysis (ICA) was performed to correct for eye-related artifacts, such as blinks. In addition, we also subsequently rejected trials with high-amplitude noise or excessive muscle activity (threshold 90 ± 10 μV from -300 – 1000ms) and interpolated excessively noisy channels using a weighted average of all neighboring channels (Perrin et al., 1989). At least 80% of trials were retained for all the included subjects.

Time-Frequency Analysis (TFA)

Frequency decomposition was performed on the artifact-free epoched EEG data using multitaper methods as implemented in the analysis software package Fieldtrip

(Oostenveld et al., 2011), in which discrete Hanning tapers were used to obtain the power estimates in linearly spaced frequencies from 3 to 30 Hz in 1 Hz increments. The window widths for the tapers were 3 cycles for 3Hz, 4 cycles for 4 – 7Hz, 5 cycles for 8 – 14Hz, 7 cycles for 15 – 20Hz, and 10 cycles for 21 – 30Hz. The total power values were contrasted between the different conditions, so no baseline correction in the frequency domain was performed for the oscillatory power analyses.

Statistical Analysis

For statistical analysis, we first calculated the mean accuracy (correct trials divided by the total number of trials for each condition), the RT, and the variability (SD) for WM probe responses as a function of the different event types (i.e., prior interference or matching). Next, behavioral data (accuracy and RT) were analyzed using two separate repeated-measures ANOVAs. The first rmANOVA had two factors: Task (DO WM, nonDO WM) and Congruency (congruent, incongruent) as a within-subjects factor. The second rmANOVA was performed with two within-subject factors: Task (DO WM, nonDO WM) and Matching (matched, non-matched).

To assess the neural processing behind conflict resolution during WM retrieval, we explicitly focused our ERP analyses on the P300 component and our time-frequency analysis on frontal-midline theta (fm-theta) power. Based on visual observation and previous literature (Ergen et al., 2014), the P300 was measured from 250 – 600ms in a central-parietal ROI (Channels Cz, CPz, CP1, CP2, Pz, P1, P2). The extracted values were analyzed with repeated-measures ANOVA to test for statistical significance ($p < 0.05$) using SPSS statistical software.

Furthermore, to evaluate the potential fm-theta effects, we performed statistical analyses on oscillatory power data that was time-locked to the WM probe, focusing on the congruency effects (Inc minus Cong trials). We extracted the mean theta-band (4 – 7Hz) power from a pair of midline-frontal electrodes (Fz, FCz) (Luu, Tucker, & Makeig, 2004). Power estimates from the midline-frontal region were then averaged across a section spanning the theta band and two time windows of interest (TOI: 200 – 400ms and 400 – 600ms), and then subjected to statistical analysis (Nigbur, Cohen, Ridderinkhof, & Stürmer, 2012). Additionally, to test the interference congruency effects and speed of processing, rmANOVAs were performed, followed by t-tests when required to interpret significant interactions ($p < 0.05$).

4.3 Results

4.3.1 Behavioral results - Descriptive Statistics

Shown in Table 6 are the descriptive statistics for the behavioral responses during retrieval (1) as a function of the prior color-discrimination interference (i.e., trials where the memoranda clashed with the Stroop-like distraction task during the maintenance period) and (2) as a function of match-to-sample (i.e., matched or non-matched). Both dual-tasks had faster RTs following a congruent color-discrimination (Stroop) condition ($p < .001$), regardless of whether the interference from the Stroop-like distraction had overlapping features with the memoranda. The retrieval as a function of match-to-sample showed faster RT for matched than non-matched ($p < .001$) condition, independent of prior interference. There was no difference in accuracy between the matched and the non-matched conditions on both our dual-tasks. Although, the accuracy during WM retrieval improved as a function of congruency only during the DO WM task *(p* = 0.11) but not during the nonDO WM task *(p* = .970) (see Figure 10). This better accuracy (mean accuracy of 94.6% vs. 92.7%) implies a potential facilitation effect only occurring when the feature domains overlap (i.e., color – color – color).

Table 6 Group mean (SD) values for behavioral performance during the WM probe (i.e., retrieval) as a function of prior congruency interference during maintenance and as a function of match-to-sample.

Behavioral data (Probe Response)						
	Prior Stroop Congruency			**Match-to-Sample**		
TASK	**Cong**	**Inc**	***p*-value**	**Match**	**Non-match**	***p*-value**
DO WM						
RT (ms)	578 (86)	622 (61)	< 0.001*	592 (78)	631 (73)	< 0.001*
Accuracy (%)	94.6 (4.0)	92.7 (5.1)	0.011*	94.0 (4.9)	93.2 (4.1)	0.217
nonDO WM						
RT (ms)	605 (60)	653 (70)	< 0.001*	566 (79)	606 (86)	< 0.001*
Accuracy (%)	93.5 (6.5)	94.0 (6.1)	0.970	93.8 (7.5)	93.2 (6.6)	0.669

Behavioral performance during retrieval due to prior interference

The rmANOVA results for accuracy on the WM probe did not revealed a main effect of task F (1,29) = 0.005, *p* = .943, $\eta^2 < 0.001$, but did reveal a main effect of congruency (higher accuracy preceding Cong trials), F (1,29) = 5.231, *p* = .030, $\eta^2 = 0.153$, as well as a significant task x congruency interaction, F (1,25) = 6.463, *p* = 0.017, $\eta^2 = 0.182$. Specific post hoc t-test contrasts examining this interaction revealed an effect of congruency on WM retrieval during the DO WM task, reflecting higher accuracy when preceded by a congruent Stroop-like event, t (1,29) = 3.421, *p* = .002. There was not, however, an effect of congruency during the nonDO WM task, t (1,29) = 1.607, *p* = .119. This finding suggests that interference is greater during the DO WM task, as seen by the specific effect in accuracy, only when there was an overlap in cognitive features. The rmANOVA for the RTs as a function of congruency showed a main effect of task (i.e., faster for DO than nonDO WM task), F = 24.832, $p < .001$, $\eta^2 = .461$), and a main effect of congruency (i.e., faster following congruent trials), F = 55.898, $p < .001$, $\eta^2 = .658$). However, there was no interaction between task and congruency for the RTs (F = 0.192, $p = .665$, $\eta^2 = .007$). Overall, the least demanding condition was the congruent trials within the DO WM task.

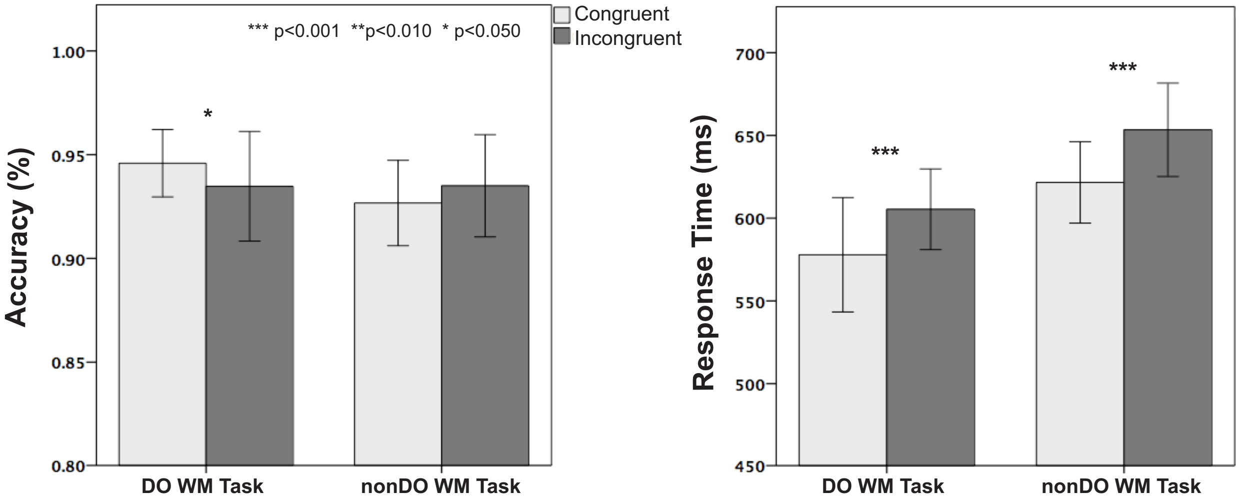


Figure 10 Behavioral data results. Mean accuracy and RT for the DO WM and the nonDO WM task during the retrieval phase as a function of prior color-discrimination interference.

Behavioral performance as a function of match-to-sample

Results for the rmANOVA on the WM probe accuracy as a function of match-to-sample did not show any main effects nor an interaction effect, F (1,29) < .343, $p > .378$. On the other hand, rmANOVA results for the RTs showed a main effect of task (i.e., faster for nonDO than DO WM task), F (1,29) = 13.841, $p = .001$, $\eta^2 = .323$, and a main effect of matching (i.e., faster for matching than non matching trials), F (1,29) = 34.850, $p < .001$, $\eta^2 = .546$, although no interaction, F (1,29) = 0.021, $p = .885$, η^2 =

.001. As anticipated, the DO WM task displayed slower WM retrieval responses, indicating a greater interference effect due to the nature of the color-discrimination distraction, regardless of its congruency. Also, matching trials showed faster responses than the non-matched trials (see Table 6).

4.3.2 Neural effects of Stroop-like interference on subsequent WM probe

Based on the significant difference in congruency on both the accuracy and RT, we decided to collapse the conditions across the matched and non-matched-to-sample trials. In other words, further EEG data analysis will concentrate on trials that are time-locked to the WM probe as a function of prior congruency interference for the DO WM and nonDO WM task, independently. This arrangement would reveal the neural mechanisms behind the facilitation effect found during the congruent trials, specific to the DO WM task.

P300 amplitude modulation in response to facilitation

The results of the rmANOVA using task and congruency as within-subject factors for the P300 (250 – 600ms) revealed a main effect of task, F (1,29) = 4.721, $p = .038$, $\eta^2 = .140$, a main effect of congruency, F (1,29) = 7.765, $p < .001$, $\eta^2 = .658$, and an interaction between these two factors, F (1,29) = 5.186, $p = .030$, $\eta^2 = .152$. Specific pairwise comparisons revealed significant differences between congruent and incongruent trials during the DO task (t (1,29) = 5.906, $p < .001$) and during the nonDO task (t (1,29) = 2.40, $p = .023$), where the P300 amplitude was larger for congruent trials in both dual-tasks. Overall, the largest amplitude of the P300 was for the congruent trials peaking at approximately 400ms during the DO WM task. Furthermore, Figure 11 illustrates the grand-average ERP waves for the DO WM

(Figure 11A) and nonDO WM tasks (Figure 11B). The grey shaded rectangles were placed to highlight the analyzed time frame for the P300 ERP component, which are represented in a bar graph in Figure 12 for easier visualization of the interaction. The increase in the P300 amplitude may be reflective of the facilitation effect.

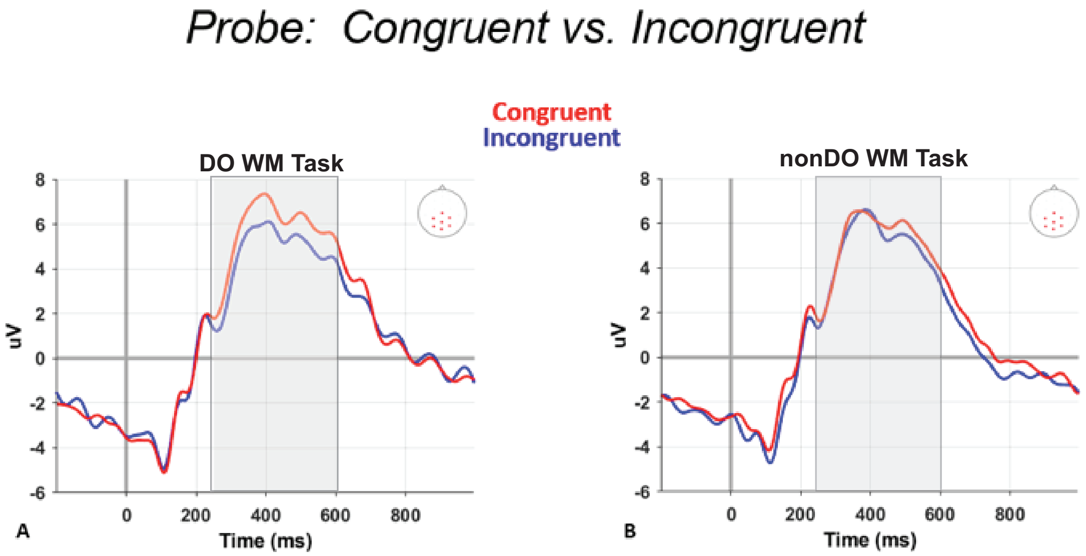


Figure 11 Grand-average ERP waveforms time-locked to the WM probe onset for the DO WM task (A) and the nonDO WM task (B) as a function of color-discrimination interference prior to the WM probe (i.e., retrieval). The ERPs were measured over a seven-channel region of interest (ROI). The channel layouts are on the upper right corner for each panel. The grey rectangles indicate the time frame (250 – 600ms) used for the analysis of the P300 component.

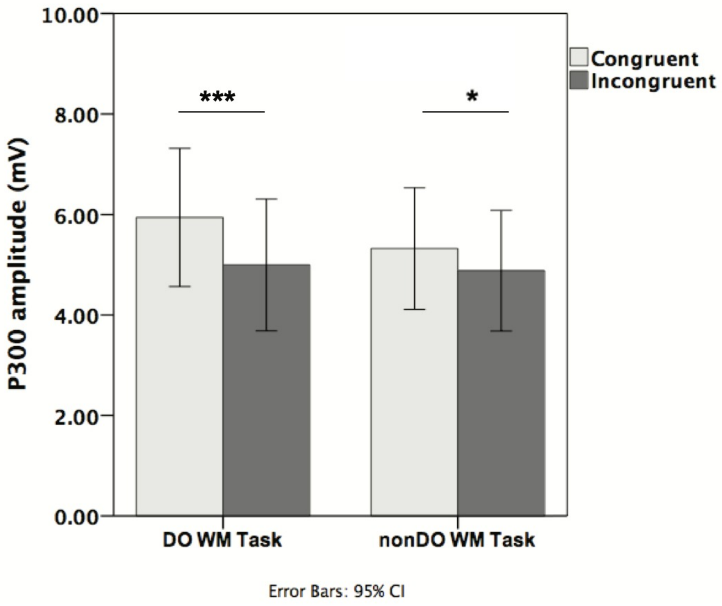


Figure 12 Grand-average P300 component activities during retrieval for the two dual-tasks separated by prior interference (i.e., Cong and Inc trials). ***** *p*-values < .001**

Frontal-midline theta modulation during retrieval in response to prior interference

We had hypothesized that retrieval of a memorandum following a greater cognitive interference, would lead to a greater cognitive effort reflected by a larger increase in fm-theta power (Eschmann et al., 2018). The rmANOVA performed for fm-theta (4-7 Hz) for the 1st time point of interest (200 – 400ms) revealed no main effect of task or congruency, and no interaction effect, F (1,29) < 0.923, *p* > .345. The rmANOVA for fm-theta power for the second time point of interest (400 – 600ms) did not revealed a main effect of task, F (1,29) = 0.86, *p* = .772, η^2 = .003. However, there was a marginal main effect of congruency, F (1,29) = 3.051, *p* = .091, η^2 = .095, and a marginal interaction, F (1,29) = 5.463, *p* = .122, η^2 = .080. A paired student t-test (uncorrected) was followed, the DO WM task revealed a significant difference between congruent and incongruent trials, t (29) = -2.132, p = 0.040, but no difference for the nonDO WM task, t (29) = -0.151, *p* = 0.881 (see Figure 13A & 13B). Figure 13C and 13D show the topographical maps of the color-discrimination congruency effect (Inc minus Cong trials) distribution, which are greatest around Fz electrode between 500 – 600ms. The larger fm-theta power suggests that fm-theta activity might reflect the resources needed for conflict resolution.

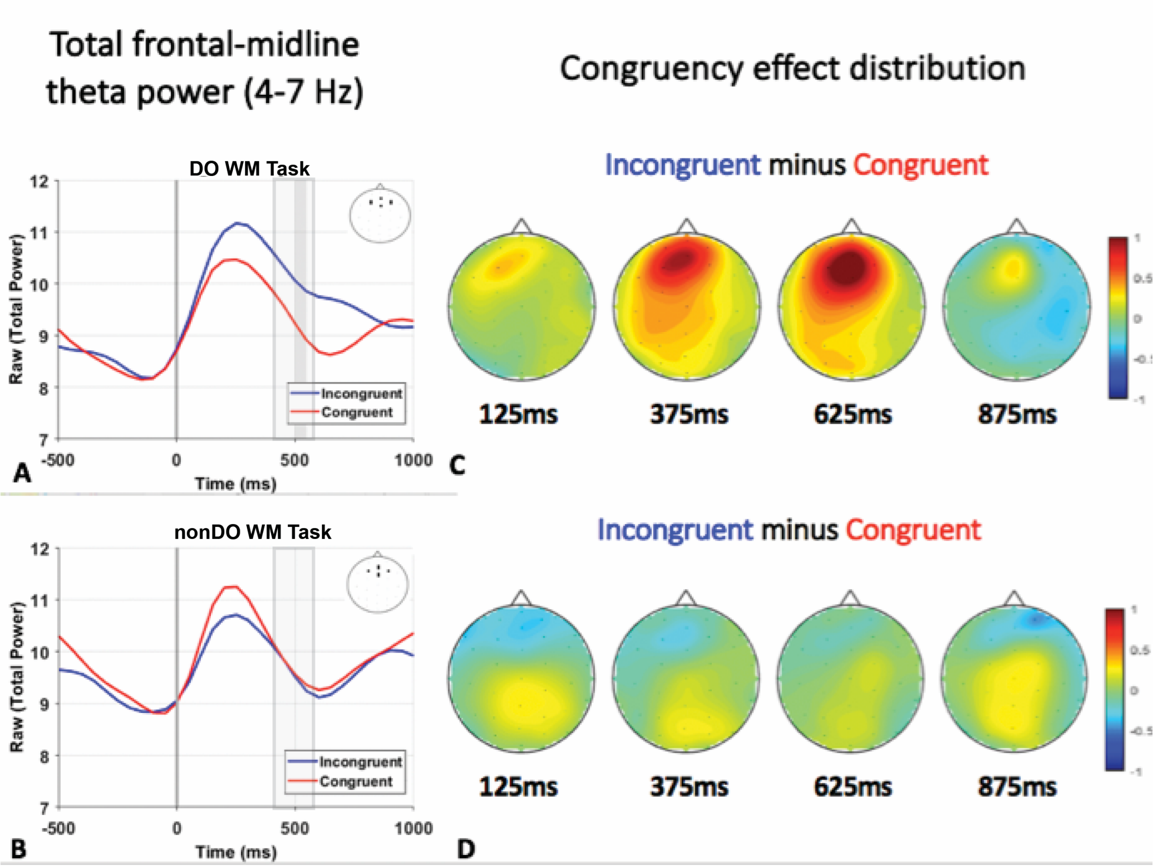


Figure 13 The averaged total theta power (4 – 7Hz) time-locked to the WM probe as a function of prior congruency interference is shown for the DO WM task (A) and the nonDO WM task (B). The electrode sites for the ROI used for the traces are shown on the top right corner of each graph. The blue line represents activity following an incongruent color-discrimination task, and the red line represents activity following a congruent one. The vertical darker grey line shown inside the light grey shaded area (A), illustrates the time

points at which Inc and Cong theta power were significantly different ($p < .05$). The shaded grey area was the time point used to average fm-theta (400 – 600ms) and obtain the topography plots. In the topography plots, the activity differences (prior Inc minus prior Cong) were plotted during the WM probe presentation during the DO WM task (C) and during the nonDO WM task (D). Warmer colors indicate positive dB values, and colder colors indicate negative dB values.

4.4 Discussion

The present study used a dual-task design to examine the neural mechanisms entailing conflict resolution during WM retrieval due to prior cognitive interference. Both our dual-tasks elicited different types of cognitive conflict during WM maintenance, which could be more or less demanding (i.e., incongruent vs. congruent) and within the same or different feature domain (overlapping vs. non-overlapping). We were interested in measuring the behavioral and neural differences in WM retrieval processes preceded by the different types of cognitive conflicts. Specifically, we wanted to know if the P300 amplitude or the fm-theta power modulated with the different interference effects between the domain overlapping (DO) versus the non-domain-overlapping (nonDO) dual-tasks.

Maintaining a color- or number-word in WM memory while having to perform a task during the maintenance phase makes the WM item or memoranda more vulnerable to interference. The DO WM task was meant to create an overall greater interference than the nonDO WM task given the shared features between the memoranda and the Stroop-like distractions (i.e., color-color-color). Although, in the congruent trials during the DO MW task, the color-discrimination task may also serve as a reinforcing event, leading to a facilitation effect during retrieval.

4.4.1 Behavioral effects time-locked to the WM probe

Our behavioral performance showed that having to maintain a numerical representation in WM while performing the color discrimination task, created less cognitive conflict than having to maintain a color representation. This finding is indicated by the faster response time during the nonDO WM task than the DO WM task, regardless of prior congruency. When conditions were separated by prior congruency, we found that response times (RTs) were faster for congruent than incongruent trials – producing the slowest retrieval response during the DO WM task with prior incongruent discrimination. This finding indicates that RT is sensitive to interference, potentially due to the general cognitive limits resource.

Additionally, we found that the memoranda were enhanced for trials with a congruent color-distraction during the DO MW task only, reflected by greater accuracy performance. In addition, we can speculate that accuracy was not affected during the nonDO WM task because the resources needed to accomplish that dual-task were orthogonal to each other. Thus, during the nonDO WM task, the external and internal representations were not completing for similar resources as in the DO MW task. This seems to be reflected by the electrophysiological measures, which we will discuss next.

4.4.2 Event-related potentials (time-locked to the WM probe)

P300 effects

We focused on the P300 amplitude differences during WM retrieval as a function of whether the Stroop-like distraction task was congruent or incongruent (Figure 11 & 12). Results showed a decrease in P300 amplitude at central-parietal sites for the conditions with prior incongruent interference during both dual-tasks, where having less attentional resources available for the maintenance of the memoranda might reflect the reduction in the P300 component at retrieval. These findings are complementary to other studies exploring interference during a Stroop task (S Hanslmayr et al., 2008) or cognitive efforts during an N-back task (Pergher et al., 2018). In Pergher et al. (2018) study, they implemented an N-back WM task, where both younger and older adults showed a decrease in P300 amplitude for the 3-back compared to the 1-and 2-back task (Pergher et al., 2018). In other words, the less demanding task showed greater P300 amplitude, consistent with what was observed in the current study. Together these studies support the observation that the P300 amplitude decreases with increased task load or interference, which is reflective of the diminished ability of attentional resources needed for conflict resolution.

Frontal-midline theta (fm-theta)

As previously mentioned, theta band power (4 – 7Hz) might also be sensitive to cognitive control mechanisms in WM (Eschmann et al., 2018; Scharinger et al., 2017) and has also been found to modulate with task difficulty (Chen et al., 2017). Specifically, increases in fm-theta are suggested to organize neural processes during a decision point where the information is integrated to inform action selection (Enriquez-Geppert et al., 2014). Previous studies have reported greater theta power over frontal electrodes during the incongruent condition in a classic Stroop task (S Hanslmayr et al., 2008; Tang, Hu, & Chen, 2013). Their time-frequency analysis revealed an increase in theta (4 – 7Hz) power for incongruent items, which emerged around 400msec and was strongest at 600 – 800msec. They concluded that the activation of theta oscillations for the Inc and negative priming condition likely reflects the activation of central executive processes, which are part of our WM system (A. Baddeley, 2012). The question we were interested in was whether conflict processing prior to WM retrieval would affect retrieval? If so, would there be a difference in fm-theta band power between our two experimental tasks?

To the best of our knowledge, this is the first study showing the fm-theta power modulations during the retrieval of a memorandum with prior interference. There were no significant differences in fm-theta power between incongruent and congruent trials during the nonDO MW task. One possibility for this outcome could be that the resources needed to suppress interference were better compartmentalized, providing similar cognitive effort levels. On the other hand, there was a significantly larger fm-theta power, specific to the 2nd time point of interest (400 – 600ms) following incongruent trials during the DO WM task. This finding could indicate that the strength of fm-theta power might reflect cognitive efforts (S Hanslmayr et al., 2008).

4.4.3 Conclusion

In closing, the aim of this chapter was to provide evidence on how behavior performance and neural correlates differ depending on whether the interference from the Stroop-like distraction, which was presented during the maintenance phase, was more (e.g., Inc trials) or less conflicting (e.g., Cong trials). Additionally, how interference would be reflected if the clash occurred within the same (e.g., DO WM task) or different (e.g., nonDO WM task) feature domains. Only during the congruent trials in the DO WM task was the memorandum reinforced, leading to a facilitation effect, which was reflected by having better accuracy, faster response times, and presented a larger P300 amplitude. Although, the P300 was sensitive to both our task when detecting congruency, that is, it displayed larger amplitude for the congruent trials regardless of whether the internal and external feature domain overlapped. On the other hand, fm-theta activity seems to be more sensitive to interference. There was a greater increase in frontal-midline theta power during the incongruent than in the congruent trials during the DO WM task, indicating the greater need to allocate cognitive resources. These results thus further our understanding of how the behavior and neural mechanisms are sensitive to interference and how facilitation effects are portrayed.

5. General discussion

5.1 Summary of findings and outline

The overarching purpose of this dissertation was to contribute to the growing understanding of the neural basis of working memory and attention, emphasizing the impact that physical exercise (PE) may have on such processes. Experiment 1 (pre-exercise intervention) demonstrated a positive association between decreases in theta power and behavioral performance during the delayed-match-to sample (DMS) working memory (WM) task. While alpha power decreases correlated with response time (RT) during the visual attention search (VAS) task. Experiment 2 (post-exercise intervention) was the first 4-month physical exercise intervention study in sedentary healthy young adults to quantify the exercise-induced effects on working-memory and attentional-related neural oscillations (Chaire et al., 2020). Only the exercise group showed an increase of alpha power over time, which correlated positively with changes in aerobic fitness and RT during the VAS task, suggesting that physical exercise modulates EEG neural oscillatory activity specific to visual attention. We attributed this exercise-induced change in alpha power to “neural efficiency.”

Experiment 3 revealed the behavioral and neural correlates involving conflict resolution due to prior interference during the maintenance phase of a WM task. The behavioral results during WM retrieval demonstrated a facilitation effect during the congruent-Stroop trials, specific to the domain-overlapping (DO) WM task, indicated by having better accuracy and faster RT during such trials. The P300 amplitude was more significant for congruent than incongruent trials regardless of whether the memorandum (i.e., color or number word) and the color Stroop-like distraction features overlapped. The frontal midline theta (fm-theta) showed distinctions between the DO and the non-domain overlapping task (nonDO) WM task, displaying a marginally larger fm-theta for the incongruent trials during the DO WM task, which may be reflective of the need for greater allocation of cognitive resources to tackle conflict resolution during WM retrieval.

The following chapter expands on how a physical exercise, whether acute or chronic, impacts working memory and attention, and discusses other relatable studies (Section 5.2). Also, the current results have implications for the characterization of EEG neural oscillatory activity during working memory, visual attention task, and their interaction (Section 5.3). Lastly, this chapter will mention the implications EEG as a technique can offer when studying such processes (Section 5.4).

5.2 Impact of physical exercise on the brain

Experiment 2 provides tentative evidence in support of exercise-induced changes in EEG neural oscillatory activity. Specifically, we found that sedentary young adults, who participated in a 4-month aerobic exercise regimen, showed increased frontal alpha power when performing a visual attention search (VAS) task but not during the DMS WM task, as we had initially expected. Additionally, frontal alpha power correlated with aerobic fitness changes, where the more considerable increase in aerobic fitness had a more substantial increase in anterior alpha power. Also, frontal alpha power correlated positively with task performances (RT - VAS task; see Figure 5). These findings led us to conclude that physical exercise may enhance attentional functions by the influence of neural circuitry at the anterior cortical region. The current findings go in hand with several rodent studies using embedded electrodes and with human studies using different techniques, such as ERPs (e.g., P300), near-infrared spectroscopy (NIRS) analysis, and fMRI, which I will further discuss throughout the next sections.

Several studies have focused on evaluating cortical activity and changes in athlete's alpha power compared to novices in several different sports. Decreases in alpha power, which some refer to event-related desynchronization (ERD), positively correlate with cortical activation. Such studies’ results are sometimes conflicting, as some indicated a stronger alpha ERD, while others observed a weaker and less prominent alpha ERD. There is not an established pattern as to whether particular athletes demonstrate a stronger or weaker alpha ERD. However, the majority of studies demonstrate that elite athletes in sports such as shooting, karate, gymnastics, and table tennis, displayed a weaker alpha ERD in task-relevant brain areas compared to novices during sport-specific tasks (Babiloni et al., 2010; Del Percio, Babiloni, Marzano, Iacoboni, Infarinato, Vecchio, Lizio, Aschieri, Fiore, Toràn, et al., 2009; Del Percio et al., 2008; Di Russo, Pitzalis, Aprile, & Spinelli, 2005; Wolf et al., 2014). That is, these subjects performed experimental tasks at similar levels, but athletes had a weaker alpha ERD (i.e., less cortical activation) to accomplish the same task as novices. Several researchers refer to this effect as neural efficiency (Babiloni et al., 2010; Del Percio, Babiloni, Marzano, Iacoboni, Infarinato, Vecchio, Lizio, Aschieri, Fiore, Toràn, et al., 2009; Wolfgang Klimesch, Doppelmayr, & Hanslmayr, 2006).

Notably, one could argue that this effect could be related to an athletes’ expertise on the sport rather than having a higher fitness level than novices. Although, researchers have also investigated the relationship between cortical activity and exercise and have observed that improvements in AF (VO_2 max) were accompanied by a reduction in cortical activity (Ludyga et al., 2016; Ludyga, Hottenrott, & Gronwald, 2017). In a study conducted by Ludyga et al. (2016), they ran a 4-week cycling intervention training where they measured the cortical activation of 22 cyclists (27 ± 4 years; 7 female) during a high and low cadence training (LCT). They observed that improvements in aerobic fitness, an indicator of endurance capacity, were associated with decreases in cortical activity only after the high cadence training (HCT). Ludyga et al. (2016) interpreted these results in terms of the neural efficiency hypothesis. That is, the intensity of exercise after 4 weeks of training was no longer high enough to cause a redistribution of cortical activity towards regions involved in planning and executing motor commands.

The previous study indicated the enhanced capacity for resource allocation during a sports-specific task. In Experiment 2, the EEG neural oscillatory measures were taken during two specific cognitive tasks. Such results are in line with the previously mentioned studies, showing a significantly smaller decrease in frontal alpha power in the post intervention (i.e., weaker alpha ERD) than in the pre intervention. This exercise-induced effect was not present in the control group. Note that the change in frontal alpha power (post intervention minus pre intervention) represents a significant increase in alpha activity over time. This increase in alpha power predominated in the frontal electrodes during the visual attention search (VAS) paradigm, suggesting that physical exercise may enhance the “neural efficiency” of trainees. In other words, the trainees are utilizing less cortical activation to accomplish the same task. Additionally, this and the previous mentioned study observed the exercise-related efficiency effect to be localized in the frontal brain region (Chaire et al., 2020; Jonasson et al., 2017; Ludyga et al., 2016).

The neurotrophic hypothesis claims that a pronounced release of distinct neurochemicals (e.g., BDNF) occurs in response to exercise, triggering a complex neurobiological process evoking functional and/or structural brain changes that facilitate improvements in memory functions (Kirk I Erickson et al., 2011; Ruscheweyh et al., 2011) and executive functions (Jonasson et al., 2017). Hence, we assumed that treadmill running would cause changes in the brain's molecular and structural basis, therefore potentially modulating the participant's EEG neural oscillatory power (i.e., increase in alpha power over time) and transfer as an improvement in behavioral performance. However, we did not observe improvements in mnemonic discrimination, or decrease in response time, or increase in accuracy during the attention-search.

Moreover, all participants (regardless of group assignment) have an overall decrease in performance throughout the DMS task. It can be argued that the images shown in the post intervention were more difficult than the ones shown in the pre intervention, yet, there should have been less of an accuracy decline for the exercise group if the exercise intervention were to increase mnemonic discrimination (Suwabe et al., 2017). As for the VAS task, while the accuracy remained the same for both groups, the control group had slower reaction times after the intervention than the exercise group, although the average groups' RT were not significantly different. A reason could be because participants were performing near ceiling (see Table 3).

Also, several factors may have played a role in the lack of behavioral differences due to physical exercise, such as age, aerobic fitness level, working memory capacity, and to an extent, a combination of all of the above. The following section will elaborate on these factors.

5.2.1 Factors influencing the lack of behavioral effects

The vast majority of studies focusing on the effects of physical exercise on cognitive functions have been directed towards the developmental or aging trajectories undergoing cognitive changes and less so focused on younger adult population (Kirk I. Erickson et al., 2015; Jonasson et al., 2017; Maass et al., 2015; Moriya et al., 2016). An example is a recent review (2018b) on the effects of physical exercise training on cognitive functions, in which out of the nine longitudinal studies presented, seven were concentrated on the older adult population, and two focused on children (Sousa et al., 2018a). Older adults tend to have worse memory, manifesting as greater susceptibility to cognitive deterioration. Physical exercise has been found to ameliorate cognitive decline in older adults (Consortium, 2017; Duzel, van Praag, & Sendtner, 2016; Kramer & Erickson, 2007; Prakash et al., 2011). Hence, the impact of exercise-induced effect in older adults might be more robust compared to young adults who are considered to be in the prime stage of their lives, leaving them with less potential for exercise-induced cognitive improvements (Sousa et al., 2018b).

Furthermore, cross-sectional research demonstrates that individuals with lower baseline cognitive performance benefit the most from exercise (Huang et al., 2015; Sibley & Beilock, 2007b). For example, Sibley et al. (2007) found that only those healthy young adults (N=48, M= 21.5 ± .65 years) lowest in working memory performed better during an Operation- and Reading-Span task after a single 30-minute self-paced bout of exercise on a treadmill (Sibley & Beilock, 2007a). Their finding adds to the idea that the impact of exercise on cognition is not uniform across all individuals and that individuals with lower memory capacity have more potential for cognitive improvements. In Experiment 2, a greater number of subjects were recruited from the University's medical campus; therefore, we can assume that our participants have higher memory capacity than an average healthy young adult, adding another reason for not finding any behavioral increases after 4-months of physical exercise.

5.2.2 The influence of aerobic fitness and acute exercise on cognitive processes

Exercising regularly is a highly effective strategy for maintaining cognitive health throughout the lifespan, and it is known to increase an individuals' aerobic fitness (AF), which is typically established by one's maximum oxygen uptake levels (VO_2max). Notably, AF is a complex measure, a composite dependent on primarily anaerobic and aerobic efficiency of muscle, muscle speed and strength, and body composition. Whether it is changing because of increased activity or lack thereof, it is in continuous variation affected by physical activity, metabolism, sleep, stress, and genetic profile. Between 40% to 50% of an individual's genetic profile influences their aerobic fitness level (Bouchard, 2012). Nonetheless, AF has been a strong predictor of cardiovascular health (DeFina et al., 2015) and has a positive association with memory functions (for review, see Rigdon & Loprinzi, 2019). The majority of cross-sectional and longitudinal studies rely on AF measures (i.e., VO_2max) to understand the relationship between physical activity with behavioral performance and neurocognitive function. During Experiment 2, it was important to select sedentary healthy young adults to participate in the study, not only to have a similar low-level fitness baseline but also to have a greater margin to improve their AF from our 4-month PE intervention.

Cross-sectional studies are faster to conduct and, therefore, more abundant than longitudinal intervention studies (Sousa et al., 2018b). However, cross-sectional studies do not show changes over time within individuals; they rely on comparing an individual's aerobic fitness levels. Nonetheless, a small number of cross-sectional studies have helped quantify the exercise-related benefits as a mean of oscillatory neural correlates (Chang et al., 2015; Wang et al., 2015). Kao et al. (2020) quantified the acute effects of exercise on behavioral and neuroelectric indices during a WM N-back task. This study consisted of 23 young adults (M = 19.2 ± 0.6 years) walking for 20 minutes on a treadmill at an intensity of roughly 65% of their maximum heart rate followed by a 1 & 2-back WM task. They did not show exercise-induced improvements in mean accuracy and RT during the N-back tasks. Also, there were no significant effects on fm-theta. They did, however, revealed an increase in frontal alpha power in the 2-back, which was observed following the aerobic exercise condition. Their findings suggest PE upregulated frontal neural activation involved in top-down cognitive control processing as WM load increased (Kao, Wang, & Hillman, 2020). This finding goes along with our correlation between performance during the VAS task and the alpha power changes (i.e., accuracy).

Previous studies have documented that participants with higher aerobic fitness levels have better cognitive functioning than those with lower AF levels**.** Particularly, older adults with higher fitness levels have been reported to possess a greater brain cortical functional connectivity related to cognitive control (Voss et al., 2010) and attention (Prakash et al., 2011). Other researchers, such as Dupuy et al. (2015), suggest that individuals with higher aerobic fitness levels perform better during visual attention tasks regardless of the participants' age. Their study obtained data from 22 young women (average age = 24.6 ± 3.6) and 36 older women (average age = 62.9 ± 5.4) performing a modified Stroop color test. They found that overall, females with higher VO_2max performed better in the computerized Stroop task than females with a lower VO_2max. Together, these studies demonstrate that an individual's aerobic fitness level, appears to be an essential factor influencing the brain's cognitive abilities.

Furthermore, ERP measures such as the P300 have given insight into how PE affects behavior and neuroelectrical performance after an acute bout of exercise. In a review by Sousa et al. (2018), seven out of eight studies reported increased P300 amplitude after an acute exercise (Sousa et al., 2018a). For example, a study by Tsai et al. (2014) assessed the effects of acute exercise on a visuospatial attention task in young adults with different aerobic fitness levels. They found that the group with higher fitness levels exhibited larger P300 amplitude after the acute exercise. It is, therefore, logical to assume that already engaging in an acute bout of exercise may increase neural activation and physiological arousal, which facilitates the allocation of more attentional resources during a cognitive task (Tsai et al., 2014).

5.3 Theta and alpha power during working memory and attention processes

5.3.1 The neural correlates of WM – fm-theta power

Despite the numerous studies quantifying EEG neural oscillations, there continues to be an inconsistency on whether theta power increases or decreases with working memory. The majority of the studies published show an increase in theta power during the encoding, maintenance, and retrieval of a WM item (Liang Tien Hsieh & Ranganath, 2014; Levine et al., 2005; Liang et al., 2017; Maurer et al., 2015). However, throughout the DMS task we observed a decrease in fm-theta power during the maintenance phase, which also correlated with behavioral performance. Nonetheless, some intracranial EEG (iEEG) studies have found that memory formation correlates with a decrease in theta power (Burke et al., 2013; Guderian et al., 2009).

A recent iEEG study by Brzezicka et al. (2019), investigated the patterns of theta power changes as a function of memory load during maintenance in three areas critical for WM: dorsolateral prefrontal cortex (DLPC), dorsal anterior cingulate cortex (dACC), and hippocampus. The participants consisted of a wide age range, the youngest adult being 17 years and the oldest 70 years (M = 37.6 ± 16.2 years, N = 13,). Their findings showed a theta power increase for both the hippocampus and the dACC but a decrease in the DLPFC during the maintenance. Such a decrease was proportional to memory load; that is, adults found to have a relatively larger decrease in theta power were overall faster in accessing WM. Increases in theta power observed in the dACC and the hippocampus did not correlate with behavioral performance. Their study revealed a pattern of theta power decrease in the DLPFC that was predictive of behavior (Brzezicka, Kamiński, Reed, et al., 2019).

Relatedly, the neurocognitive correlation obtained from Experiment 1 estimated a relationship between fm-theta power and working memory (WM) performance during the DMS task, where higher accuracy (i.e., corrected hit rate) and faster response time correlated with decreases in theta power values. In other words, the relatively larger decrease in fm-theta power during the maintenance phase, the faster participants recognized a lure, and the more accurate they were at mnemonic discrimination. These correlations add to the existing evidence that fm-theta power is related to the activation of relevant visual information that is actively being held in memory.

A limitation of Experiment 1 (i.e., in Chapter 2) was that I did not assess the theta and alpha power for lures and hits or target-absent and target-present trials separately. This was not possible due to the scarce number of trials, specifically in the lure condition. Thus, it is uncertain if theta and alpha power differs within each paradigm. Previous neuroimaging studies have documented different neural mechanisms between presenting novel stimuli, lures, and a repeated image. This phenomenon is known as repetition suppression, in which a decrease in fMRI hippocampal (DG/CA3) activity is observed when a repeated stimulus is presented compared to a novel or lure stimuli. Acquiring EEG on stimuli with subtle differences within both of our experimental paradigms might give an insight about the underlying mechanisms of phenomenon such as repetition suppression.

5.3.2 The role of cortical activation in visual attention – alpha power

Decrease in alpha band power (9-12Hz) happens during a broad set of cognitive processes. In some circumstances, this decrease is thought to reflect cortical activation concerning cognitive functions such as general attentional demands and inhibitory processes (Wolfgang Klimesch, 2012; Womelsdorf & Fries, 2007). Experiment 1 showed a decrease in alpha power during both the DMS and VAS task, where alpha power decrease was strongest over posterior electrodes relative to the center and frontal electrode sites. It also correlated with the reaction time for the visual attention search (VAS) task. Notably, alpha power decrease was larger for the more demanding task, suggesting that the degree of attentional resources needed, plays a role in modulating alpha power (Van Diepen, Foxe, & Mazaheri, 2019; Worden, Foxe, Wang, & Simpson, 2000).

The neurocognitive correlations for alpha power only correlated with the VAS task and not the DMS task. The alpha band power values evaluated for the correlations were averaged from the posterior electrodes, given that alpha band power had the largest decrease in posterior regions. As expected, a correlation existed between alpha power and behavioral performance, although this correlation was only significant during the target-absent trials (see Figure 5). Similarly, when we correlated the changes in behavioral performance (post minus pre intervention values) and changes in alpha band power (see Chapter 3), the correlation was significant only for the target-absent trials (see Figure 10). This outcome might have happened because target-absent trials are more engaging given that participants spent significantly longer time and attentional resources to ensure that the target was absent. Therefore, explaining why a significant correlation was observed during the target-absent condition and marginal during the target-resent trials.

5.3.3 EEG measures of conflict resolution in WM from prior interference

Working memory and attention are interrelated cognitive processes; what we maintain in WM can affect our attention and, in turn, impact the way we interact with stimuli in our environment (Awh, Jonides, & Reuter-Lorenz, 1998; Kiyonaga & Egner, 2014). Likewise, our environmental interaction can also influence the information we try to maintain in WM (Oberauer, 2019). Measuring the underlying neural cascade of conflict resolution processes during WM retrieval can help us understand the internal and external brain processes that occur from prior interference. Note, that the interference arises during the maintenance phase from the clash between the internal representation (i.e., the word being encoded) and the external representation (i.e., the Stroop-like distraction task). With the idea that the interference will differ depending on whether their features overlap. The key difference between our two dual-tasks was that one requires encoding a color representation (e.g., “red”) and the other a number representation (e.g., “five”).

Oberauer (2019) and others have demonstrated that engaging perceptual attention to a secondary task during the retention interval is susceptible to interference (see review Oberauer, 2019; Samrani, Marklund, Engström, Broman, & Persson, 2018). On the other hand, attending to a congruent external stimulus, in some cases, may reinforce the memoranda if the internal and external representations are congruent (e.g., having “red” as the sample stimuli, showing a red patch during the maintenance phase, and having “red” as the probe stimuli). In a study by Barrouillet and Camos (2012), they coined this event as attentional “refreshing” of the memorandum (Barrouillet and Campos, 2012), which leads to a strengthening of the memoranda (e.g., the word “red”). Hence, researchers can manipulate the maintenance phase to either increase interference or further enhance the memorandum’s activation by introducing an element that reinforces it.

In Experiment 3 (i.e., Chapter 4), WM retrieval during the two dual-tasks had different congruency effects, depending on whether the memoranda’s and the Stroop-like distraction’s features overlapped domain-wise (i.e., semantically). Behaviorally, having the Stroop-like distraction task in the same feature domain led to a greater difference in accuracy between incongruent and congruent trials during the DO WM task only. This indicates that the Stroop-like distraction task allowed for the rehearsal or refreshing of visual contents, which led to the facilitation of retrieval. This outcome is represented by the higher accuracy and faster response time for congruent trials during the DO WM task. Accuracy was not affected during the nonDO WM task because the resources needed to accomplish the task were orthogonal to each other. That is, the external and internal representations were not competing for similar resources as in the DO WM task, nor were the memoranda being facilitated (see Table 4). The EEG effects will be discussed in the next two subsections.

5.3.4 Facilitation of P300 during WM retrieval

The P300 amplitude is known to modulate with interference variations (S Hanslmayr et al., 2008), and task demands due to increased WM load (Pergher et al., 2018; Pratt et al., 2011). Hanslmayr et al. (2018) conducted a study, in which 21 young adults (M = 24.9 years; 16 females) performed a classic and modified versions of a Stroop task. This experimental paradigm was design to create a linear increase in interference from congruent and neutral trials producing a smaller conflict, to incongruent and negative priming trials creating a larger interference. They found that around 400msec after stimulus onset, the congruent and the neutral items elicited stronger positivity at fronto-central sites. Our findings indicate that the time window around 400msec is not only sensitive to interference in the Stroop task but continues to be present well into the retrieval section.

In Experiment 3, we see that the P300 activity response to WM retrieval corresponded to the behavior performance in that the decrease in P300 amplitude may be reflective of a diminished ability of attentional resources needed for conflict resolution. Although, another possibility could be that the increased P300 amplitude is a sign that the memoranda was reinforced or facilitated during the DO WM task following congruent versus incongruent trials. Notably, the other three P300 components had similar amplitudes, indicating that the P300 activity during the DO WM retrieval following congruent Stroop-like distraction stimuli could be explained by reinforcement on memoranda on congruent trials. This increase in P300 amplitude was analogous to having better accuracy and faster response for congruent trials during the DO WM task.

5.3.5 Modulation of fm-theta power during retrieval by prior interference

Fm-theta band activity can serve as a neural marker of the dynamics of interference in selective episodic retrieval (Staudigl et al., 2010) and in conditions with higher need for cognitive control (Eschmann et al., 2018). In particular, fm-theta is involved in the resolution of different types of interference occurring at distinct processing stages

(Nigbur et al., 2012). In Experiment 3, we found that fm-theta power during WM retrieval was significantly larger for the incongruent than the congruent interference during the DO WM task, which may be reflective of the need for greater allocation of cognitive resources to tackle conflict resolution during WM retrieval (see Figure 13). During the nonDO WM task, there was no difference in fm-theta power during retrieval between congruent and incongruent trials. This absence of modulation involving interference suggests that participants equally engaged cognitive control during the nonDO WM task. The strength of fm-theta power reflects the engagement of cognitive control with greater power is associated with greater cognitive control demands (S Hanslmayr et al., 2008).

5.4 Future directions and outlook

Previous studies have shown that subjects with higher-fitness levels can cognitively benefit the most from engaging in physical exercise (Budde, Brunelli, Machado, Velasques, & Ribeiro, 2012). Perhaps training participants with initially different aerobic fitness levels (high vs. low) could yield a difference in cognitive performance after a long-term physical exercise intervention, where the higher-fit subjects have a higher chance of increasing their behavioral performance. Another idea could be to separate groups by MW capacity, where participants with lower WM capacity have an advantage of benefiting from a PE regimen compared to those with already high WM capacity. An experimental design that includes young adults would benefit the most with these types of arrangements.

Moreover, it would be beneficial for future studies to incorporate accelerometers or activity bracelets during the intervention for monitoring every physical activity, such as using a bike, playing sports, and engaging in other physical activities. The monitoring of daily activity could be an incentive for participants to increase their fitness outside of the laboratory setting. An advantage of this could be that participants increase their activity even more. On the downside, this could increase the variability of how the participant gained the fitness increase. Nonetheless, it would be a great idea if the overall aim were to quantify the brain changes from an interval where participants exercised or changed their sedentary lifestyle for a more active one.

The use of physical exercise is a promising tool not only for children and older adults but for healthy young adults as well. Future studies can create EEG markers or establish oscillatory patterns that could assess the potential value of cardiovascular training in a variety of different disorders, such as traumatic brain injury, depression, addiction, and anxiety disorders.

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