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Investigating the suitability of neurofeedback to improve fatigue

Simon Hanzal
(MA, MSc)

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Doctor of Philosophy

School of Psychology and Neuroscience
College of Medical, Veterinary and Life Science
University of Glasgow
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Abstract

Fatigue is an adverse subjective state occurring during demanding tasks, often coupled with vigilance decrements and changes in the associated brain signal oscillations. Surveys indicate age-related imbalances in fatigue, making older age groups a viable target to investigate fatigue in the healthy population.

In this thesis, I examined fatigue during sustained attention decline (as reflected in vigilance decrements), both behaviourally and neurally, across young and older age groups. Electroencephalographic metrics of increases in alpha and other lower frequency oscillations, both pre-stimulus and in relation to the task, were of particular interest. These oscillations have been previously associated with vigilance decrements and used in neurofeedback interventions targeting fatigue symptoms. I also examined motivational factors potentially contributing to the age-related effects. Using different adaptations of the Sustained Attention to Response Task (SART), three empirical studies examined how fatigue manifests in performance and neural activity across the young and healthy older samples.

Chapter 2 demonstrated that the SART can induce subjective fatigue and that this change relates to accuracy change. However, its key finding was a higher accuracy in older adults, with only limited age-specific fatigue effects. In **Chapter 3**, an extended version of the SART including extensive EEG measures additionally revealed neural changes over time commonly associated with fatigue (increased pre-stimulus alpha and task-related beta synchronization), but these were correlated neither to subjective fatigue nor to a performance decline. Instead, age again emerged as the primary drive of the behavioural and neural responses to the task, further showing a prospective link to motivation. In **Chapter 4**, I thus shifted focus from time-on-task to testing possible motivational effect directly. Young and older participants were equalised to the same accuracy level by titration of task difficulty. Initially, higher motivation helped older participants match the young group's performance. Then, following an unexpected motivational initiative, young participants became motivated and showed larger accuracy improvement compared to the older group. Fatigue had little impact on performance or age effects.

I conclude that sustaining attention over time can incur a subjective experience of fatigue, but an accompanying shift in neural oscillations is uncorrelated and likely only reflects covert changes in attentional processes. My findings thus challenge the assumption of a tight coupling of fatigue to performance decline and neural pattern changes in sustained attention. This also casts doubt on the efficacy of neurofeedback treatments of fatigue by targeting these patterns. Instead, I highlight the interplay of age and motivation as drivers of performance (and brain dynamics) during sustained attention and posit them as a more promising focus for future interventional research.

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I would like to dedicate this work to the glory of God, who is the source and main inspiration for my love for seeking truth through scientific inquiry. I am thankful to Him for this wonderful world He made for us to discover, for making the brain an unsolvable but beautiful mystery and for guiding me all the way to the submission of this thesis.

Author's Declaration

I declare that, with the exception of explicit reference indicated in the text, this thesis represents my own work and it does not include any work submitted towards any other degree.

Simon Hanzal

Abbreviations

ADHD	Attention Deficit Hyperactivity Disorder
ANOVA	Analysis of Variance
BCI	Brain-Computer Interface
BST	British Standard Time
CFS	Chronic Fatigue Syndrome
CIS	Checklist of Individual Strength
CRT	Cathode Ray Tube
EEG	Electroencephalogram
ERP	Event-Related Potential
fMRI	functional Magnetic Resonance Imaging
GFP	Global Field Potential
IAF	Individual Alpha Frequency
ICA	Independent Component Analysis
LFP	Local Field Potential
IMI	Intrinsic Motivation Inventory
M	Mean
MFI	Multidimensional Fatigue Inventory
MoCA	Montreal Cognitive Assessment test
MRI	Magnetic Resonance Imaging
ms	Millisecond
MS	Multiple Sclerosis
mTBI	mild Traumatic Brain Injury
MW-S	Mind-Wandering State
OECD	Organisation for Economic Co-operation and Development
OSF	Open Science Framework
PMBR	Post-Motor Beta Rebound
PSF	Post-Stroke Fatigue
SART	Sustained Attention to Response Task
SD	Standard Deviation
SMR	Sensory-Motor Rhythm
tDCS	transcranial Direct Current Stimulation
TF	Time-Frequency
VAS	Visual Analogue Scale
VAS-E	Visual Analogue Scale for Energy
VAS-F	Visual Analogue Scale for Fatigue
VAS-M	Visual Analogue Scale for Motivation

Previous dissemination of findings

All empirical chapters in this thesis were preregistered on the Open Science Framework (https://osf.io) prior to the commencement of the main data collection.

Chapter 2

Conference talk: **Hanzal, S.**, Learmonth, G., Thut, G., & Harvey, M. (2022, July 13-15). *Measuring attention in the general population: An online study* [Conference talk]. EPS Meeting 2022, Stirling, United Kingdom.

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Chapter 3

Published abstract: **Hanzal, S.**, Learmonth, G., Thut, G., & Harvey, M. (2023). Neural correlates of inducing fatigue with a sustained attention task. *Journal of Vision (Charlottesville, Va.)*, *23*(9), 4923. https://doi.org/10.1167/jov.23.9.4923

Conference poster: **Hanzal, S.**, Learmonth, G., Thut, G., & Harvey, M. (2023, May 19-24). *Neural correlates of inducing fatigue with a sustained attention task* [Conference poster]. VSS Meeting 2023, St Pete's Beach, Florida, USA.

Conference poster: **Hanzal, S.**, Learmonth, G., Thut, G., & Harvey, M. (2023, July 22-26). *Neural correlates of inducing fatigue with a sustained attention task* [Conference poster]. OHBM Meeting 2023, Montreal, Canada.

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Chapter 4

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Findings related to the present thesis

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Chapter 1: Introduction

General Introduction

Background

Our daily lives are filled with many demanding tasks. Fatigue is a key experience accompanying these, both in the general population and in patients with various clinical disorders. While current research does not unanimously agree on fatigue's definition (Hockey, 2013, Chapter 1), neuroscience, in its many clinical models, generally understands fatigue as a prevention mechanism, modifying behaviour in light of demands placed on the individual (Boksem & Tops, 2008; Hockey, 2013, Chapter 2)[1].

To study fatigue, neuroscience researchers have employed tasks demanding either physical exertion (Baranauskiene et al., 2023; Behrens et al., 2023; Boolani & Manierre, 2019) or involving attentional (Reteig et al., 2019), memory (Wylie, Genova, et al., 2017) or other cognitive processes (Behrens et al., 2023). In addition to behaviour, the brain's response to the tasks is commonly measured using methods such as the electroencephalogram (EEG; Berger, 1929). Findings from these investigations corroborate present frameworks for fatigue (Pessiglione et al., 2025), often derived from clinical symptomatology (Kuppuswamy, 2022), providing markers or even targets for possible interventions. An example of these is neurofeedback, a therapeutic method where patients receive a reward for achieving a change in their brain signal (Frederick, 2012; Othmer & Othmer, 2017).

The principal aim of this introductory chapter is to review the currently proposed correlates of fatigue in the context of one chosen specific research paradigm - sustained attention - and to evaluate their relevance to intervention. More

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[1] This general framework echoes intuitions of pre-empiricist thinkers about the behavioural adversity of idleness (Aquinas, 1880, Part II-II:35; Aristotle, 1877, Sections 1100a–1101a), as well as the work of early empirical psychologists such as Thorndike, who described the negative impact of task monotony on performance quality (Hockey, 2013, Chapter 2). The fundamental assumption is arguably still evident in much research on fatigue.

specifically, there continues to be no clinically approved universal treatment for fatigue (Acciarresi et al., 2014; Castro-Marrero et al., 2017), despite the strong demand for accessible therapies without side effects (Whitehead et al., 2016). The introduction establishes the need for greater scrutiny of fatigue correlates as a target for interventions. Specifically, it underscores the necessity for further neural examination of the impact of time-on-task and age on fatigue during sustained attention.

Measurement and manipulation

One of the crucial distinctions in fatigue research is between subjective fatigue, commonly measured by self-report questionnaires or qualitative report (Vries et al., 2003), and objective fatigue (Filippi et al., 2022; Herlambang et al., 2021; Hockey, 2013, Chapter 1; Völker et al., 2016a). While task performance and brain signals are commonly included among fatigue's objective measures, they also extend to methods such as posturography, heart rate variability or eye pupillometry (Herlambang et al., 2021; Völker et al., 2016a). Characterising the relationship between subjective and objective measures underpins much of fatigue research and is understood to be one of its key aims (Jacquet et al., 2021). Yet, attempts to connect the two domains directly have so far faced mixed results (Pessiglione et al., 2025; Völker et al., 2016b). It is then proposed that either the objective element (Dantzer et al., 2014; Karshikoff et al., 2017) or the subjective one (Penner & Paul, 2017) is more important to the overall characterisation of fatigue. Here, I review findings from each respective domain and establish the continued need to research them in alignment.

Subjective fatigue

Fatigue in the healthy population

Research interest in the level of self-reported fatigue[2] in the general population stretches back over at least 25 years (Watt et al., 2000) and continues until the present day (J.-H. Yoon et al., 2023). The definition of fatigue employed in populational surveys varies depending on the trait questionnaires used, and is commonly a derivative of clinical models of fatigue (Karshikoff et al., 2017), such as the multidimensional fatigue inventory (MFI; Engberg et al., 2017; Hinz et al., 2013; Vries et al., 2003; Watt et al., 2000), a Checklist of Individual Strength (CIS; Vries et al., 2003) or direct administrations of symptom measures of Chronic Fatigue Syndrome (CFS; van't Leven et al., 2009).

Over time, surveys have gradually increased in scale, reaching a peak with the work of Yoon et al. (2023), who compiled data from over 600.000 participants to characterise fatigue at a populational level. They estimated factors predictive of fatigue, as well as its general prevalence. Based on their data, general fatigue (defined as lasting less than 6 months) was characterised as present in 24% of adults and 12% in minors, with prevalence up to 42% in specific occupations, with chronic fatigue (lasting over 6 months) present in 8% of adults, 2% of minors, and 6% in specific occupations. Females had higher fatigue prevalence than males, moderate fatigue was more common than severe fatigue, unexplained fatigue was more prevalent than explained fatigue, and Asian populations had higher overall fatigue prevalence (on this as a cultural difference, see Cumming et al. (2016)).

Alongside a marginal effect of gender, surveys have identified a connection between general fatigue and age (Watt et al., 2000) with some indicating that the

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[2] Some researchers consider fatigue measured in populational surveys to be a prolonged state rather than a trait (Filippi et al., 2022), meaning proclivity to fatigue over a longer time period. In contrast, experimental probes of fatigue (Wiemers & Redick, 2019) have generally been targeting it as a fully dynamic state (Calderwood & Ackerman, 2011). State fatigue shifts during tasks and is independent of other states (Boolani et al., 2019; Lerdal et al., 2013). State and trait fatigue are considered to be closely intertwined (Vlietstra et al., 2019). It is reasonable to predict that trait fatigue suggests heightened state fatigue. (Manierre et al., 2020).

middle-aged have higher fatigue prevalence than those of advanced age (Galland-Decker et al., 2019; Gilsoul et al., 2022), while others showed that younger individuals are more fatigued than older ones (Aggarwal et al., 2006; Engberg et al., 2017; Fuhrer & Wessely, 1995). Elsewhere, older individuals were the ones reported as experiencing higher fatigue levels (Beutel et al., 2002, 2004; Hinz et al., 2013; Vestergaard et al., 2009). In short, populational studies hint at a relevance of age in fatigue but are limited in the ability to adequately outline its core contributing factors due to the different tools, timescales and samples used (Eldadah, 2010). Overall, demographic studies underscore the timeliness of studying how age differences underpin fatigue. In addition, the surprising outcomes of lower or equal fatigue levels in the healthy older population may be explained by the increased prevalence of patients in the older age groups, who present with high fatigue levels. These patients are typically excluded from surveys, but if added to the general population, would make the older adults group the most fatigued (K. F. Cook et al., 2011).

Fatigue in specific clinical populations

As mentioned, aside from studies of fatigue in the general population, high prevalence of fatigue has been observed in several patient groups, typically those comprising older adults. Notably, fatigue in older adults was generally found predictive of earlier onset of multiple disorders (Avlund et al., 2002; Hardy & Studenski, 2008; Liao & Ferrell, 2000). Attempts have been made to synthesise accounts of fatigue in several of these clinical groups at once (Behrens et al., 2023; Chaudhuri & Behan, 2004; Kuppuswamy, 2022). Nevertheless, most research characterises fatigue only in one clinical condition, without an overarching model. A short outline below summarises fatigue in key older patient groups, its known effects on brain function and behaviour in relation to attention and outlines some proposed treatments.

Multiple Sclerosis (MS) is a condition with a common onset in older age (Holm et al., 2024). Fatigue has been richly researched in MS patients, as it is a central and truly debilitating symptom characterising the condition, with up to 80% prevalence (Giovannoni, 2006). In the context of MS, fatigue has been linked to poor functioning of the striato-thalamo-cortical loop underpinning attentional processes (Capone et al., 2020; Román et al., 2022). Time-on-task effects characterising dysfunction of this particular network were detected in its associated neural indices, including a rise in occipital alpha power (Linnhoff et al., 2023). The network involved in homeostatic, motor and cognitive control has, in addition, shown decreased activity tied to attentional cortical and subcortical networks (Kalron et al., 2020; Spiteri et al., 2019).

One explored intervention of MS fatigue is altering the cortisol awakening response (Powell et al., 2015) with modafinil. The drug utilises an N-methyl-d-aspartate as a receptor antagonist with amantadine thought to relieve fatigue by restoring balance in dopamine and cortisol levels (Ledinek et al., 2013). However, some researchers point to conflicting results about its efficacy (Penner & Paul, 2017), particularly due to comorbidity with sleep disorders. Similarly, modafinil has been found to have mixed effects or, alongside the use of antidepressants, no enhanced effects on MS fatigue (Ledinek et al., 2013). Some recent findings cast doubt on the connection of cortisol secretion to evoked fatigue response in MS patients, (Malekzadeh et al., 2020). Further study is still warranted as modafinil may have more substantial effect sizes than some other treatments (Cash & Kaufman, 2022).

Unexplained and persistent fatigue is associated with CFS, which shows severer symptomatology and is more common in older adults (Jason et al., 2009; Lewis et al., 2013). CFS arises in the healthy population in continuity with work-related fatigue (Hockey, 2013, Chapter 8), and a loss of motivation to work (Penner & Paul, 2017). CFS is considered to be the consequence of daily exposure to fatiguing events in healthy individuals (Mizuno et al., 2011) and coupled with symptoms such as lower baseline heart rate variability, decreased adaptability (Rimes et al., 2017), worse attentional control (Hughes et al., 2017) and lower cognitive performance (D. B. Cook et al., 2007). It is further reflected in brain functional activation changes in the cerebellum, temporal, cingulate and frontal cortices and negatively correlated with brain activity in the left posterior parietal cortex. CFS patients present with melatonin deficiency (van Heukelom et al., 2006) and metabolic alterations (Kujawski et al., 2021), relating CFS to a metabolic account of fatigue (C. Craig, 2015; Derache et al., 2013). However, a larger review of 25 studies focusing on CFS as well as other groups with heightened fatigue (post-HIV, lupus, cancer) found inconsistent results in support of this account (Jason et al., 2009). Instead, most differences pointed to reduced levels of coenzyme Q10, carnitine, and oxidative phosphorylation enzymes, increased oxidative and nitrosative stress, and altered mitochondrial gene expression in fatigued patients compared to healthy controls (Filler et al., 2014).

An interesting aspect of CFS is its frequent use as a framework for other fatigue-related disorders and its screening in the general population (van't Leven et al., 2009). The recent post-covid fatigue is often seen as having much overlapping symptomatology (Araja et al., 2021; El Sayed et al., 2021). Of note are a few pharmacological treatments of CFS which have recently been considered. Oxaloacetate has been used in both CFS and long-Covid (Cash & Kaufman, 2022). It works on the principle of boosting energy through increasing metabolic activity. Yet, these early pilots are considered to require further work (Cash & Kaufman, 2022).

Fatigue is present in both nonfatal strokes and mild traumatic brain injury. Post-stroke fatigue (PSF) and mild Traumatic Brain Injury (mTBI) fatigue closely align in their symptomatology, leading to a theoretical connection between their associated fatigue symptoms (Kuppuswamy et al., 2022). Strokes are more common in older adults, as their prevalence increases with age (Akyea et al., 2021). PSF has been noted to have a long-term effect on 29-77% of stroke populations (Acciarresi et al., 2014) when measured using the fatigue severity scale (FSS). On the MFI, PSF showed a prevalence of between 50-56% (Cumming et al., 2016). Recovery rates differed, with a third of patients showing no recovery from fatigue up to 6 years after the stroke (Elf et al., 2016).

Fatigue has been found in 33-44% of TBI patients (Cantor et al., 2012) with more prevalent hospitalisation in older adults (Thompson et al., 2006), those with prior cognitive impairment, emotional problems, unemployment and reduced physical activity prior to acquiring the injury (Visser-Keizer et al., 2015). In a systematic review of 22 studies, TBI-induced fatigue was found to be persistent over time and affected by injury severity, depression, anxiety, sleep problems, pain, cognitive impairment, but also coping strategies (Mollayeva et al., 2014). It was characterised by inter-hemispheric inhibitory disbalance (Ondobaka et al., 2022) and altered activation of the basal ganglia (Penner & Paul, 2017), areas associated with attentional deficits. Lesion studies following penetrating TBI linked fatigue to altered ventromedial prefrontal cortex function (Pardini et al., 2010) TBI patients reported higher baseline fatigue in relation to worse performance on a selective attention task, showing further connections to attentional deficits (Belmont et al., 2009; Ziino & Ponsford, 2006).

Subjective fatigue in behavioural studies

Factors related to fatigue in observational studies contrast with findings in experiments where fatigue is induced in healthy individuals. Experiments identified an increased influence of additional factors like time of day (Maciejewska & Moczarska, 2023), personality (Calderwood & Ackerman, 2011), sleep quality (Boolani & Manierre, 2019; Lim & Dinges, 2010; Oken et al., 2006; Quiquempoix et al., 2022; Roach et al., 2012) and general subjectively perceived state of health (Boolani et al., 2019) on reported subjective fatigue. This shows that experimentation provides insights into fatigue beyond the contributions of populational surveys.

Importantly, since psychological experiments are demanding tasks in themselves, they are commonly considered to give rise to fatigue (Behrens et al., 2023). Furthermore, fatigue continues to be mentioned as a general factor contributing to changes in participant performance over time (Cassarino et al., 2019; Vallesi et al., 2021; van Berkel et al., 2011). Its effects have also been elicited in effortful and difficult laboratory tasks (Behrens et al., 2023; Darnai et al., 2023; Massar et al., 2018; Wilhelm et al., 2022). There, fatigue is characterised as occurring whenever the response to the task is deemed ‘not proportional’ (Karshikoff et al., 2017). In many instances, the employment of such tasks resulted in a coupled increase in subjective fatigue. Subjective ratings of cognitive fatigue increased in MS patients on a cognitive task (Claros-Salinas et al., 2013), in patients with stress-related exhaustion after a verbal fluency task (Krabbe et al., 2017), and in healthy controls on a 2-back task (Wylie et al., 2019). Exposure to 30 minutes of a cognitively demanding Stroop task elicited mental fatigue when measured with the visual analogue scale (VAS; Trecroci et al., 2020). Subjective fatigue increased over time on a prolonged Sudoku task (Gergelyfi et al., 2015). Subjective fatigue increased after engaging with a brain-computer interface (BCI) device under various levels of mental workload (Käthner et al., 2014). A subjective score also increased in an experimental rendition of a driving task (Gharagozlou et al., 2015).

Interestingly, subjective fatigue tends to arise earlier than associated behavioural decrements. Self-reported symptoms of mental fatigue were shown to alter faster than behaviour in the most effortful tasks (Nieznański et al., 2020). Likewise, increases in fatigue alongside stable performance were detected in working memory experiments (Pergher et al., 2021; Wójcik & Nęcka, 2024), in a hard version of a divided attention task (Nakagawa et al., 2013). Subjective fatigue increased in a ‘heroic’ 4-hour verbal test task, while performance remained stable (Ackerman et al., 2010) or even slightly improved.

Age differences in subjective fatigue arising during experimental tasks have mostly been investigated in the context of physical fatigue (Baranauskiene et al., 2023; Bisson et al., 2014; Mänty et al., 2015). Some findings have suggested older adults to be less fatigued (or de-energised) by experimental tasks (Cardini & Freund, 2020). However, most experiments point to matched levels of subjective fatigue in both young and older age groups after difficult tasks (Gilsoul et al., 2022, 2024) or some heightened age-related fatigue following physical activity only (Jones et al., 2020; T. Yoon et al., 2008). A review of the available research shows that age is understudied in experimentally induced fatigue and that existing research is inconclusive. This confirms the relevance of age to the continued investigation of subjective fatigue also outlined earlier in the description of the populational studies.

Objective fatigue in sustained attention

Measurement in sustained attention

Objective fatigue is commonly studied by inducing a measurable performance decline over time. Most time-on-task performance studies show increases in errors if tasks are sufficiently difficult, and this is commonly described as reflective of fatigue (Gergelyfi et al., 2015; Marcora et al., 2009; Stoll et al., 2016; Van Cutsem et al., 2017). It is then tempting to classify all behavioural decrements as objective signs of fatigue, similarly to the measurement of its subjective levels.

However, performance in research tasks is specific to the studied process (Behrens et al., 2023; Hockey, 2013, Chapter 2). For illustration, performance observed in attention may be affected by wholly different factors than performance in memory (Niogi et al., 2008) or cognition (Vallesi et al., 2014). If experimentally induced fatigue is compared in parallel across multiple such psychological processes (attention, memory, cognition, motor), it is difficult to address confounds specific to each of the processes. Instead, studying objective signs of fatigue in just one such process should allow a clearer outline of the fatigue mechanisms specific to that process. As was discussed, fatigue is common in disorders affecting attention. Therefore, the following review will consider sustained attention-style tasks as a tool to investigate objective fatigue. This will in turn refine the present investigation to fatigue specifically during sustained attention tasks.

Sustained attention has been defined as the ability of a self-directed maintenance of cognitive focus and performance (Slattery et al., 2022). It has been measured alongside its subjective report (Seli et al., 2015) and prolifically by lapses of attention (Robertson et al., 1996). The specific behavioural deficiency in sustained attention is described as the vigilance decrement, reflected in a slowing of reaction times or increase in error rates (Lara et al., 2014; Oken et al., 2006; Pattyn et al., 2008). Commonly related to time-on-task effects (Pattyn et al., 2008; Pershin et al., 2023), vigilance decrements have been detected in fatigued patients (Brosnan et al., 2022) and associated with other symptoms of fatigue and sleep problems (Roach et al., 2012; Walker & Trick, 2018). Mind-wandering (Martínez-Pérez et al., 2023) is also commonly seen as arising alongside the vigilance decrement (Carriere et al., 2013; Hawkins et al., 2019).

Fatigue can be studied via vigilance decrements in several research paradigms, but the most commonly used one is the Sustained Attention to Response Task (SART; Robertson et al., 1997). The SART is an experimental paradigm designed to measure sustained attention. It involves participants pressing a key to react to frequent stimuli while withholding the response to rare targets. As a static probe, it has been used clinically to identify correlates of attentional failures such as coma severity and white matter damage in TBI patients (Robertson et al., 1997). Treatment effects in narcolepsy patients on pitolisant and modafinil have been compared using the SART, with a log-transformed total error count reflecting narcolepsy levels (van der Heide et al., 2015). It has likewise been used as a probe in relation to time-on-task effects. A 70-minute intelligence test and a 40-minute dual task decreased vigilance, as reflected in worse performance on later SART probes (A. S. Smit et al., 2004). The SART has further been used to detect vigilance decrements and changes in task strategy (Lara et al., 2014). It has many adaptations, for instance, using naturalistic stimuli to increase its ecological validity (Cassarino et al., 2019; Smilek et al., 2010) as well as its external validity in the healthy population (Head & Helton, 2012).

Beyond the use of the SART, there are other tasks known to induce decrements and behavioural changes, specific to sustained attention. A 21-minute go/nogo task was seen to increase commission errors (Pershin et al., 2023) and a related iteration showed an increase in errors, reaction times and associated fatigue measures (Kato et al., 2009). Reaction times during a go/nogo task also increased in a patient group (Claros-Salinas et al., 2013). A sustained attention task with rare go trials saw an increase in error and reaction time after 20-30 minutes (Reteig et al., 2019). Increased reaction times were found as a result of both a successive and simultaneous vigilance task (Gartenberg et al., 2018) and in a sustained attention task relying on boredom induction (Head & Helton, 2012). A vigilance decrement was reported in other versions of the sustained attention task with rare go trials (MacLean et al., 2009) or rare nogo trials (Martínez-Pérez et al., 2023). Errors increased over time during a colour-change detection task (Wascher et al., 2014). While the task is not directly described in terms of sustained attention, it produced related decrements in allocation and focus of attention. Performance deteriorated over time during driving, relying on constantly sustained attention (Thiffault & Bergeron, 2003). A decrease in vigilance reflected by lower reaction times was reported after 3 hours in a driving task monitoring inattention (Schmidt et al., 2009; Walker & Trick, 2018).

This outline shows that most investigators agree that time-on-task affects sustained attention performance, yet the critical underlying processes are still underexplored and debated. While fatigue is considered one of the explanations, others have mentioned effort perception, affective valence, self-regulation and time perception (Krabbe et al., 2017). Individual differences in cognitive vulnerability to fatigue from sleep loss and circadian misalignment, as well as extended work hours and shift work have been suggested to affect the offset of some of these effects (Shigihara et al., 2013). Others have proposed a strong link between these behavioural effects and motivation, instead of fatigue (Gergelyfi et al., 2015; Hopstaken et al., 2016). Lastly, some researchers have failed to find a relationship between subjective fatigue and sustained attention decline (MacCoon et al., 2014; Schwid et al., 2003) and some even questioned the connection conceptually (Gunzelmann et al., 2011). As fatigue is then only one of the factors affecting sustained attention performance, the subsequent section will cover other major influences on sustained attention performance in the general population to better inform the rest of the thesis.

Impact of age on sustained attention

A strong effect of age on performance during the SART and other related sustained attention paradigms has been found consistently (Vallesi et al., 2021), so age-specific findings will now be reviewed to highlight that a sustained attention investigation of fatigue cannot be done without a consideration of this age effect.

The primary age difference often encountered in the literature is the retained attentional control of older adults during sustained attention tasks (S. Hsieh et al., 2015; McAvinue et al., 2012), leading to an advantage in nogo accuracy, defined as correct response in nogo trials (alternatively termed no-go or omission trials; Staub et al., 2015). Older adults have shown a preserved ability to allocate top-down attentional resources (Madden, 2007), which is thought to help resolve perceptual difficulties otherwise arising from ageing (Bourisly & Shuaib, 2018; Zhuravleva et al., 2014). This ability has also been described as an on-task controlled processing mode (Brache et al., 2010; Jackson & Balota, 2012; Staub et al., 2015). Consequently, older participants have been conceptualised as equipped with a strategy to obtain greater accuracy during sustained attention (Robison et al., 2022; Vallesi et al., 2021). This is referred to as the behavioural masking effect in older age, corresponding to a performance able to match or outperform young controls (Cheyne et al., 2013). Concretely, older adults are characterised as prioritising accuracy (Carriere et al., 2010; Statsenko et al., 2020; Staub et al., 2015) or even as showing an accuracy bias (Hübner et al., 2021). This has been observed in the SART (Wiemers & Redick, 2019) but also in a vigilance task (Brache et al., 2010). In its full extent, it is outlined in a recent meta-analysis by Vallesi and colleagues (2021).

The findings do not suggest that higher nogo accuracy means overall behavioural superiority of older adults in sustained attention. Sustained attention is understood to decline beginning in the early 40s (Fortenbaugh et al., 2015), as reflected in multiple behavioural metrics. The most common one (although only present in some sustained attention paradigms) is slower response time (Jackson & Balota, 2012). Age differences in selective attentional tasks were reflected in slower reaction times (McLaughlin et al., 2010), and older adults also responded more slowly than young adults when presented with blurred objects and incongruent scenes (Lai et al., 2020). In a visual attention paradigm, this was further accompanied by a deficiency in accuracy. And despite a nogo accuracy advantage, older adults can still show deteriorated accuracy on attentional tasks probing regulation and control of attention (McLaughlin et al., 2010). Older adults have further been found to have worse go (also termed commission trial) accuracy (S. Hsieh et al., 2015; McAvinue et al., 2012), related to a generally accepted motor decline arising from ageing (Seidler et al., 2010). Older adults also performed worse in situations such as switching attention from a temporal to a spatial task (Huizeling et al., 2021) or trying to divide their attention (Fraser & Bherer, 2013). Other research also highlights more complex metrics which bespeak a negative age effect, such as poor dual-task performance (Vallesi, 2016), slower cognitive restoration (Cassarino et al., 2019) and, in some cases, difficulty re-engaging with a task following an error (Jackson & Balota, 2012), characterised as post-error slowing. Other age-related adverse factors, such as old-age frailty, have likewise been associated with poorer sustained attention ability (O'Halloran et al., 2014). These findings highlight a lasting role of cognitive decline in older age, contrasting with the interestingly preserved ability to exhibit high nogo accuracy.

Underpinning age differences in sustained attention with fatigue

Almost no research has explored the role of fatigue in different age groups undertaking sustained attention tasks. There seem to be no direct investigations into the connection, although some papers come close to making a link. Brache et al., (2010) successfully used a vigilance task to induce a decrement in accuracy in young but not older adults. They interpreted the finding as reduced arousal in the young participants or a switch to a less demanding speed-based task strategy. Yet, they did not suggest a direct link of the decrement to fatigue. The same pattern was later demonstrated in the SART (Staub et al., 2014). Although subjective fatigue was not measured, the age difference was underpinned by subjective differences in the perception of success, effort and frustration, which could be argued to be components of the subjective experience of fatigue. Manipulation of break length in a fatiguing Stroop task improved fatigue in the young and middle-aged, but not older participants. While the task induced cognitive, not attentional fatigue, the authors connected the findings to related research on sustained attention (Gilsoul et al., 2024). Vallesi et al. (2021) marginally investigated fatigue as contributing to age differences in sustained attention. While the meta-analysis did not detect any reliable effects, age was still proposed as a viable factor for future research work.

Notable age differences exist in connection to mind-wandering during sustained attention (Fountain-Zaragoza et al., 2018). Generally, older adults are less prone to mind-wandering (Diede et al., 2022; Jackson & Balota, 2012). Observations of mind-wandering differences in older age have even been associated to the underlying differences in strategy during sustained attention (Diede et al., 2022) and to behavioural preservation in advanced age (Bailey et al., 2020; Fountain-Zaragoza et al., 2018). Increased sustained attention accuracy in older adults has also been related to lower state and trait mind wandering levels (Seli et al., 2017). It can thus be argued that time-on-task fatigue occurs in close relation to increases in mind-wandering (Walker & Trick, 2018) and that mind-wandering is theoretically connected to fatigue in the SART (Hawkins et al., 2019). This can be taken as early evidence for a link between the accuracy advantage of older adults and their experience of fatigue. Still, research is needed to test this hypothesis directly.

In summary, the prevalent effect of age on performance during sustained attention continues to attract interest in the literature. Since these differences exist, they may generate new findings about vigilance decrements in young and older age groups, in connection to fatigue. However, there are other important factors to consider, notably age differences in sustained attention in terms of motivation. Vallesi and colleagues (2021), alongside other researchers (Jackson & Balota, 2012; Staub et al., 2013, 2014), favour this account. Because of this, the topic of motivation will now be addressed and incorporated into the present discussion.

Underpinning age differences with motivation

Motivation is a highly abstract construct (Rust & LeDoux, 2023) but can be defined as an orienting and invigorating impact of prospective reward on behaviour (Kok, 2022). It is likely comprised of multiple factors with inter-related dynamics (Howard et al., 2021; R. M. Ryan & Deci, 2019). A helpful distinction is that of intrinsic and extrinsic motivation (Herlambang et al., 2021; Kok, 2022). Dickinson (1989) posits that intrinsic motivation, in particular, relates to time-on-task behaviour. It decreases over time due to the repetitiveness of the task, reflecting a re-evaluation of the task as internally unrewarding.

In reviewing factors involved in fatigue, Hockey discussed motivation as an underlying driver of psychophysical testing of vigilance decrements (2013, Chapter 5). He highlighted that untracked motivational distractors can impact performance. Researchers confirmed the effects of some of these: social facilitation (McCambridge et al., 2012), cognitive bias in human judgement (Neal et al., 2022) and even the impact of the experiment being located in the laboratory as opposed to a naturalistic environment (Hockey, 2013, Chapter 5; Rubin & Telch, 2018). Motivation has, in addition, been directly shown to affect time-on-task dynamics. Motivational arousal can increase with time-on-task (Brehm & Self, 1989), serving as feedback for assessing task goals leading to time-on-task changes in performance (Robison & Nguyen, 2023).

For some time now, researchers in the working memory domain have discussed the influence of motivation on older adult behaviour (Friedman & Castel, 2013; Hennessee et al., 2018; Sutin et al., 2024). Older adults are considered to be more motivated to maintain effortful behaviours (Ennis et al., 2013; Forstmeier & Maercker, 2008; Hess et al., 2021), and even to show smaller vigilance declines

(Staub et al., 2014). Interestingly, this baseline older adult performance advantage can be negated with an experimental removal of their underlying high motivation (Löckenhoff & Carstensen, 2007). A recent meta-analysis of cognitive control and episodic memory (Swirsky et al., 2023) also investigated this effect. No overall age-related difference in motivation to improve memory task performance were found, but there were substantial differences based on the type of motivators. Older adults were motivated by socioemotional rewards (such as curiosity, interest in research and self-relevance) more so than younger adults who prioritised pragmatic and financial rewards.

It needs to be acknowledged that this effect of motivation on older adult performance was mainly highlighted in working memory paradigms (Swirsky et al., 2023). Findings testing them in connection with sustained attention are very limited. So, even though motivational decrements closely correspond to the posited time-on-task fatigue effect, empirical work is only now beginning to consider this in the context of sustained attention (Strayer et al., 2024). For these reasons, I incorporated an exploration of motivational factors in this thesis to clarify their connection to age effects and fatigue.

Sustained attention fatigue and brain function

Resting-state brain activation related to fatigue

Neuroscience research seeks to underpin psychological tasks with associated neural patterns (G. Li et al., 2020) across various involved brain functional networks[3] (Benwell et al., 2018). These are commonly studied with functional

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[3] An influential model proposed by Posner notably divides attention into three networks: the alerting, orienting and executive control network (Petersen & M. I. Posner, 2012; M. I. Posner & Dehaene, 1994). Together, they have a role in selecting, orienting and controlling of information going into the brain. Sustained attention can then be seen as a regulatory mechanism distributed in the networks (Demazure et al., 2021). Another network with involvement in sustained attention is the salience network, chiefly comprised of a cortico-striatal-thalamic-cortical loop: cortical nodes in the dorsal anterior cingulate cortex, anterior insula, dorsolateral prefrontal cortex and inferior parietal lobule, as well as subcortical nodes

magnetic resonance imaging (fMRI) or tracking various EEG patterns (Donoghue et al., 2022), namely Time-Frequency (TF) oscillation patterns (Macdonald et al., 2011). Oscillations related to fatigue can be broadly categorised into 1) global changes in activation in the resting state, pre- and post-task probes or raw pre-stimulus baseline windows, or 2) occurring directly in response to a stimulus after baseline correction and tied to the mental processes specific to a sustained attention task. As both pattern categories are distinct, the present review will treat them separately.

The predominant pre-stimulus pattern associated with fatigue is a rise in the so-called alpha oscillations. These occur around the frequencies of 8-12Hz (Bazanova & Vernon, 2014) and have been ascribed several crucial functions in sustained attention (Clayton et al., 2018) and further been closely connected to decreases and increases in attention (Walz et al., 2015).

Alpha oscillation increased over time in a visual Simon task, described as eliciting changes in the allocation of attention (Arnau et al., 2021). They increased during effortful attention (Talukdar et al., 2019) and have frequently been measured as a result of fatigue in driving (Fonseca et al., 2018; Gharagozlou et al., 2015; Lal & Craig, 2002; Zhao et al., 2012). Based on these results, resting state alpha has been suggested as a marker of fatigue (Aziezah et al., 2020). In connection to rises in the alpha band, oscillations in the adjacent slower theta frequency band (around 4-8Hz) have also been reported to increase during attentional tasks (Arnau et al., 2021; Maciejewska & Moczarska, 2023; Talukdar et al., 2019; Tanaka et al., 2012; Zhao et al., 2019) and to correspond to the same underlying process as alpha (Arnau et al., 2021; Huizeling et al., 2021), although some consider it a distinct process (Maciejewska & Moczarska, 2023). Similarly, increases in the adjacent

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in the caudate nucleus, mediodorsal thalamus and dopaminergic brainstem nuclei (S. K. Peters et al., 2016). The network's association with sustained attention deficits is well documented. For example, the loop showed reduced connectivity in clinical conditions, like obsessive-compulsive disorder (J. Posner et al., 2014). Finally, vigilance decrements could be linked to the sleep-wake brain systems, comprised of the hypothalamus, the serotonin and norepinephrine projection systems (Oken et al., 2006).

beta oscillatory band (around 13-30Hz) have been detected with respect to the onset of fatigue in a range of tasks, including a go-nogo style task (Liu et al., 2010). Describing this broadband increase, multiple researchers have proposed that the signal occurring in the lower frequencies corresponds to one undifferentiated cluster of a fatigue-related rise (Arnau et al., 2021; Lal & Craig, 2002; Tran et al., 2020). Lower frequency band resting state signal increases have thus been previously proposed to be biomarkers of fatigue (Bazanova & Vernon, 2014; Krigolson et al., 2021). Yet, others have challenged this account, as pre-stimulus alpha fluctuations are notably related to many behaviours (Melcón et al., 2024; Slagter et al., 2016; Zazio et al., 2020).

The aforementioned approach to the resting-state signal analysis relies on the study of canonically defined frequency bands. In contrast, a newer approach has recently gained recognition, relying on the analysis of both periodic and aperiodic components of the resting state EEG signal (Donoghue, Dominguez, et al., 2020; Donoghue et al., 2022). There is a good basis for considering the signal this way, as aperiodic components have already been mapped onto some brain functions relevant to attention (Gao et al., 2017; Jacob et al., 2021). The newly considered aperiodic components are thought to broadly reflect a general balance between inhibitory (gabaergic) and excitatory (glutamatergic) neural activity (Ostlund et al., 2022) and related to attentional processes (N. Li et al., 2024; Waschke et al., 2021). Aperiodic components have been investigated in connection with age and thought to isolate age differences observable in the oscillatory signal (Cellier et al., 2021; Merkin et al., 2023; Montemurro et al., 2024). They have been further noted to differ across various clinical conditions, such as developmental dyslexia (Turri et al., 2023) and Alzheimer’s disease (Martínez-Cañada et al., 2023), where their dynamics corresponded to a well-known disbalance between excitation and inhibition. Conversely, they show smaller spatial functional specificity than their periodic counterparts (Kasten et al., 2023), although certain specifics still exist, such as a link of occipital aperiodic components to attentional processes (Waschke et al., 2021). Aperiodic analysis is still in its infancy, and findings relating to fatigue absent. Analytical steps are currently experimental and flexible, especially with respect to baseline correction and identifying an ideal cut-off lower frequency for component computation. In this thesis, I incorporated aperiodic analysis to analyse resting state signal alongside the more established approaches, particularly because of its relevance to ageing. This aligns with recent trends in the literature and provides greater sensitivity to relevant signal patterns.

In addition, other dynamics occur in pre-stimulus activity during time-on-task. Individual Alpha Frequency (IAF), defined as the maximum alpha power detected in an individual (Aziezah et al., 2020), has been shown to rise over time alongside rises in power (Benwell et al., 2019). IAF was affected by cortical connectivity (Sun et al., 2014) and corresponded to general cortical excitability (Babu et al., 2018) or engagement (Bernhardt et al., 2019). Interestingly, some findings show that IAF over frontal, parietal and occipital lobes indicates fatigue, but only in connection with time-dependent decreases in alpha power (Aziezah et al., 2020). Where an alpha decrease occurred (Ishii et al., 2019; Jap et al., 2009; Tanaka et al., 2012), it was interpreted as functionally corresponding to a focus on the perception of fatigue or attentiveness to fatigue (Ishii et al., 2019; Tanaka et al., 2012). Ultimately, these findings may point to a multi-component nature of the alpha oscillations, possibly explaining the inconsistency between alpha increases and decreases and IAF stability. This cautions against a single functional interpretation of alpha change, even in the context of the pre-stimulus signal (Arnau et al., 2021; Ishii et al., 2019; Jap et al., 2009; Tanaka et al., 2012).

Sustained attention and task-related brain function

The review can now turn to task-related patterns. These are identified by locking averaged signal TF windows to the presentation of stimuli. This analytical technique elicits a diverse array of signal patterns, more specific to the mental processes employed in the experimental tasks. As each task presents with different performance metrics and parameters, these correspond to varied post-stimulus neural dynamics. As a result, the review is constrained to patterns identified predominantly in connection with sustained attention and closely related paradigms. Notably, most research focuses on the analysis of different experimental conditions averaged across time rather than time-on-task changes in the signal (as exemplified in Sahu and Jain, 2024). Therefore, existing findings leave significant gaps in the understanding of time-on-task processes. In most cases, the decrement is not directly tested in relation to subjective fatigue measures.

Krigolson et al. (2021) found that over time, frontal theta decreased over central and frontal regions in an oddball task utilising attentional control (Krigolson et al., 2021) and in a vigilance task, described as associated with cognitive effort (Byrne et al., 2020). Theta was also found to decrease in a smaller sample undertaking the SART task (Ulgen et al., 2023). Conversely, general frontal theta increases were detected in effortful and mental vigilance during the SART (Linnhoff et al., 2023). Frontal theta increases were also observed in an attentional cognitive task (Wascher et al., 2014).

Alpha increased occipitally in both healthy controls and MS patients during a sustained attention task (Linnhoff et al., 2023). Task-related alpha also increased in a go/nogo task relying on continuous attentive performance (Pershin et al., 2023) and was seen as reflecting change in the allocation of attentional resources and increases in mental effort in order to maintain vigilance. However, alpha decreased in an attentional control task (Krigolson et al., 2021). Elsewhere, alpha differentiated between internal and external attention by decreases in difficult mental arithmetic but subsequent dramatic increases in a purely mental task (Magosso et al., 2019). Prolonged cognitive activity in a Simon task relying on maintained attention to stimuli likewise showed a lower alpha power increase and a decrease in upper alpha power, proposed to denote fatigue (Wascher et al., 2014). This was linked to depletion in cognitive resources, increased effort to maintain performance and reduced efficiency of stimulus processing. The two separate alpha frequencies further point to a multi-modal account of alpha, as highlighted in the work of other research groups (Barzegaran et al., 2017; Benwell et al., 2019; Knyazeva et al., 2018). They emphasise a possible presence of several functionally independent mechanisms oscillating within the alpha range.

The effects of time have been observed in other frequency bands, particularly in lower beta oscillations (14–25Hz). This signal commonly occurs in a pattern characterised as the post-movement beta-rebound (PMBR) which primarily reflects changes in motor execution (Pfurtscheller et al., 1996). The PMBR has been mapped to the motor cortex (Jurkiewicz et al., 2006) and its function researched widely in motor tasks (Heinrichs-Graham et al., 2017; Parkes et al., 2006). Some researchers have further suggested that the pattern also follows after attentional processes (Coleman et al., 2023). For example, changes in beta-band activity were associated with the regulation of attentional effort during time-on-task, in addition to motor preparation (Liu et al., 2010). A related finding was also observed in multi-component variations of frontal beta in monkeys around spontaneous pauses in work (Stoll et al., 2016). The reset of beta power after the modulation reflected the maintenance of cognitive control. Importantly, there was also an influence of time-on-task on the signal, but this was noted to have an effect independent of cognitive control. An earlier study also observed an increase in beta oscillations while using the SART to measure attentional decline between two time points (A. S. Smit et al., 2004). Lower amplitude and longer time-to-peak of PMBR was connected to motor fatigue (Pakenham et al., 2020) and has also previously been connected to task-related mental fatigue (Liu et al., 2010). All these findings point to a gap in what is known about beta oscillation change over time-on-task, but with a potential relevance to fatigue in the present study.

Age differences in sustained attention brain activity

There are several findings investigating neural age differences during sustained attention, driven by an interest in the known effect of age on performance. Age is associated with improved occipito-parietal functional connectivity and encoding when carrying out attentional tasks (Wiegand et al., 2014). These increases in control have been proposed to correspond to increased sensitivity to contextual information (Lai et al., 2020). This in turn has been related to stronger inhibitory attentional function (Doesburg et al., 2016). In an fMRI study that showed dedifferentiation of functional brain activity, older adults were nonetheless noted to compensate for cognitive decline by recruiting alternative frontal and temporal brain regions involved in attentional control (Angel et al., 2022). Conversely, younger participants were shown to have less attentional inhibition (Brache et al., 2010). Recently, performance in the SART has been related to structural patterns in the ageing brain using MRI. Their cerebral white matter density contributed to better accuracy, with grey and white matter volumes greatly mediating the relationship of ageing and sustained attention (Treacy et al., 2024).

Ageing also affects the resting-state power spectral density components associated with attention (Cesnaite et al., 2023). The key among these is the ‘1/F’ component, seen to reflect that the combined noise and power in the frequency-decomposed signal exponentially decreases with higher frequencies (Pathania et al., 2021). Concerning the discussed pre-stimulus signal, older adults have previously shown a flattened 1/F response in the right frontal lobe, alongside differences in IAF from young adults (Cesnaite et al., 2023; Waschke et al., 2021). A possible reason for this is the multi-component structure of the alpha peaks (higher occipito-parietal alpha and lower occipito-temporal alpha) reduced into a single component in older age, the so-called anterior shift in age (Knyazeva et al., 2018). More recent developments in data analysis have enabled the clarification of age differences in 1/F dynamics. Merkin et al. (2023) used aperiodic analysis to isolate the 1/F component of the signal from the underlying periodic peaks. Older adults then showed lower aperiodic offset and smaller aperiodic exponent than younger adults (Merkin et al., 2023). Some findings showed that the difference in peak alpha is then partly or even fully removed by isolation of these components (Merkin et al., 2023) and explains age differences in alpha oscillation (Deodato & Melcher, 2024).

Regarding task-related signals, alpha and beta differences between young and older groups were detected in a go-nogo task, reflective of sustained attention (Schmiedt-Fehr et al., 2016). Other researchers have found differences in brain function of areas linked to top-down attentional resources, such as differences in theta and alpha oscillatory activation (Huizeling et al., 2021) and in Event Related Potentials (ERP) associated with these oscillations (Studenova et al., 2023). These include the P300 (a positive potential appearing around 300 milliseconds after the stimulus) in incongruent trials of an attentional oddball task (Kaufman et al., 2016) and increased components of non-target P300 (Wiegand et al., 2014), in response to the SART (Chan, 2001) and an increase in attentional control-related P300 (S. Hsieh et al., 2015). Other findings indicate differences in the beta oscillatory response in go/nogo tasks again in connection with age, with older adults displaying a weaker beta motor rebound after successful response inhibition (Schmiedt-Fehr et al., 2016). ERP researchers have found that reduced reaction time benefits from alerting cues in older participants were reflected by reductions in a related N1 ERP component (the first negative peak in amplitude following the stimulus), responsible for alerting (Kaufman et al., 2016). In the context of sustained attention, ageing has been noted to affect inhibitory neurotransmission of cortical to subcortical regions, this is reflected in ERP research too (Bourisly & Shuaib, 2018; L. Li et al., 2013).

My review has shown that older adults' ability in sustained attention is known to be underpinned by structural and functional brain differences, reflecting ageing-related decline and heightened attentional inhibition. In contrast to these often time-averaged study designs, there are practically no findings that would illustrate age differences in time-on-task changes in sustained attention, reflecting the very much under-researched behavioural domain. As previously shown, both fatigue and motivation may be the key underlying processes behind age differences in sustained attention. Despite these significant gaps in our understanding, neural treatments have nonetheless been used to target candidate fatigue markers, including studies in both older adults in the healthy general population as well as patient groups.

Interference with fatigue through neurofeedback

Several studies have attempted to treat fatigue symptoms by modulating neural activity. Neurofeedback is a tool of particular interest among these neuromodulation techniques since it directly utilises and targets some of the previously discussed fatigue-related patterns across its diverse experimental protocols.

Older neurofeedback research has reported general improvements in fatigue symptoms using various protocols relying predominantly on alpha up- or down-regulation (Luctkar-Flude & Groll, 2015) and some benefits of neurofeedback were found in fibromyalgia patients, as seen in a continuous performance test (Caro & Winter, 2011). Cognitive performance supposedly improved in older adults following neurofeedback training relying on a protocol targeting an adjacent frequency, the sensory-motor rhythm (SMR; around 12-15Hz), and theta oscillations. The neurofeedback resulted in increased post-training theta and alpha as well as performance improvements in vigilance decrements, sustained in a 1-month follow-up (Marlats et al., 2020). A more comprehensive test suggested an improvement in fatigue and quality of life in a controlled trial of patients with chemotherapy-induced neuropathy as a side effect of cancer treatment. After 20 sessions of targeting motor-related beta bursts, there was a beneficial effect for at least 4 months (Prinsloo et al., 2018). However, It must be acknowledged that many commonly used neurofeedback protocols for the treatment of fatigue symptoms have inherited certain methodological flaws from the application-driven older work[4]. Most of these older findings are now considered to require methodological improvements to attain clinical standards (Ros et al., 2020; Sorger et al., 2019).

Conversely, a systematic review of 99 fMRI neurofeedback experiments concluded that neurofeedback reliably modulates specific brain regions albeit with the difficulty of translating the effect into clinical or behavioural outcomes, including fatigue (Richard et al., 2018). A different narrative review reached a similar conclusion about the use of neurofeedback for depression, where fatigue commonly co-occurs as one of its symptoms (Melnikov, 2021). It was found not to have any specific effect over placebo in Attention Deficit Hyperactivity Disorder (ADHD) patients, where fatigue was included among associated symptoms, 13 months after a post-intervention that targeted the theta-beta ratio (Neurofeedback Collaborative Group, 2021). A recent study attempting to influence fatigue in a post-Covid-19 cohort (Orendáčová et al., 2022) lead to improvements in some comorbid symptoms but had no effect on fatigue. A meta-analysis of the use of neurofeedback generally targeting the alpha band to improve chronic pain, looking at 10 randomised and 13 non-randomised trials, found short-term reductions in pain intensity, but with lower certainty and a risk of bias as well unbalanced methodology, and little improvement in fatigue symptoms (Hesam-Shariati et al., 2022).

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[4] Neurofeedback was firstly developed in the 1950s, during a period of a cognitive shift in psychology. This also sparked long-lasting research interest into the ability to observe and regulate one's own EEG signal (Frederick, 2012). The initial approach focused on the identification of high or low alpha wave states (Othmer & Othmer, 2017), but since then, experimental protocols have widened significantly in scope and methodology. Soon, clinical trials tested the effect of various theory-driven EEG oscillatory bands, including alpha and the SMR (Sterman et al., 1974). Various application-oriented pathways emerged around target patterns of uncertain utility, such as the 'infraslow' EEG signal (0-0.1Hz). Even recent literature reports the effects of these approaches (Leong et al., 2018), while still highlighting the need to carefully consider control conditions (Sorger et al., 2019).

Some more recent investigations point to the effect of neurofeedback, but they are mostly not specific enough for the presently discussed fatigue symptomatology. As an example, alpha power lateralisation feedback was successfully utilised to enhance covert visuospatial attention (Schneider et al., 2020). In addition, up- and down-regulation of alpha was used in a temporal expectancy task to measure performance decline. This single-blind, counterbalanced, sham-controlled crossover design introducing both up- and down-regulation in each participant found that up-regulation impaired initial attention performance but slowed down the deterioration of attention over time, while successful down-regulation had no impact on attention performance compared to the sham condition (Nan et al., 2024). A general effect of neurofeedback was also seen in an intervention targeting cognitive and psychomotor performance in healthy adults (Dessy et al., 2020), yet not showing much differentiation among the targeted frequency bands (He et al., 2020). While these newer approaches with more robust methodology confirm an effect of neurofeedback, the ability of neurofeedback to give rise to general neural changes contrasts with its mixed behavioural efficiency (Zilverstand et al., 2017; Zotev et al., 2018) and lack of specificity to fatigue symptoms. One ongoing explanation for the general effect is the experience of social support shared among both the neurofeedback and placebo conditions (Neurofeedback Collaborative Group, 2021). When factoring in adequate control conditions, investigations often continue to lead to null findings, such as a recent rigorous comparison of neurofeedback with tDCS, leading to no detected difference from placebo (Rêgo et al., 2022).

In summary, a review of the neurofeedback interventions related to fatigue generally shows a dissociation between the targeted frequency bands and their supposed outcomes, with scant robust results for improvements in fatigue directly arising from the targeted fatigue-associated patterns. There is thus a continued need to improve experimental rigour and constrain the investigation to avoid ‘general’ neurofeedback effects. Future works needs to adhere to more rigorous design practices and a more thoroughly examined link to the targeted pathology, in this case, fatigue.

Thus, the present work aims to inform future neurofeedback and other interventions for fatigue by clarifying the link of theoretically supported oscillatory patterns to fatigue. Moreover, the investigation is constrained to fatigue during sustained attention to isolate a reliable effect in one process. I hoped that the work could later be generalised to other processes and inform working interventions, including neurofeedback.

Thesis at a glance

In three related experiments, one for each empirical chapter, I sought to clarify factors underlying performance in sustained attention in the general population, with a specific focus on the roles of fatigue, age and motivation. In doing so, I hoped to inform a prospective and empirically valid neurofeedback-based fatigue intervention. Failing that, to warn about the limited utility of neurofeedback interventions relying on the modulation of EEG oscillations or other scalp signal markers supposedly reflective of fatigue.

Chapter 2 aimed to demonstrate that sustained attention tasks are a viable means of eliciting fatigue-related changes. The Sustained Attention to Response Task (SART) was chosen and used to investigate time-on-task effects on subjective fatigue and performance in the general healthy population. The feasibility of coupling a change in performance on the task with trait fatigue and a change in state fatigue was tested and confirmed using an online research paradigm. A 10-minute version of the SART in a large representational sample showed that accuracy was maintained at a cost of increased fatigue. However, the key finding was better SART accuracy in older adults, yet only limited age-specific links to fatigue. A direct investigation into the neural correlates of these effects was then attempted in **Chapter 3**.

In **Chapter 3**, neural and motivational dimensions were added to investigate age-related fatigue changes in a first-of-its-kind incarnation of the SART as a time-on-task EEG test of fatigue. The previous chapter’s effect of inducing subjective fatigue by exposure to the SART was followed up with a longer, 45-minute version, aiming to induce stronger performance decrement effects that were absent in **Chapter 2**. Again, I found a rise in subjective fatigue change and also a change in brain dynamics, but these were unfortunately neither correlated, nor demonstrably linked to performance decline. Concretely, the experiment showed change over time in two key signal patterns: a rise in pre-stimulus alpha synchronisation and fronto-central task-related beta synchronisation. In addition, a motivational manipulation elicited a separate decrease in fronto-parietal task-related beta synchronisation. There was no overall vigilance decrement, despite extending time-on-task to 45 minutes. Again, age was the key factor influencing accuracy during the SART and now, in addition, the detected neural patterns. The experiment thus highlighted the limitation of interpreting neural changes as reflecting fatigue. Instead, the data pointed to motivation and age-related performance strategy, rather than fatigue, as a further factor impacting sustained attention, which was then tested in **Chapter 4**.

The final empirical **Chapter 4** was a behavioural experiment attempting to elicit changes in SART performance by investigating motivational effects. Young and older participants undertook a customised version of the SART, which matched participant accuracy levels by titration of task difficulty to remove any trace of baseline differences. Both groups were then given a motivational manipulation to perform better at the difficulty level they reached during the titration. While both groups responded, the young participants improved their accuracy much more. In addition, subjective measures revealed a higher motivation of older participants to perform well from the start, while young participants reported becoming motivated after the motivational manipulation. No decisive link of fatigue to age or performance was found. The experiment thus confirmed that age-driven performance effects in the SART are underpinned by motivation rather than fatigue.

Overall, I conclude in **Chapter 5** that the two key patterns showing change during sustained attention (above all the rise in pre-stimulus alpha oscillations) have only a tentative link to subjective fatigue and vigilance decrements or maintained performance in the context of sustained attention. Changes in the neural patterns more accurately bespeak age and motivational differences. I explain that, contrary to expectation, fatigue did not underpin the strong age differences I found in sustained attention. I then question the utility of neurofeedback as an effective remedy for fatigue, given the weak link of the relevant neural signals to subjective fatigue. Instead, I encourage further study of motivation as a more apparent factor affecting performance decline and playing a potential role in future interventions tackling behavioural deficiency during sustained attention.

Chapter 2: Probing sustained attention and fatigue across the lifespan

Abstract

Trait fatigues reflects tiredness that persists throughout a prolonged period, whereas state fatigue is defined to be short term after 'intense and/or prolonged effort'. We investigated the impact of sustained attention (using the SART) on both trait and state fatigue levels in the general population. A JsPsych online version of the SART was undertaken by 115 participants, stratified across the whole adult lifespan. While pre-task trait fatigue was a strong indicator of the initial state fatigue levels, undergoing the task itself induced an increase in reported subjective state fatigue, and an accompanying reduction in subjective energy rating. Consistent with this finding, greater subjective state fatigue levels were associated with reduced accuracy. In addition, age was the best predictor of inter-participant accuracy (the older the participants, the greater the accuracy), and learning (i.e., task duration reducing reaction times). Moreover, a ceiling effect occurred where participants with higher trait fatigue did not experience greater state fatigue changes relative to those with low trait scores. In summary, we found improved accuracy in older adults, as well as a tight coupling between state fatigue and SART performance decline (in an online environment). The findings warrant further investigation into fatigue as a dynamic, task-dependent state and into SART performance as an objective measure and inducer of fatigue.

Introduction

Fatigue is one of the most common symptoms experienced by people with a range of clinical conditions, for example, PSF affects up to 50% of stroke survivors (Cumming et al., 2016). Fatigue has also been estimated to affect up to 17% of the general population (Aritake et al., 2015). In the clinical populations, definitions of fatigue vary and are often specific for the respective populations in which they occur. PSF for instance has been described as a subjective lack of physical or mental energy (or both) that is perceived by the individual to interfere with usual or desired activities with the closely related 'chronic fatigue' described as a negative whole-body sensation, not proportional to recent activity (L. Wilson et al., 2011). There is similar variability in defining fatigue within the general population. Researchers either extend the definition from a particular syndrome, typically chronic fatigue syndrome (van't Leven et al., 2009) or frame fatigue more generally within experimental cognitive research, e.g., as a lapse in sustained attention (Wylie, Dobryakova, et al., 2017). One frequently adapted model describes fatigue as a change from baseline state in response to either physically or mentally challenging tasks, which induces a depletion of cognitive resources and lowered vigilance (Thiffault & Bergeron, 2003). Another mechanism of fatigue induction could be via boredom, where repetitive and unstimulating tasks lead to an inability to maintain sustained attention (Gergelyfi et al., 2015).

Trait fatigue is measured both in clinical studies (Acciarresi et al., 2014; Mead et al., 2007; L. Wilson et al., 2011) and the working population (Caldwell et al., 2019; Engberg et al., 2017; Vries et al., 2003). It has been characterised as an innate tendency to exhibit fatigue (Filippi et al., 2022). Long-term trait fatigue depletes the ability to readily engage in moderately demanding tasks (Möckel et al., 2015). Alternatively, measures used for self-reported assessment of trait fatigue are comprised of recalled experiences of fatigue over specified time windows and dimensions (e.g., the multidimensional fatigue inventory, MFI (Smets et al., 1995)). This type of recent, self-reported fatigue has also been described as 'prolonged state fatigue' (Filippi et al., 2022) in order to distinguish it from an innate tendency to become fatigued (sometimes also described as 'trait fatigue'). Short-term state fatigue, on the other hand, is a more transient mental state (Chen et al., 2020). It undergoes dynamic shifts throughout the day, based on external factors corresponding to undertaken activities and tasks (Völker et al., 2016b). States are prone to shift, and this is reflected in performance changes across tasks that require sustained focus or attention (Reteig et al., 2019). State fatigue can be studied subjectively through self-report measures that are designed to capture subjective experience at any given time. Many researchers use a simple, one-item measure of subjective state fatigue (Shigihara et al., 2013) to link reported momentary fatigue to the objective task performance (Kluger et al., 2013; Völker et al., 2016a; Xu et al., 2018). However, measures of state fatigue comprising several items would offer greater construct validity (Clark & Watson, 2019). There has been a tight coupling of state fatigue with energy, where several studies (Boolani & Manierre, 2019; Filippi et al., 2022; Wender et al., 2022) utilised combined measures of state fatigue comprised of energy and fatigue subscales. Although the two scales seem to be closely related, findings of divergent changes in both suggest that they constitute two related, unipolar aspects (Filippi et al., 2022). Accordingly, a more in-depth investigation of state fatigue benefits from inclusion of both of the two separate subscales. Furthermore, few studies have investigated changes of subjective state fatigue during effortful tasks (Guillemin et al., 2022), and it is also unclear how fluctuations in subjective state relate to objective changes in task performance. Tests of state fatigue with attentional paradigms suggest that the ability to concentrate for a prolonged period decreases over time (Ishii et al., 2014; Smilek et al., 2010). Therefore, a fatiguing task is perhaps the most immediate exogenous influence on state fatigue over and above the initial baseline stemming from trait fatigue measures. Furthermore, coupling the changes in (subjective) state fatigue with task performance would enable a direct link between (objective) reduced task performance and (subjective) fatigue measures.

SART and fatigue

It is known already that tasks that require continuous and maintained mental effort are likely to elicit changes in fatigue (Reteig et al., 2019). A self-directed maintenance of cognitive focus (Robertson & O'Connell, 2010) can be characterised as sustained attention, and a frequently researched task that relies on sustained attention is the sustained attention to response task (SART; Robertson et al., 1997; Vallesi et al., 2021; Weinstein, 2018). Performance on the

SART is typically measured in terms of response accuracy with a focus on commission errors (i.e., when erroneous responses are made in no-go trials), reaction times, and standard deviations in reaction times. The sensitivity of the task to fatigue lies in its tendency to provoke unintended motor response commission errors, with lapses in attention. Regarding trait fatigue, an initial comparison of the SART with the cognitive failures questionnaire (Broadbent et al., 1982) showed a modest negative relationship (Robertson et al., 1997). The questionnaire was principally developed to reflect trait predisposition to attentional lapses, yet investigations into larger and more diverse populations with alternative procedures and methods of analyses have shown limited support for this association (Smilek et al., 2010). However, measures relating to state fatigue have been easier to link to task performance, and indicated some change over time (van Schie et al., 2012). Thus, the SART may be a reliable means of measuring as well as experimentally inducing changes in state fatigue levels (Nieznański et al., 2020) while detecting whether these are related to trait fatigue.

Age and the SART

At present there is a gap in our current understanding of fatigue across the healthy adult life span. Somewhat counterintuitively, surveys recurrently suggest fatigue to reduce with advancing age (Aritake et al., 2015; Engberg et al., 2017; van't Leven et al., 2009; Watt et al., 2000). Yet, ageing has also been noted to lead to deficits in attention (Knyazeva et al., 2018), difficulty in attentional switching (Fraser & Bherer, 2013) and lowered task-related attentional improvement (Wiegand et al., 2017). On the other hand, both McLaughlin et al. (2010) and Staub et al. (2015) reported higher SART retention of accuracy with more advanced age, and a task closely resembling the SART showed stability of commission error rates across different age groups (S.-S. Hsieh et al., 2016). This goes in opposition to older adults reporting deficits in sustained attention (Harty et al., 2013) while keeping lower mind-wandering levels (Nicosia & Balota, 2021; Vallesi et al., 2021) and occasional evidence for a gradual decline both in reaction times and accuracy in subsets of the ageing population in a version of the SART (Rizzo et al., 2021). Differences in type of fatigue assessed may reconcile these diverging findings, and we thus investigated SART performance and trait and state fatigue systematically across the life span.

Online research

Recently, interactive behavioural experiments have been moved online to platforms such as Qualtrics (Bridges et al., 2020; Garaizar & Reips, 2019; Majima et al., 2017). While these studies were of particular interest due to the increased risks of conducting face-to-face laboratory experimentation during the global pandemic, the online implementation of cognitive experiments has been shown to achieve precision comparable to the laboratory environment, whilst providing researchers access to wider, more diverse demographic groups (Kuroki, 2021). We leveraged the online approach for the study of SART and fatigue (for gaining new insight, but also out of necessity due to the pandemic).

Aims

We hypothesised that trait fatigue could either negatively affect task performance directly, or that trait fatigue would predispose participants to higher levels of pre-task state fatigue. In turn, we proposed that this pre-task state fatigue would cause further in-task changes to state fatigue, and consequently to performance on the SART. We investigated this by first recording trait fatigue measures, using a subjective self-report questionnaire. Participants then provided their momentary, pre-SART state fatigue through a subjective self-report measure, performed an extended version of the SART and then reported their post-SART state fatigue. In relation to our pre-registered protocol (available at https://osf.io/hzwvp), we specifically aimed to:

1) Investigate the correlational relationship between changes in state fatigue and performance changes on SART over time. Specifically, that no-go accuracy will decrease, and reaction times will increase as a) state fatigue increases, and b) state energy decreases.
2) Assess the relationship between no-go trial accuracy and reaction time on the SART and reported trait and state fatigue. Specifically, that no-go accuracy will be lower, and reaction times will be slower in participants with a) high trait fatigue, b) high state fatigue and c) low state energy.

3) Determine the relationship between subjective trait fatigue and state fatigue, as well as changes in state fatigue as a result of the task. Specifically, that trait fatigue would be a) positively correlated with pre-task state fatigue and b) negatively correlated with pre-task state energy. We also expected to observe greater SART-induced c) increase in state fatigue when pre-task trait fatigue was high, and d) decrease in state energy when pre-task trait fatigue was high.
4) Carry out the research project online, targeting the general population across the whole lifespan and so test the viability of an online environment for general research on sustained attention. Based on previous divergent findings, we expected to observe difference in a) no-go accuracy and b) reaction times with increasing age.

Methods

Participants

We ran a power analysis on the largest anticipated test to be performed, a two-sample independent t-test with an expected power (1 – ß) of 0.80, α = 0.05 and an expected Cohen's d of 0.4 (J. Cohen, 2009). As there was no prior evidence as to how state fatigue may relate to the other proposed measures, we powered the sample size calculation for a medium effect size based on a pilot study with 10 participants (see methods section). The power analysis was conducted using the 'pwr' in R (Champely et al., 2020), determining that a minimum of 100 participants was required. Based on the pilot study (see below), we expected a drop-out rate of 10%, and because we wanted to recruit 6 stratified age cohorts of equal size, the total number of participants recruited for the study was raised to 120.

Participants were recruited from the general adult population (age ≥ 18) through the online platform Prolific (http://www.prolific.com). They were recruited in 6 equally large, stratified age cohorts (18-29, 30-39, 40-49, 50-59, 60-69, 70+) to compensate for overrepresentation of younger participants in the Prolific participant pool. All participant data was acquired within 24 hours of the study portal opening on 28th of March 2021 at 8am (BST). Most participants carried out the task within the first two hours of its publication on Prolific (84%). Participants were admitted to the experiment if they indicated at least moderate proficiency in the English language and reported an absence of any cognitive or neurological conditions or uncorrected vision.

Measures

The Visual Analogue Scale for Fatigue (VAS-F, (Lee et al., 1991)) was used as the state fatigue measure. It captures changes in subjective state fatigue through 18 items divided into two subscales: one for fatigue (13 items) and one for energy (5 items), with scores from 0 (no fatigue) to 100 (maximum fatigue). It has shown excellent reliability of α = 0.93 and α = 0.91 for the two scales, respectively (Lee et al., 1991). Two items of outdated language were replaced by closest possible synonyms: ‘worn out’ to ‘drained’, and ‘bushed’ to ‘run down’ to avoid repetitiveness and a poor understanding of the items. Subsequent internal consistency tests confirmed no impact on the measure’s reliability.

The MFI was used to acquire trait fatigue measures (Smets et al., 1995). This scale has been used to measure fatigue in a variety of settings and age groups and is comprised of 5 subscales with 4 items each (20 items in total) on a 5-point Likert scale. It is the most comprehensive measure to date combining many aspects of trait fatigue in one larger scale. It has a reliability of α = .84. and shown to lack floor and ceiling effects as well as item redundancy (Lin et al., 2009).

Task

The SART is a task in which participants react to numerical stimuli presented in rapid succession in the middle of the screen. The general population has response times ranging from 300 to 400ms (Hawkins et al., 2019; Seli, Jonker, et al., 2013). We expected our data to contain time offsets of about 30ms due to the online nature of the task, expected from hardware (keyboard sampling, keyboard cable) and software (operation system, web-browser) differences (compared to a stable laboratory environment (Bridges et al., 2020)). In the conventional SART, the typical standard deviation is reaction times between 50ms to 100ms. We expected a greater standard deviation in response times in our online sample in comparison to the conventional experiments, due to possible lower accuracy and variability of the devices the participants could use to access the task (Bridges et al., 2020). Whilst a very high accuracy rate was expected on the go trials (> 90%), we expected no-go accuracy rate to vary greatly across participants (Seli, Jonker, et al., 2013; L. Wilson et al., 2011).

A custom implementation of the SART using JavaScript code, relying on the jsPsych package (de Leeuw, 2015) hosted on an external, secure server was used to run the experiment. There was a practice block of 36 trials, followed by four blocks of 117 trials, each with a break (timed by the participants) between each block, 502 trials in total. This number was chosen to achieve a duration of around 10 minutes for the experimental part and around 20 minutes for the whole study (based on the prior piloting). Each trial consisted of a number between 1-9 presented in the centre of the screen at a 64-pixel size for 250ms. The number disappeared for 900ms before the next one was presented. Participants were instructed to respond to any number apart from the number 3 by pressing the space bar (go), whilst withholding their response for the number 3 (no-go). They were asked to balance speed and accuracy in their responses as both were used as measures of performance. For each participant, the numbers were sampled randomly, with each number appearing the same number of times, and all numbers were distributed evenly. Altogether, the no-go stimuli appeared 56 times in total, representing 11.11% of the presented stimuli.

Procedure

Upon receiving the notification of a new study available on Prolific, participants were redirected to a survey web portal on Qualtrics (2021, Provo, UT, USA). The platform was chosen because it follows strict ethical protocols for participation and provides access to a stratified participant demographic (Boas et al., 2020). Participants were first introduced to the experiment and asked for their consent. They then provided their basic demographic information, self-reported information about possible visual deficiencies and other conditions that would impact their performance in the experiment, they then filled in the MFI and VAS-F. The Qualtrics platform then performed call-backs to a server hosting the JavaScript code, forming a pop-up within the Qualtrics survey in which participants carried out the experimental tasks. They underwent a practice session for the SART, completed four blocks of the SART with breaks between them and then provided their VAS-F again. Finally, they were debriefed. To avoid expectation bias in the practice block, participants were only given general feedback about their accuracy without specified desirable outcomes.

Statistical analyses

All data analysis was carried out in R (R Core Team, 2022) using the packages ‘tidyverse’ (Wickham et al., 2019), ‘psych’ (Revelle, 2023) and ‘moments’ (Komsta & Novomestky, 2022). Further packages used for graphical depiction were: ‘ggpubr’ (Kassambara, 2023), ‘viridis’ (Garnier et al., 2023) and ‘Cairo’ (Urbanek & Horner, 2023).

The behavioural data was pre-processed to acquire accuracy scores both for go and no-go trials. Go trial responses classed as anticipation errors (< 150ms; Hawkins et al., 2019) were discarded. Participant reaction times were log-transformed to normalise the distribution of the residuals of the subsequent models. As per the pre-registered protocol, participants with responses that fell into either of two anticipated deliberately erroneous approaches to completing the experiment were removed from further analysis: One was responding to all trials and withholding responses randomly at the rate of the occurrence of the no-go stimuli (> 89% go stimuli correct and < 11% no-go stimuli correct), the other to randomly respond at the rate of occurrence of the no-go stimuli (< 11% go stimuli correct and >89% no-go stimuli correct), in any of the four experimental blocks. Participants who did not complete all the blocks were likewise removed from the analysis. Finally, participants showing more than one failure to correctly answer the attention check questions were excluded from the analysis also.

Correlation matrices were acquired for the five subscales of the MFI and then used to compute the Cronbach's alpha (Claros-Salinas et al., 2013). Cronbach's alpha scores were also obtained for the pre- and post-test levels of the VAS-F. State fatigue change was obtained by subtracting the pre-task VAS-F score on both the fatigue and energy subscales from the post-task VAS-F score on both of those scales. Accuracy change scores were acquired by subtracting the no-go accuracy score in the last block from the no-go accuracy in the first block.

Pilot study

A pilot study with 10 participants was conducted to determine the viability of the online environment for conducting a SART experiment. These results also informed the power calculation and resulted in a formulation of the accuracy thresholds for the SART. In response to the pilot, we also implemented attention checks to ensure that participants fully attended to the questions. These were in the form of an extra item on the MFI, pre-task VAS-F and post-task VAS-F asking the participant to answer with a specific numeric value. In line with the platform recommendations, participants were excluded from data analysis and refused payment if they failed more than one of the three checks.

Results

Exclusions

Four participants failed more than one attention check and so were not included in the sample. A further 16 participants (11.4%) attempted the task but stopped without finishing. Further participants were recruited in their place until the complete sample size of 120 was achieved. For the final analysis a total of 5 participants were excluded from the sample: Two participants experienced an unknown technical fault, two were removed for failing to achieve the minimum SART performance and one was removed for reporting a lack of sufficient English language knowledge. This left the total of participants at 115 (95.83% of complete total recruited), see Fig 2.1.

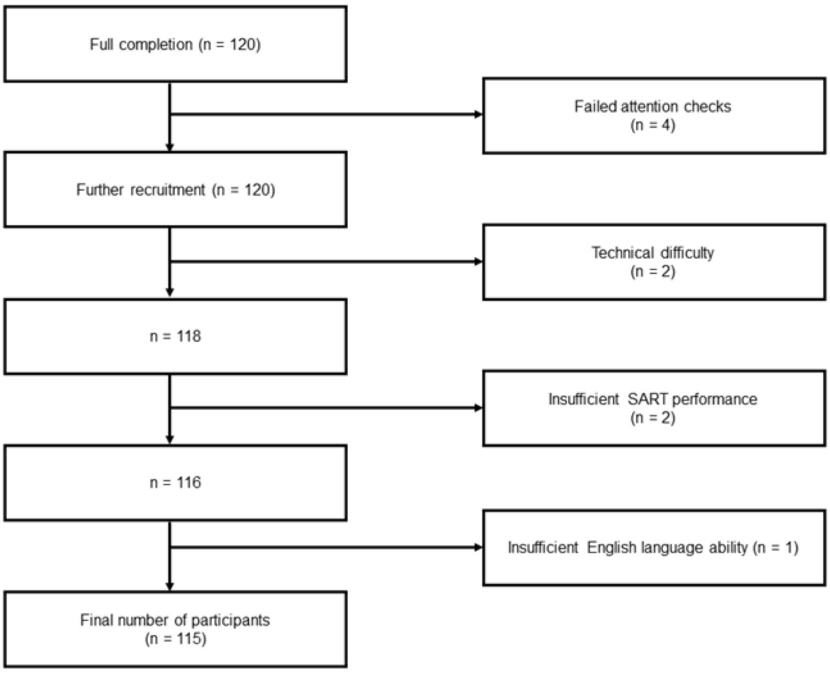

Fig 2.1 A flowchart depicting the exclusion process in the study.

Participants

A total of 115 participants were analysed after exclusions. The sample was comprised of 61 women and 54 men (46.96%), with a mean age of 48.43 (SD = 18.08) equally represented across the stratified adult age lifespan (range = 18-81). The sample was comprised of 27 different nationalities, predominantly

European (n = 100, 86.96%), with the most frequent being British (n = 51, 44.35%), Polish (n = 12, 10.43%) and Italian (n = 7, 6.09%). The sample was socio-economically diverse, including 26 (22.61%) individuals with no higher education, 26 (22.61%) individuals with college-level or vocational training, 35 (30.43%) individuals with an undergraduate degree and 28 (24.35%) individuals with postgraduate and/or higher degrees. Sixty (52.17%) individuals were in some form of employment, whilst 13 (11.30%) comprised students and 42 (36.52%) were unemployed, retired, on leave or furloughed. No participants reported complications related to eye-conditions or cognitive difficulties which could have impeded performance. All European participants completed the study in the morning, within two hours of the study release on Prolific. Finally, 32 (27.83%) participants reported that they currently had, or suspected that they had had, Covid-19 infection. However, only 5 (4.35%) reported a definite diagnosis with Covid within the previous 3 months.

The study was approved by the University of Glasgow College of Science and Engineering Ethics committee (Approval number: 300200069). Digital consent was obtained from all participants by completing an online checkbox form.

Questionnaires

The participants gave both their pre-task fatigue (M = 364.49, SD = 284.82) and energy (M = 264.06, SD = 114.01) scores as well as their post-task fatigue (M = 415.27, SD = 325.04) and energy (M = 241.08, SD = 118.87) scores. Change scores were thus obtained by subtracting the pre-task score from the post-task score for fatigue (M = 50.78, SD=186.14) and energy (M = -22.98, SD = 91.76). As the change scores included post-task state fatigue levels in their calculation, we decided not to consider post-task scores separately, contrary to what we indicated in the pre-registration.

Pre-test fatigue scores predicted post-test fatigue scores, F(1, 113) = 234.70, p < .001, R2 = .680. Likewise, pre-test energy scores were predictors of post-test energy scores, F(1, 113) = 102.80, p < .001, R2 = .480, showing consistency within participants across the two time points.

The participants completed the MFI as a measure of trait fatigue. Subscale and total scores were calculated. The sample had a mean score around the midpoint of the scale (M = 51.43, SD = 13.82, range = 20 - 87). Even on the subscale level, the MFI showed a similar means for general fatigue (M = 10.77, SD = 3.43, 4-19), physical fatigue (M = 10.54, SD = 3.56, 4-20), mental fatigue (M = 10.12, SD = 3.59, 4-20), reduced activity (M = 10.28, SD = 3.36, 4-20) and reduced motivation (M = 9.71, SD = 3.15, 4-18). The results were similar to those found in other populational studies (Ishii et al., 2014; Völker et al., 2016b) as opposed to results with means above the threshold score of 60 (Purcell et al., 2010) indicative of a clinically fatigued population.

Cronbach's alphas of the MFI, as well as of the pre-test VAS-F and the post-test VAS-F, were obtained. We expected a Cronbach's alpha of 0.8 on all the scales (Cronbach, 1951). We found a Cronbach alpha of 0.92 for the MFI total, 0.78 for general fatigue, 0.81 for physical fatigue, 0.81 for reduced activity, 0.70 for reduced motivation, and 0.86 for mental fatigue. The pre-task state fatigue scale (VAS-F) showed an alpha of 0.95, energy (VAS-E) was 0.95. Overall pre-task was 0.96. Post-task overall was 0.97, fatigue 0.97 and energy 0.95. Except for general fatigue and reduced motivation, all values reached 0.8, implying that the items in the questionnaires were internally consistent. The VAS-F showed very high internal consistency.

SART

After removal of the trials with very short reaction times (< 150ms, 3.0% of data), and although the sample mean reaction times matched the times expected based on prior studies (364.47ms, SD = 5.15ms), they appeared not to be normally distributed (they had a heavy rightward skewness (2.02) and were leptokurtic (12.44)). So, the reaction times were corrected by log-transformation, leading to more acceptable skewness (.50) and kurtosis (4.54). The mean within-participant standard deviations in reaction times were 99.87ms (SD = 7.76) and normally distributed (skewness = .22, kurtosis = 2.69). No-go accuracy was 68.23% (SD = 15.84%) and go accuracy was at ceiling, 98.86% (SD = 3.07%).

Accuracy change scores (M = -3.34%, SD = 18.82%) were acquired by subtracting the nogo accuracy score in the last block of the task, from the first block. This showed no skewness (-.19) and no kurtosis (2.96). A multiple linear regression was run to predict no-go accuracy change from each of the five individual subscales of trait fatigue, change in reaction time, change in state energy, change in state fatigue and interaction between change in state fatigue and change in state energy. The overall model was significant, F(10, 104) = 2.51 p = .010, R2 = .190 and only fatigue change was found to be a predictor of accuracy change with a negative relationship between accuracy change and fatigue change, ß < .001, t = 2.82, p = .006, showing a small to medium effect size (J. Cohen, 2009): the greater the fatigue change, the larger the drop in accuracy across the blocks. While fatigue change was associated with accuracy change, energy change and the other variables were not significant. Fig 2.2 depicts both relationships to fatigue and energy. The variance inflation factor remained under 3 for all model variables.

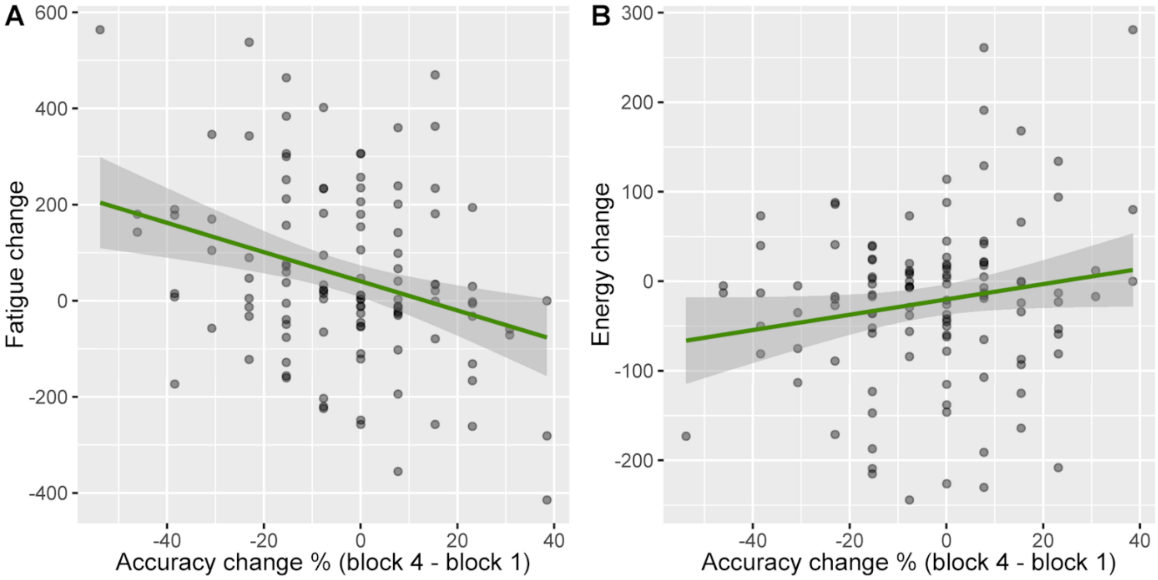

Fig 2.2 Linear relationship between accuracy change, fatigue change and energy change. (A) Relationship of accuracy change between the last and the first block and fatigue change before and after the task with 95% confidence intervals and (B) accuracy change between the last and the first block and energy change before and after the task. with 95% confidence intervals.

A multiple linear regression was run to predict no-go accuracy from block number, age, total MFI score, pre-task state energy score, pre-task fatigue score and interaction of all the subjective fatigue measures. The overall model was significant, F(8, 451) = 9.40 p < .001, R2 = .140. Only age was found to be a predictor of accuracy, ß = .003, t = 5.89, p < .001: the older the participants were, the more accurate they were at withholding no-go responses during the SART. The relationship between age and accuracy is depicted in Fig 2.3. The variance inflation factor remained under 3 for all model variables.

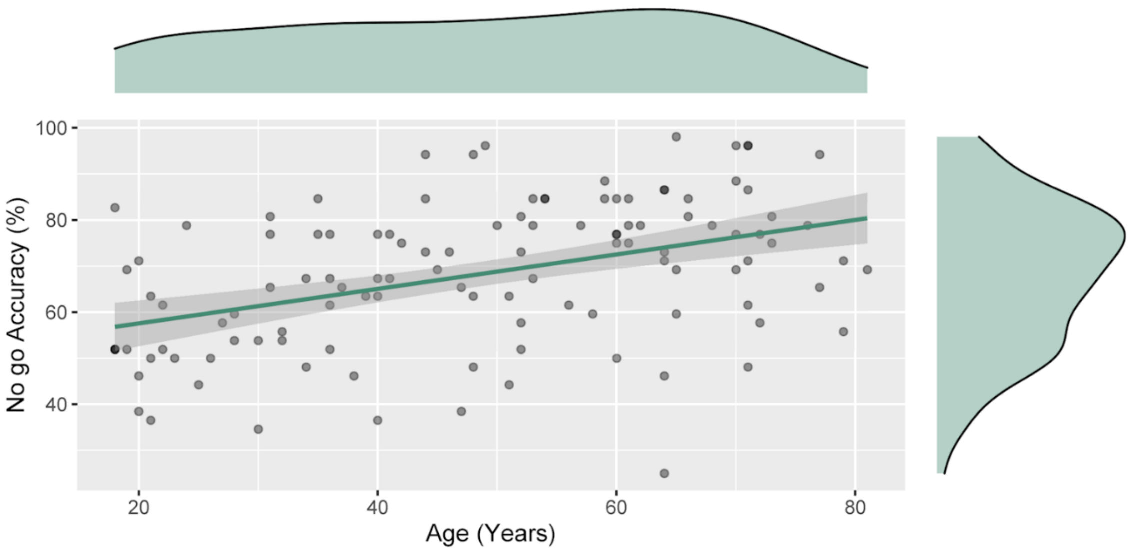

Fig 2.3 Linear relationship between participant age and overall participant no-go accuracy with 95% confidence intervals. Density plots indicating the distribution of the participants across ages 18-81, as well as the no-go accuracy distribution.

A multiple linear regression was run to predict correct go-trial reaction time from block number, age, total MFI score, pre-task state energy score, pre-task fatigue score and the interaction of all the subjective fatigue measures, yielding an overall significant model, F(8, 451) = 11.00 $p < .001$, R2 = .16, and only block number found to be a predictor of reaction time, ß = .014, t = 8.94, $p < .001$, with a reduction in RTs in relation to task block number (Fig 2.4).

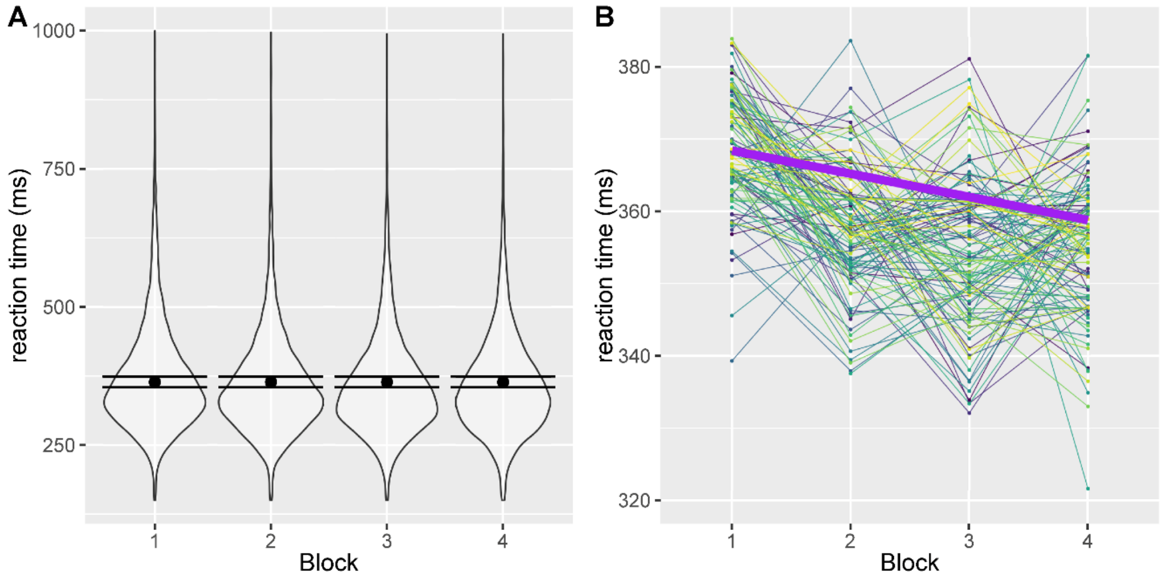

Fig 2.4 Reaction times on the SART across time. Distribution of reaction times at trial block level across the four blocks including mean reaction times and standard deviations with reaction times within each participant across the four task blocks distinguished by colour (including the overall linear trend across the four blocks).

A simple linear regression showed that mean reaction time did not predict no-go accuracy, F(1, 113) < .001, p = .970, R2 < .001.

Initial state fatigue

We expected the state fatigue change and the energy change induced by the SART to be predicted by the scores on the five MFI subscales. Likewise, we expected a relationship between the MFI subscales and the pre-task VAS-F scores. A multiple linear regression examined the relationship between all 5 of the MFI subscales and pre-task fatigue, and another examined the relationship of the 5 MFI subscales to pre-task energy, see Fig 2.5.

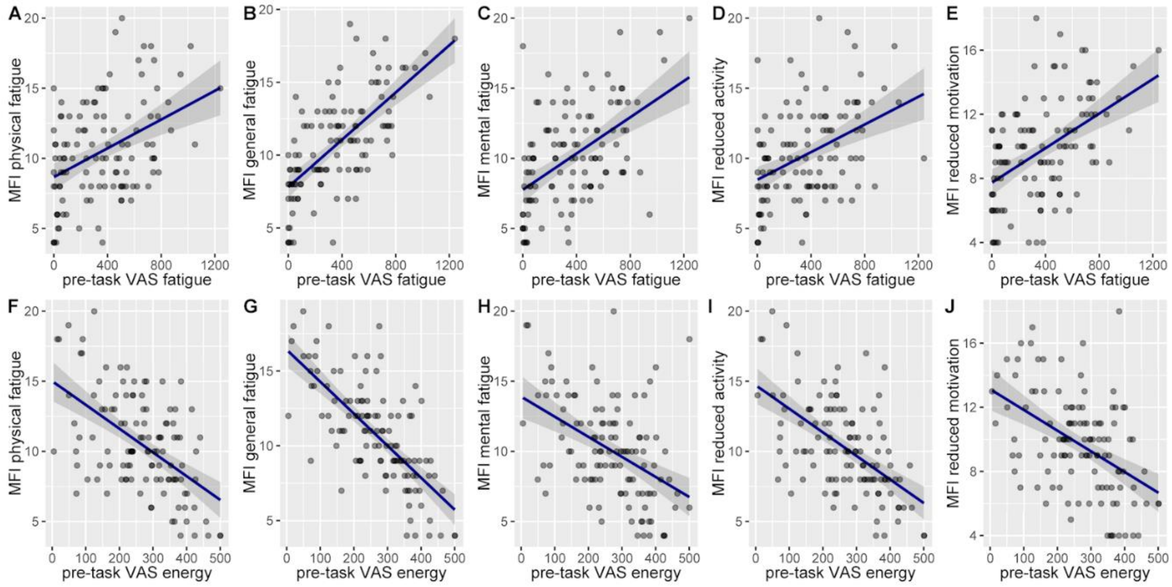

Fig 2.5 Trait-state fatigue relationship (including highlighted 95% confidence intervals) on all MFI and pre-task VAS subscales. (A) VAS fatigue and MFI physical fatigue. (B) VAS fatigue and MFI general fatigue. (C) VAS fatigue and MFI mental fatigue. (D) VAS fatigue and MFI reduced fatigue. (E) VAS fatigue and MFI reduced motivation. (F) VAS energy and MFI physical fatigue. (G) VAS energy and MFI general fatigue. (H) VAS energy and MFI mental fatigue. (I) VAS energy and MFI reduced activity. (J) VAS energy and MFI reduced motivation.

The overall model predicting pre-task state fatigue was significant, F(5, 109) = 25.10 p < .001, R2 = .535). Pre-task state fatigue was positively related to mental fatigue (β = 14.80, t = 2.26, p = .026), physical fatigue (β = 28.10, t = 3.05, p = .003) and general fatigue (β = 60.69, t = 6.75, p < .001), but was not related to reduced activity (β = 9.84, t = 1.10, p = .275) or reduced motivation (β = 7.94, t = .880, p = .380).

The overall model predicting pre-task state energy was also significant, F(5, 109) = 29.11 p < .001, R2 = .572). Pre-task state energy was negatively related to general fatigue (β = 22.34, t = 6.47, p < .001) and reduced activity (β = 12.60, t = 3.66, p < .001), whilst showing no relationship to mental fatigue (β = 2.88, t = 1.14, p = .256), physical fatigue (β = 6.75, t = 1.90, p = .060) or reduced motivation (β = 3.48, t = 1.01, p = .317).

State change

However, state change only modestly corresponded to the MFI scores. The overall model was significant, F(5, 109) = 2.38 p = .043, R2 = .099). State fatigue change was negatively related to reduced activity (ß = 18.84, t = 2.31, p = .023), with a small effect size. This meant that participants who had higher reduced activity scores had a smaller increase in their state fatigue during the task. There were no other relationships between state fatigue change and any of the other 4 MFI subscales: mental fatigue (ß = 5.67, t = .950, p = .344), physical fatigue (ß = 6.74, t = .803, p = .424), general fatigue (ß = 5.30, t = .648, p = .518) or reduced motivation (ß = 14.78, t = 1.80, p = .074). The same model was run to predict state energy change from the five MFI subscales, F(5, 109) = 3.10 p = .012, R2 = .125. Again, reduced activity was also a positive predictor of energy change, ß = 10.30, t = 2.60, p = .01 with a small effect size. This showed that participants with higher reduced activity scores reported less energy loss during the task. No relationship was found with the other scales: mental fatigue (ß = 1.17, t = .403, p = .688), physical fatigue (ß = 3.38, t = .829, p = .409), general fatigue (ß = 1.35, t = .341, p = .734) and reduced motivation (ß = 6.16, t = 1.55, p = .124). Therefore, the direction of the relationship was the opposite of our pre-registered prediction. We predicted that we would observe more task-induced fatigue and energy loss in participants who started the experiment with high levels of reduced activity (see Fig 2.6).

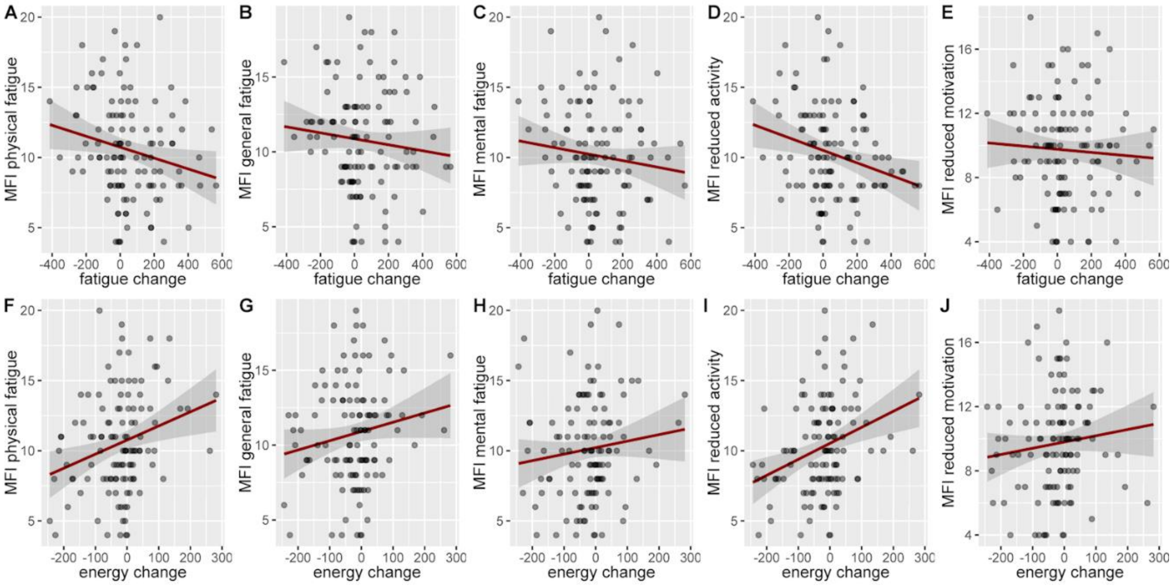

Fig 2.6 The fatigue and energy state change and trait fatigue relationship in the sample with highlighted 95% confidence intervals. (A) VAS fatigue change and MFI physical fatigue. (B) VAS fatigue change and MFI general fatigue. (C) VAS fatigue change and MFI mental fatigue. (D) VAS fatigue change and MFI reduced fatigue. (E) VAS fatigue change and MFI reduced motivation. (F) VAS energy change and MFI physical fatigue. (G) VAS energy change and MFI general fatigue. (H)

VAS energy change and MFI mental fatigue. (I) VAS energy change and MFI reduced activity. (J) VAS energy change and MFI reduced motivation.

All the European sample (86.96%) completed the study in the morning, contrary to the pre-registration, so no analysis was conducted on the difference between morning and evening due to the high imbalance between the two conditions. Likewise, too few participants identified as having experienced Covid symptoms 3 months prior to their participation (4.35%), and so Covid was not considered in the analysis. Employment was too diversified to be categorised for the analysis and so it was not considered either.

Discussion

Fatigue and SART

Participants reported fatigue and energy levels before and after carrying out an online version of SART. Levels of state fatigue were predicted by scores from the MFI, which was used to reflect trait fatigue, illustrating that pre-task state fatigue levels were initially rooted in long-term internal trait fatigue. In addition, the findings show that undergoing the SART does induce changes in state fatigue. Participants got fatigued and lost energy during the task, as demonstrated by the clear difference between the pre- and post-task subjective fatigue and energy levels. Furthermore, the change was reflected in their task performance: If performance on the task dropped, more fatigue and less energy were experienced. So, the objective measure of accuracy change between the first and final blocks corresponded to the change in reported subjective fatigue. In fact, state fatigue change as a predictor of accuracy change outperformed initial trait fatigue levels. This was true even though participants received no feedback and were not given any expectations about the desired performance. Our data thus demonstrate a tight coupling between drops in SART accuracy and changes in state fatigue.

We detected an unexpected relationship between state fatigue change and trait fatigue opposite to our original prediction. Change in state fatigue was smaller with higher levels of trait physical fatigue and reduced activity present before the task. This may indicate a ceiling effect, or limited capacity for fatigue change, if a relatively higher fatigue state is already present: when fatigue is high prior to the start of the task, no further increase may be possible given the nature of the task. Our selection of the SART to induce fatigue was motivated by its ability to induce errors in the withholding of a behavioural response caused by lapses in sustained attention. The prolonged, and repetitive nature of this task may have induced a different type (or a different degree) of fatigue compared to a task that, for example, depletes cognitive resources due to high complexity (Botvinick & Braver, 2015; Gergelyfi et al., 2015) or involves high working memory load (Wylie et al., 2019). It may be the case that participants with high trait fatigue did not experience greater state fatigue changes because they had a higher tolerance for unstimulating, repetitive tasks, and it is possible that the use of a challenging task may have produced different results in this regard, which should be investigated in future research. The findings parallel those of Boolani and colleagues (Boolani et al., 2020), who likewise detected that higher trait fatigue in individuals meant the inability to get further fatigued. The effect has also been suggested to occur due to depleted cognitive reserve on part of the participants, preventing any further rises in fatigue (Fuller et al., 2021).

Age and learning effects

Age proved to be the strongest predictor of overall performance over any other measures or variables (the older the participants the greater the accuracy), confirming and reproducing the outcomes of a recent meta-analysis by Vallesi and colleagues (2021). We propose this finding to be a robust indicator of an underlying age-specific difference, likely the cognitive approach to the task (see further elaboration under ‘future directions’).

In agreement with prior findings (Nieznański et al., 2020; van Schie et al., 2012), participants in this large sample sped up over time. There was no speed-accuracy trade off, accuracy remained the same whilst reaction times reduced. This improvement in speed thus showed a gradual increased familiarity with the task and accommodation to the experimental paradigm (Reteig et al., 2019). Interestingly, this effect occurred regardless of age. It highlights the need to track performance across a larger time window (ideally 40 minutes or longer; Reteig et al., 2019), should future attempts aim to achieve a measurable decline in SART participant performance.

Online environment

The achieved go and no-go accuracy rates as well as reaction times when adjusting for errors caused by performing the study online (Kuroki, 2021) matched those in other studies carried out in the general population (Dang et al., 2018; Seli, Jonker, et al., 2013). Notably, the described online performance appears comparable with samples in the laboratory studies (Robertson et al., 1997; Seli, Jonker, et al., 2013). Thus, the findings support the notion that online behavioural research can closely match the laboratory setting, whilst reaching diverse participant groups, which would be harder to recruit in laboratory studies. They also demonstrate the feasibility of obtaining decrement effects despite reduced experimental control over participants than in laboratory settings, such as less influence on timing of breaks between blocks. To our knowledge, this is the first time that the SART has been implemented online, and it achieved very comparable data to laboratory settings. The study thus successfully shows the suitability of such efforts for future attempts to investigate ageing as well as the link between subjective measures of fatigue and SART performance change. It also provides a characteristic profile of fatigue and baseline fatigue rates prior to experimentation in online samples across the whole adult lifespan with the exception of advanced age, as well as the influence of fatigue levels over the course of the experiment.

Limitations

The original pre-registered models were based on concrete linear predictions between one predicted and one predictor variable, but we considered several variables within one model, not all of which were directly mentioned in the pre-registration. Nonetheless, the models broadly reflect the anticipated pre-registered relationships. This approach helped us to detect the unanticipated link between increased trait fatigue and reduced state fatigue change. It is possible that this particular effect was influenced by regression to the mean, driving a drop in ceiling state fatigue levels when re-tested at a second timepoint. Nevertheless, it remains a valid exploratory finding and does not exhaust the full potential of the available dataset. Further work may consider other analytical approaches to clarify this correspondence of trait to state fatigue, including a promising use of non-linear models already utilised elsewhere (Bolsinova & Molenaar, 2018).

We are aware that other factors could have impacted state fatigue and there is added uncertainty in the use of an online environment, which is usually alleviated by more precise laboratory control over the experiment: factors pertaining to the sleep cycle and time of day which could impact the vigilance decrement (Lara et al., 2014) were not considered, and other insufficiently addressed factors include individual problems in nourishment (van't Leven et al., 2009), gender, work exhaustion, smoking or undetected underlying health conditions which could in turn have contributed to the reported trait and state levels of fatigue.

Future directions

It was interesting to see that age had a greater impact on overall SART performance than initial fatigue levels, yet this may be the case only for a generally healthy population (as tested here). Research into clinically fatigued populations is warranted to see whether fatigue becomes a significant predictor of SART performance, as the SART may be much more challenging for patients with diagnosed clinical fatigue conditions. This study highlights the significance of SART as an objective measure of fatigue change, and it may well prove to be a sensitive, objective means of assessing and monitoring fatigue in clinically fatigued populations.

Reverting back to the age effect, the present findings provide clear evidence of a stable age effect in the standard implementation of the SART. The used sample size allowed us to treat age as a continuous variable and so show a linear relationship between higher accuracy and age. There are clear differences which occur in the attentional processes necessary to undertake this task with increasing age. One existing explanation is that the task is either perceived as more interesting and challenging, and so carried out more dutifully with advancing age. Thus, older participant performance hints at a motivational advantage (Vallesi et al., 2021) and reliance on a more accuracy-based cognitive strategy (Knyazeva et al., 2018). At the same time, it may paradoxically show that improved performance means greater difficulty and necessity to actively engage cognitive resources when performing the task. The task could be perceived as more routine and automatic by younger participants due to its relative simplicity (Vallesi et al., 2021). They would therefore opt for a speed-based strategy. In contrast, older adults may experience a more innate motivational drive to excel at the task (Braun et al., 2015; Macdonald et al., 2011). Future work could investigate this phenomenon in more detail by utilising motivational manipulations and probing attitudes to experimentation in participants. Pairing future studies of the SART with neural measures tracking the employment of cognitive resources independent from subjective report would enable the detection of this speculated effect. Recent research has started to investigate oscillatory neural correlates of performance on the SART (Braun et al., 2015; Knyazeva et al., 2018) focusing on the link between the SART and brain oscillations in particular (Braun et al., 2015;

Macdonald et al., 2011; Majima et al., 2017). Further research could link changes in the oscillatory signal to this objective performance and the subjective experience of fatigue, and this would help to ground research on fatigue in clinically relevant theoretical conceptualisations (Ishii et al., 2014; Johansson & Rönnbäck, 2013) as well as help to better understand innate and lasting proclivity to fatigue. Another open avenue of research is the comparison of this attentional approach to other paradigms and tasks with higher cognitive demands (Jacquet et al., 2021; K. J. Peters et al., 2022) or using a task-switching approach (Mangin et al., 2022).

Conclusion

In summary, we investigated the impact of undergoing the SART in a large online sample comprising all adult age groups. We found that an increase in reported state fatigue was reflected in reduced SART performance. We also found that age, not trait predisposition to fatigue, was the greatest predictor of overall performance on the task. Pre-task trait fatigue led to a ceiling effect in state fatigue change only. We propose that the SART is a sensitive, objective means to induce and measure changes in state fatigue.

Chapter 3: Oscillatory markers of vigilance, task-induced fatigue and motivation during sustained attention: Evidence for decoupled alpha- and beta-signatures

Abstract

Reduced vigilance can be captured in measures of attentional lapses in sustained attention tasks, but just how these lapses relate to task-induced fatigue and motivation to maintain optimal performance is unclear. We used the Sustained Attention to Response Task (SART) to induce fatigue and manipulated motivation levels for the last block of the task in young and older participants (N = 34), while recording electroencephalography to track electrophysiological markers of vigilance change, motivation and fatigue. Despite significant increases in subjective fatigue and mind wandering over 45 minutes, no vigilance decline in the task was observed. However, the age groups differed markedly in their response strategies from the outset (adopting distinct speed-accuracy trade-off strategies) with faster/more erroneous responses in the younger and slower/more accurate responses in the older participants. Pre-stimulus alpha power increased over time, but although this mirrored the subjective rise in fatigue/mind wandering that also occurred over time, these were not correlated. Post-stimulus activity showed two distinguishable beta signatures: a fronto-central topography as a marker of response strategy and a fronto-parietal distribution modulated by motivation *per se*. We speculate that these two signatures contribute to offset performance declines over time.

Introduction

Sustaining attention requires a constant, self-directed maintenance of vigilance (Robertson & Garavan, 2004) both across various daily activities (Massar et al., 2018; Roach et al., 2012; Walker & Trick, 2018), and bespoke experimental tasks (Head & Helton, 2012; Reteig et al., 2019). Continuously engaging in sustained attention tasks can result in changes in performance (Reteig et al., 2019; Stoll et al., 2016) that have been characterised as the vigilance decrement (Oken et al., 2006; Robertson & Garavan, 2004). However, the onset of a vigilance decrement will vary across experiments and studied populations, with some studies pointing to a continued ability of participants to concentrate and maintain focus during sustained attention tasks (Lara et al., 2014; Nakagawa et al., 2013), while others suggest impairments in accuracy and reaction times with increasing time-on-task (Pershin et al., 2023; A. S. Smit et al., 2004; van Schie et al., 2012).

Differences in motivation, both between-and within- participants, may account for some of this variability. For instance, it has been suggested that motivation can be a key influence in the reappraisal of task strategies (Earle et al., 2015; Gilsoul et al., 2022), which can lead, through the self-regulatory mechanism of attentional effort (Sarter et al., 2006; Stoll et al., 2016), to improved behavioural measures in sustained attention tasks (Oken et al., 2006). This was tested by Reteig et al. (2019), who reactivated participants' motivation after 60 minutes spent on a sustained attention task, by offering an additional monetary reward if they managed to out-perform 65% of the other participants in the final part of the experiment. Although Reteig et al. found that the motivational manipulation restored the vigilance decline to some extent, this was not reflected in the tested EEG measures of attentional control, except for variability in a neural theta-response. Hence, a neural link between the effect of motivation and vigilance change remains tentative (see also Awh et al., 2012). In the present study, we sought to re-examine the role of motivation in vigilance decrements by manipulating motivation in the course of a sustained attention task while recording its EEG markers (similarly to Reteig et al., 2019). We anticipated motivated participants to show different performance and oscillatory patterns compared to the unmotivated group.

In addition, we sought to investigate state fatigue. Performance declines in sustained attention tasks are often accompanied by mental fatigue. The exact mechanisms driving such fatigue are still unclear (Kuppuswamy, 2022), but are likely caused by either a depletion of cognitive resources (Jacquet et al., 2021; Krigolson et al., 2021), or by monotonous tasks leading to a disengagement of the sustained attention networks (Richard et al., 2018). Notably, previous work highlights that the effect of fatigue on vigilance decrement may be decoupled from the effect of motivation (Gergelyfi et al., 2015) and hence taking into account fatigue in the study of neural markers of vigilance change, in addition to motivational factors, is relevant. Unlike Reteig et al., (2019), who used a sustained attention-style task where the goal was to detect rare targets in an oddball paradigm (and where the typical errors were omissions), we used the Sustained Attention to Response Task (SART; Robertson et al., 1997; Weinstein, 2018) in which failures in sustained attention manifest in commission errors (false positives) arising from erroneously responding to infrequent no-go stimuli. Performance changes in the SART are influenced by response strategy and age (Dang et al., 2018; Lara et al., 2014; K. M. Wilson et al., 2016), can capture lapses into a less attentive state (Manly et al., 1999), as well as task monotony (Head & Helton, 2012), so the mapped effects extend well beyond the task itself (A. S. Smit et al., 2004). Prolonged versions of the SART therefore represent an optimal method for exploring the relationship between vigilance decrements and potential differences in strategy linked to motivation and fatigue.

In terms of neural substrates and/or correlates of the vigilance decline, both the relevant anatomical networks and some of its potential neural markers have been identified. The vigilance network is responsible for sustained attention (Milyavskaya et al., 2021), as well as executive function (Holtzer et al., 2011), exerting attentional control over the incoming visual stimuli (M. I. Posner & Dehaene, 1994) via modulation of early visual centres and network interactions needed to carry out the task (Clayton et al., 2015; Corbetta et al., 2002). It has also been linked to task-induced fatigue (Shen et al., 2016) and brain activity potentially associated with this network has been observed to change over the course of a task (Benwell et al., 2019; G. Li et al., 2020; Macdonald et al., 2011). Accordingly, activity changes in the vigilance network should track its gradual disengagement (Ishii et al., 2014; Johansson & Rönnbäck, 2013) and thus make the network a viable focus for the study of neural changes due to the vigilance decrement.

In EEG research, activity of the vigilance network has been broadly characterised as occurring in the oscillatory alpha frequency band (Clayton et al., 2015; Sadaghiani & Kleinschmidt, 2016) extending over frontoparietal brain areas (Clayton et al., 2015; Corbetta & Shulman, 2011). Previous literature further suggests patterns of change in alpha oscillations connected to a decline in performance in sustained attention (Braun et al., 2015; Nan et al., 2024; Oken et al., 2006). There is some evidence of a connection between posterior alpha increase and task-induced fatigue (Barwick et al., 2012; Jacquet et al., 2021; Tanaka et al., 2012) as well as general fatigue levels (Maciejewska & Moczarska, 2023), while others maintain the connection is uncertain (Huycke et al., 2021; Talukdar et al., 2019). Oscillatory activity related to attentional control may also extend beyond the alpha-band: Changes in beta-band activity have been associated with the regulation of attentional effort during time-on-task, in addition to motor preparation (characterised as beta-rebound; Z. Li et al., 2022; Liu et al., 2010; Stoll et al., 2016). Thus, analyses of oscillatory signals focusing on the alpha and beta band should contribute to a better understanding of the neural processes underlying vigilance changes and clarify their contribution to fatigue and motivation.

Finally, it is well documented that there is large inter-individual variability in SART performance across the population (Hanzal et al., 2024b; Vallesi et al., 2021). In particular, different age groups tend to adopt either an accuracy (Dang et al., 2018; Reteig et al., 2019) or speed-based (Lara et al., 2014; Statsenko et al., 2020) strategy. These strategies are then prone to change (for example, switching from an emphasis on achieving high accuracy, to responding faster) during the task (van Schie et al., 2012). This could reflect differences in the underlying levels of fatigue, as suggested by surveys of general population fatigue (Gilsoul et al., 2022; J.-H. Yoon et al., 2023), or instead an age difference in motivational levels (Carr et al., 2022; A. D. Ryan & Campbell, 2021).

In brief, in this pre-registered study, we aimed to investigate the behavioural and EEG measures of vigilance and fatigue in young and older participants as a function of time-on-task during prolonged (45 minutes) SART performance. We induced higher levels of motivation in half of the participants during the final experimental block to investigate whether motivation could improve performance and change EEG markers of fatigue and also tested for differences between age-groups. Our results reveal three dissociated frequency-specific EEG signatures of increased state fatigue/mind wandering with time-on-task (pre-stimulus alpha), of age specific response strategies (post-stimulus fronto-central beta) and of motivation (post-stimulus fronto-parietal beta), on the backdrop of maintained task performance (no vigilance decline was observed). Unexpectedly, the reported increase in pre-stimulus centro-parietal alpha-power was not correlated with the reported rise in state fatigue/mind wandering.

Methods

Participants

The hypotheses, design and analysis plan were pre-registered prior to data collection and can be accessed via OSF (https://osf.io/y2vgc/). A total of 41 healthy adults aged between 18 and 87 years old were recruited from the University of Glasgow subject pool and the local area and were given monetary compensation for their time. The study was approved by the University of Glasgow College of Science and Engineering Ethics committee (Approval number: 300210156). Written consent was obtained from all participants. Participants were balanced for gender and were asked to report any existing medical conditions, eye-sight correction and medications which might impact their performance. Seven participants were excluded due to excessive noise and artefact in the EEG signal. The final sample consisted of 34 participants (F = 16) split into two groups based on age: young (n = 18, F = 9, mean age = 22.61, SD = 1.85, range = 20-26) and older adults (n = 16, F = 7, mean age = 66.50, SD = 8.45 years, range = 55-87). Two participants were left-handed, one was a smoker and all participants reported low to moderate caffeine consumption (estimated mean units per day over the past week = 1.31, SD = 1.12, range = 0-4), corresponding to the maximum recommended daily dose of 400mg of caffeine (Mitchell et al., 2014). They also reported an average of 7.34 hours of sleep per day (SD = 0.85, range = 6-9). All young participants were enrolled university students and the older group had similar levels of tertiary education (n = 6, 37.50%) compared to the UK average for their age group (39.60%; OECD, 2023).

All participants were screened for cognitive difficulties using the Montreal Cognitive Assessment test (MoCA; (Nasreddine et al., 2005)), reflecting scores representative of a healthy population (Borland et al., 2017) in both young (mean score = 28.28, SD = 1.49, range = 26-30) and older adults (mean = 25.81, SD = 2.74, range = 22-30). A short (3 minute) computerised visual screening assessment was administered at the beginning of the session to exclude potential visual pathologies. The task was adapted from a similar experiment investigating lateralised visual attention in both young and older groups (Learmonth et al., 2017) and shortened to 32 trials. A Welch's t-test identified no between-group differences in target detection within the visual regions where the SART stimuli were to be presented, t(32) = 1.45, p = 0.16.

Subjective Measures

Changes in state fatigue were assessed by the Visual Analogue Scale for Fatigue (VAS-F). The VAS-F measures 18 items across two subscales (fatigue = 13 items and energy = 5 items), with scores of 0 = low fatigue to 100 = high levels of fatigue. It has excellent test-retest reliability of α = 0.93 and α = 0.91 for the two scales, respectively (Lee et al., 1991). As in Hanzal et al., (2024b), two items on the scale were replaced with synonyms: 'worn out' was changed to 'drained', and 'bushed' to 'run down' to avoid repetitiveness and dated language. The spontaneous subscale from the Mind Wandering measure (Carriere et al., 2013), comprising 4 items on a 7-point Likert scale was administered to measure changes in mind-wandering during the experiment.

Sustained Attention to Response task (SART)

The study used a custom version of the SART (Robertson et al., 1997; Fig 3.1B). In each trial, participants were instructed to maintain fixation on a centrally presented cross and attend to a numeric stimulus (0-9) presented at an angular distance of 1° for 250ms. The fixation reappeared for a variable duration of 3000-4000ms before progressing to the next number. The stimuli were black on a white background and presented using a 21-inch CRT monitor (Samsung, SyncMaster 1100MB) with a screen resolution of 1280x1024 pixels and a refresh rate of 100 Hz. Participants were seated 60 cm from the screen, maintaining horizontal eye level with the centre of the display. Participants were instructed to click the left mouse button with their right index finger in response to all numbers that appeared (go trials), apart from 3 and 6 (no-go trials). The participants did not receive any feedback about their individual response times or accuracy. The stimuli were pseudo-randomised to ensure equal frequency and random distribution throughout the experiment.

Procedure

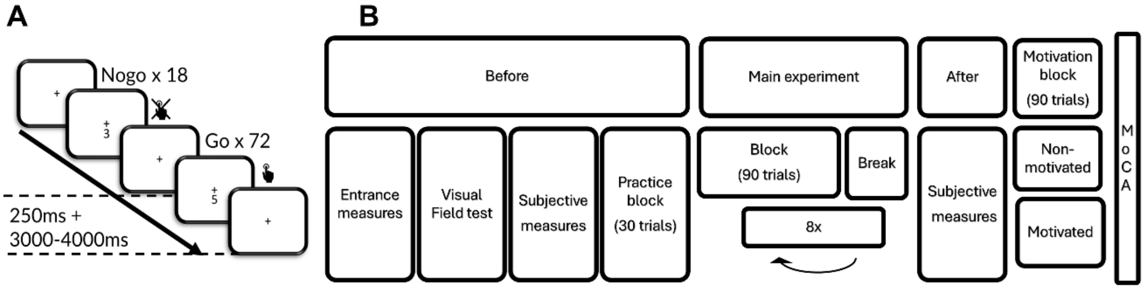

Fig 3.1 (A) Outline of the SART. (B) Outline of the experimental procedure. Before the task, participants completed the entrance demographic information, the visual field test and were administered the subjective measure questionnaires assessing state fatigue and mind wandering (VAS-F, MW-S). For the main experiment, participants performed 8 blocks of the SART task, allowing tracking of vigilance over time. After completing the experiment, the participants again completed the subjective measure questionnaires (VAS-F, MW-S) and proceeded to the final motivational block of SART performance. The MoCA was administered at the end to assess potential presence of cognitive impairments in the sample.

The experimental procedure is outlined in Fig 3.1. Participants were provided with an information sheet and gave written, informed consent to take part. They then provided basic demographic information and reported visual deficiencies, as well as any other relevant medical conditions. A 64 Ag/AgCl BrainCap (BrainProducts, Gilching, Germany) was fitted according to the international 10/20 system (American Electroencephalograpic Society, 1991), including two horizontal electro-oculographs, and impedance reduced to <25KΩ using Signa gel. Participants then completed the VAS-F and MW-S and a brief visual field test to map visual acuity. They then underwent a SART practice session of 30 trials and were given general feedback about their accuracy on the practice block. In the main experiment, participants completed eight blocks of the SART (90 trials, 72 go, 18 no-go trials, random presentation), each lasting five minutes and 20 seconds, with self-paced breaks between each block, followed by the VAS-F and MW-S to record post-task subjective states. Continuous EEG data was recorded at a 1000Hz sampling rate. The first eight blocks of the SART were followed by one further, unannounced, block of 90 trials (Block 9) to manipulate motivational state. Half of the participants were randomised into a motivated group and were instructed to try to maximise their performance on the last block (no guidance was given regarding potential strategies to achieve maximal performance). They were informed that the participant with the best performance during this block would receive an additional bonus of £50. The other half were only informed that the experiment includes an additional block and asked to undertake the block with the same instructions as the previous blocks. Finally, the participants were screened for mild cognitive decline using the MoCA and debriefed.

Analyses

Behavioural analyses

All behavioural analyses were carried out in R (R Core Team 2024) using the packages 'tidyverse' (Wickham et al., 2019), 'psych' (Revelle, 2023), 'moments' (Komsta & Novomestky, 2022), 'readxl' (Wickham et al., 2019), 'broom' (Robinson et al., 2024), 'ez' (Lawrence, 2016), 'lmerTest' (Kuznetsova et al., 2020), 'lme4' (Bates et al., 2015), 'emmeans' (Lenth et al., 2024). Further packages used for graphical depiction were: 'ggpubr' (Kassambara, 2023), 'viridis' (Garnier et al., 2023) and 'Cairo' (Urbanek & Horner, 2023). Performance analyses of the effect of age-group and time on the chosen metrics relied on an examination using randomised block- and participant- level modelling. The lmer function of the 'lme4' package (Bates et al., 2015) was used to construct corresponding random mixed effects model and to fit individual participant and block slopes and intercepts, with the lmerTest package (Kuznetsova et al., 2020) to estimate p-values.

Electroencephalography (EEG) analyses

Analysis of the EEG data was undertaken using the EEGLAB (Delorme & Makeig, 2004) and FieldTrip (Oostenveld et al., 2011) toolboxes for MATLAB. The continuous data was first detrended to remove drifts introduced by instrumental and physiological noise, alongside various baseline shifts. A Hamming-windowed FIR filter was then applied within the 2-45Hz frequency range, followed by re-referencing to the average signal. Independent component analysis was then run using ICLabel (Pion-Tonachini et al., 2019). The following threshold criteria were applied to identify components for automatic rejections: 1) Components that had <0.05 likelihood of brain origin and 2) Components that had >0.8 likelihood to be one of either an ocular artefact, muscle artefact, heart artefact, line noise or channel noise. All components labelled as 'Other' were visually inspected and rejected if they appeared similar to standard artefact components. This semi-automated correction method led to the rejection of a mean of 25.97 components (of a total of 64 available components per person, SD = 4.25, range = 20-37). A further 1.18 (SD = 1.40, range = 0 -3) components were manually rejected in each dataset and 0.24 (SD = 0.55, range = 0-2) preserved from automatic rejection due to incorrect ICLabel classification. The same analytical steps were then performed on the raw datasets with a lower filtering threshold of 0.5 - 40Hz, the original ICA weights were re-applied and components removed. Upon inspection of the signal, known noisy electrodes were interpolated (mean per participant = 0.76, SD = 0.96, range 0-4).

Data for analyses were selected based on the following steps:

1. Participants with insufficient neural data as outlined in data pre-processing were not included in behavioural analysis.
2. Trials with trigger information missing due to failure of transition of an event signal were identified and removed.
3. Outliers in reaction times were removed. Firstly, block and group mean and standard deviation in reaction time was computed. Blocks were considered separately due to an expected time effect and age groups were considered separately because of an expected group difference. Then, trials rising above two standard deviations of the mean were removed as attention lapses and trials two standard deviations below the mean as anticipation error (Kiesel et al., 2008).
4. Participants were also removed if they exhibited any of two identified erroneous strategies in any of the 8 main experimental blocks: a) responding to all trials at chance level (> 80% go stimuli correct and < 20% no-go stimuli correct), or b) withdrawing the response for all trials at chance level (< 20 % go stimuli correct and >80% no-go stimuli correct) in any of the eight experimental blocks.

Trials thus rejected (based on behaviour) were also identified and removed from the EEG analysis. Further trials were identified for removal based on visual inspection of the signal, detecting artefacts not removed by ICA, leading to a rejection of 4.60% of trials (SD = 2.70, range = 0.00 – 18.19%). After initial cleaning, the data was re-epoched for pre-stimulus and task-related analysis. Time-frequency (TF) analysis was performed using a transformation based on multiplication in the frequency domain method as specified in the ft_freqanalysis Fieldtrip function (Oostenveld et al., 2011), and a Hanning taper was applied to the data. The frequency range of interest was defined as 2 to 40Hz with a 1/3Hz frequency step. The number of fixed cycles per wavelength was set to 6. For all permutation testing, spatial neighbours for each electrode were defined as those being approximately 5cm distant (Maris & Oostenveld, 2007). The maximum possible number of permutations (up to 3000) was undertaken for each test. To investigate whether neural patterns differed across conditions of interest, a permutation test was run on all channels over the whole epoch (-1500ms to 1500ms), applying relative baseline correction and transforming the data to decibels.

The same data cleaning procedure as in blocks 1-8 was applied separately to the EEG recording for block 9. This led to the selection of different participant data for the motivational group, leading to 33 (older adults = 13). This slight divergence is explained by a case-by-case basis of inclusion of participants based on the overall neural data quality, which fluctuated between the two parts of the experiment, with a final overlap of 30 participants between both parts. Table 1 provides participant count for the between-group factors age and motivation. The motivational block data was notably noisier, due to a likely higher proportion of agitation and motion artefact introduced by the motivational manipulation.

Between-group factor	Main blocks		Motivational block	
	n	%	*n*	%
Motivated young	7	21	7	23
Motivated older	8	24	5	17
Non-motivated young	11	32	11	37
Non-motivated older	8	24	7	23
Total	34	100	30	100

Table 1 Outline of participant count for between-group factors age and motivation in main and motivational task blocks.

The procedure for analysing the pre-stimulus signal was guided by the recent decomposition of the signal into periodic and aperiodic components (Donoghue, Haller, et al., 2020) which have distinct associations with tasks and participant populations (Donoghue et al., 2022), e.g. ageing (Turner et al., 2023) and pathology, as in developmental dyslexia (Turri et al., 2023). This was undertaken using the ‘mne’ python package (Gramfort et al., 2013). The TF signal was examined through spectral parameterization in trial-averaged TF spectra for each channel and each participant in blocks 1 and 8, using an implementation of the aperiodic analysis through the ‘specparam’ python package (Donoghue, Haller, et al., 2020). The resulting aperiodic 1/f fit was removed from the power spectrum using subtraction. The corrected ‘periodic’ spectrum was permutation-tested using the permutation_cluster_1samp_test and permutation_cluster_test functions as implemented in the ‘mne’ python package (Gramfort et al., 2013), by supplying first and last block difference matrices per each participant. The t-statistic significance threshold was manually determined using the ppf function from the ‘scipy’ package (Virtanen et al., 2020). The adjacency sparse matrix was obtained using the native easycap 64 channel layout derived from the MATLAB ‘fieldtrip’, and extended to include N-1 and N+1 neighbours along the frequency dimension using the combine_adjacency function implemented in the ‘mne’ package.

Results

SART Task Performance

Across the two groups, the young adults had faster reaction times (mean = 429.45ms, SD = 50.37ms, range = 328.88–577.67ms; Fig 3.2A1), but lower accuracy due to elevated commission errors (i.e. a failure to withhold responses; mean = 24.46%, SD = 13.19%, range = 0%-61.11%; Fig 3.2B1), while the older group showed a reversed pattern, with slower reaction times (mean = 567.66ms, SD = 95.18ms, range = 429.99–923.98ms) but fewer commission errors (mean error = 7.72%, SD = 7.48%, range = 0-33.33%), see the same Fig 3.2A1 and Fig 3.2B1. Omission errors (missed targets) showed floor effects both in young (0.21%, SD = 1.15%, range = 0-12.5%) and older adults (mean error = 0.80%, SD = 2.03%, 0–13.89%), so they were not analysed any further.

To track possible vigilance decrements over time, we tested the effect of time-on-task (experimental blocks 1-8) and age group (young vs old) on commission errors using a random mixed effects model. The effect of time-on-task was not significant [t(32) = 0.43, p = 0.16] but lower error rates were confirmed in older participants as opposed to the young group [t(32) = 15.77, p < 0.001] with no interaction [t(32) = 0.36, p = 0.72]. An identical model was used to analyse reaction times. The effect of time-on-task was significant, indicating a slight reduction in reaction times across time [t(32)= 0.01, p = 0.049], likely due to learning effects, alongside a main effect of age group, showing faster reaction times in young participants as opposed to the older group [t(32) = 0.23, p < 0.001], with no interaction [t(32) < 0.01, p = 0.78].

We then tested the effects of the motivational manipulation using a three-way ANOVA with the factors block (block 8 vs 9), age group (young, old) and motivational group (non-motivated, motivated) separately for reaction times and commission errors. The motivational manipulation consisted of instructing half of the participants after completion of block 8 that they can earn more money if they outperform their fellow participants in the last block (block 9), while the other half were simply told that there is one final block to be completed (resulting in motivated vs non-motivated subgroups).

The analysis of the reaction times showed that there was no effect of experimental block [$F(1, 26) = 0.37$, $p = 0.55$, $\eta^2 < 0.001$] and no effect of motivation group [$F(1, 26) = 0.18$, $p = 0.68$, $\eta^2 < 0.001$], but the interaction between block and motivation was significant with a small to medium effect size [$F(2, 26) = 7.74$, $p = 0.01$, $\eta^2 = 0.02$]. Confirming the analysis above, the older group had slower reaction times than the young group [$F(1, 26) = 16.17$, $p < 0.001$, $\eta^2 = 0.42$]. Post-hoc analyses were conducted using paired sample t-tests to further explore the interaction of block and motivation. These revealed that in the non-motivated group, reaction time increased between blocks 8 and 9 [$t(17) = -2.47$, $p = 0.02$], while remaining stable in the motivated group [$t(11) = 1.65$, $p = 0.13$], hence suggesting that the motivational manipulation, albeit weakly, affected reaction times (See Fig 3.2A2). No other interaction was significant.

The analyses of the commission errors showed that there was no effect of block [$F(1, 26) = 1.54$, $p = 0.23$, $\eta^2 = 0.05$] and no effect of motivation [$F(1, 26) = 1.53$, $p = 0.23$, $\eta^2 = 0.04$]. The results also showed that the older adults were more accurate than the younger group [$F(1, 26) = 10.30$, $p = 0.004$, $\eta^2 = 0.24$]. Unlike for the reaction times results, there was no interaction between block and motivation, hence suggesting that there was no effect of the motivational manipulation on commission errors. There was a significant interaction between age group and motivation [$F(2, 26) = 4.77$, $p = 0.02$, $\eta^2 = 0.17$] but this interaction was not further explored due to the absence of an interaction with block. This 2-way interaction picks up on a difference between motivated vs non-motivated young participants independent of block that is not seen in the older participants and is almost certainly reflecting a chance effect. (As participants were only allocated to the motivation group randomly after the end of block 8, any differences prior to the allocation into the groups would be random variations. See Fig 3.2B1 for an illustration of this interaction that is seen throughout all blocks (and is not specific to block 9). No other interaction was significant.

Finally, because the two age groups showed opposite patterns in their behavioural response strategies, an exploratory analysis of speed-accuracy trade-off was undertaken, this is documented in Appendix 1.

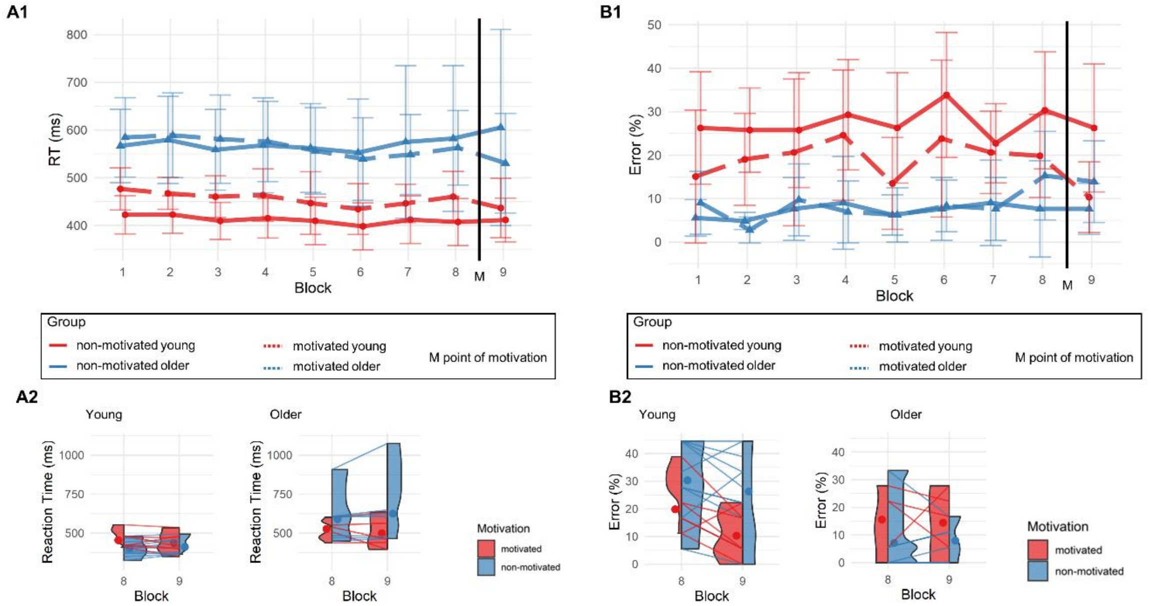

Fig 3.2 Behavioural Performance. (A1) Mean reaction time and (B1) commission errors in both experimental groups (older in blue, young in red) across time-on-task (experimental blocks 1-8) and a final experimental block (block 9) with/without motivational manipulation (motivated, non-motivated subgroup). (A2) Difference in reaction times and (B2) commission errors induced by the motivational manipulation in both age groups (young, older) as inferred from comparisons between blocks (8, 9) in both the non-motivated group (blue) and motivated group (red).

Subjective levels of fatigue and mind wandering

Subjective fatigue levels were assessed before and after task performance (pre block 1 and post block 8). From the beginning, the older group (mean = 427.56, SD = 201.22, range = 104-755) had lower baseline fatigue scores than the young group (mean = 588.89, SD = 257.61, range = 118–1054) [t(32) = 2.05, p = 0.049, see Fig 3.3A]. Likewise, from the beginning, older adults had lower mind wandering scores (mean = 3.70, SD = 1.61, range = 1.25–6.50) than the younger group (mean = 4.07, SD = 1.71, range = 1-6) [t(32) = 2.69, p = 0.01, see Fig 3.3B].

Comparing pre-task with post-task subjective scores (see Figs 3.3A and 3.3B), we found that both the young (mean change = 217.06, SD = 182.29, range = -25-646) and older group (mean change = 169.31, SD = 149.58, range = 3-485) showed a rise in their subjective fatigue levels with time-on-task. Likewise, both the young (mean change = 0.53, SD = 1.00, range = -0.75–2.50) and the older group (mean change = 1.11, SD = 1.28, range = -0.50–4.25) had an increase in mind-wandering scores.

In a 2x2 mixed ANOVA testing the effect of time (before, after), age group (young, older) and their interaction on the subjective fatigue scores, we found a large effect of time [F(1, 32) = 45.75, p < 0.001], showing that subjective fatigue scores had increased by the end of the main experiment. There was also a small difference between the groups, indicating that the young adults had slightly higher fatigue scores than the older group [F(1, 32) = 5.03, p = 0.03]. However, there was no interaction between age group and time [F(2, 32) = 0.69, p = 0.41].

Similarly, in a 2x2 mixed ANOVA testing the effect of time (before, after), age group (young, older) and their interaction on mind wandering, there was a large effect of time, explained by higher mind wandering scores by the end of the experiment [F(1, 32) = 16.80, p < 0.001]. There was again a main effect of age group, with the young adults having higher mind wandering scores than the older group [F(1, 32) = 5.61, p = 0.03]. However, there was no interaction between group and time [F(2, 32) = 2.20, p = 0.15]. To test for a link between mind wandering change and subjective state fatigue change, a linear regression was fitted to the paired observations for each participant, but the model was not significant [F(1, 32) = 2.42, R2 = 0.04, beta < 0.01, p = 0.13].

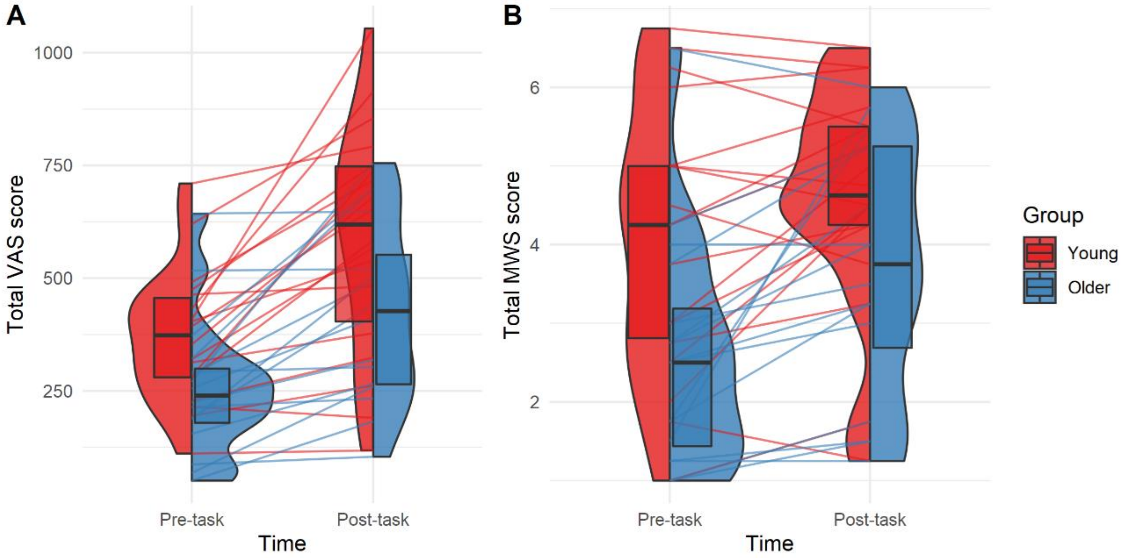

Fig 3.3 Subjective measures over time. (A) Scores of the visual analogue scale for state fatigue and (B) mind wandering before and after the experiment (Pre-task, Post-task) for each group

(young in red and older in blue), with individual participant total scores, as well as overlaid boxplots with overall medians and quartile ranges.

Electroencephalography (EEG) results

The EEG analyses aimed at identifying the brain oscillation markers of the above performance differences and the reported subjective changes, across our experimental factors. Due to the absence of the vigilance decline, we first sought to identify the EEG-changes with time-on-task as a possible marker of increased fatigue/mind wandering, or alternatively, of enhanced effort to maintain stable task performance despite the reported subjective increase in fatigue. In a second step, we examined a relation with age group and the motivational manipulation. Finally, we tested for correlations with behavioural measures. This was to disentangle EEG-markers (i) of fatigue/mind wandering *per se*, which should show changes both across age-group (enhanced fatigue in the younger as compared to the older group) and time-on-task (increasing fatigue across blocks in each group), (ii) to disentangle EEG markers of the difference in response strategy in the older vs the younger participants (deployment of effort more towards motor control/accuracy versus response speed), and (iii) of the effects of the motivation manipulation. Our results revealed an EEG signal change in (i) pre-stimulus alpha-oscillations over centro-parietal locations potentially reflective of disengagement of effort, (ii) qualitative differences in response strategy/ effort deployment in post-stimulus, task-related beta synchronisation/rebound over fronto-central sites, and (iii) of motivational manipulation in a distinct, fronto-parietal beta-signature, as outlined below.

Pre-stimulus EEG oscillations: alpha-signals increase with time-on-task, differ by age-group and are amenable to motivational manipulation

We first investigated potential oscillatory markers of time-on-task. To identify the effects of time-on-task on oscillatory activity, we first compared activity in the pre-stimulus window (-1100 to 0ms) across a broad spectrum of frequencies (3-40Hz, including the alpha- and beta-band) between experimental blocks 1 and 8, whereby we decomposed the full pre-stimulus spectrum per experimental blocks and group (Fig 3.4A) into its separate periodic (Fig 3.4B) and aperiodic components (Fig 3.4C; Donoghue, Haller, et al., 2020), and ran comparisons using cluster-based permutation statistics (Maris & Oostenveld, 2007). We then examined whether the markers of time-on-task (Fig 3.4D) co-vary with other possible contributors to task performance/vigilance, namely age-group and motivation (Figs 3.4E-F).

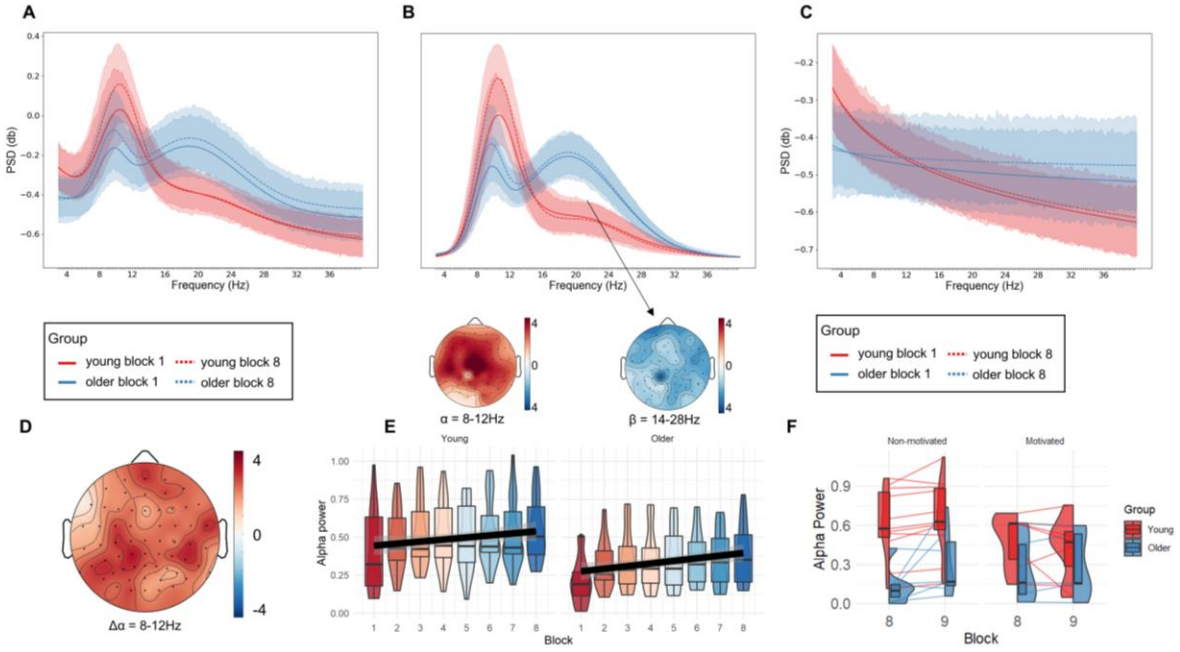

Fig 3.4 Time-on-task related pre-stimulus activity. Spectrograms for (A) total measured power, (B) the periodic signal after adjustment from the aperiodic component and (C) the aperiodic component, represented across Time-on-task (block 1 vs 8: solid line vs dashed line) and the young (in red) and older group (in blue). Transparent areas represent 95% confidence intervals. Note in (B) that the largest periodic spectral differences are observed between age groups in the alpha-band (left topography: alpha older < younger) and the beta-band (right topography: beta older > younger group). (D-E) Time-on-task of periodic alpha (8-14Hz) activity: The panels illustrate the alpha-increase with time-on-task in terms of (D) its topography (from block 1 to block 8) collapsed across age groups, and (E) its evolution across experimental blocks 1-8 for each of the age-groups separately (young vs old: left vs right). The plot illustrates the variability of the signal in individual participants, as well as the median values and quartile ranges with an overall positive linear trend fitted separately for each group. (F) Motivational manipulation and alpha-band activity: Plots denote periodic alpha-band changes from blocks 8 to 9 (with motivational manipulation), per each of the groups (younger: red vs. older: blue/ motivated: solid vs. non-motivated: dashed lines). The motivational manipulation influenced alpha-band activity by preventing further alpha-increases from block 8 to 9 in the motivated but not the non-motivated group, independently of age-group. Participant-level changes are depicted alongside median values and quartile ranges.

Examining the effect of time-on-task through cluster-based statistics of the periodic, pre-stimulus activity in experimental blocks 1 versus 8, revealed one positive cluster (cluster statistic = 3391, p = 0.007). This indicates a rise in power across time-on-task in the alpha frequency band (8-14Hz) over the majority of channels with a maximum in centro-parietal locations (see Fig 3.4D).

To characterise the alpha-increase with time-on-task over all experimental blocks 1 to 8 and to further test for possible co-variations with age-group differences and motivational effects, we first determined the electrode with the highest cluster t-statistic (CP1) based on results from blocks 1-8. Then we extracted the periodic alpha signal (8-14Hz band) in that electrode for the pre-stimulus epoch from across all blocks 1-9.

Fig 3.4E illustrates the periodic alpha-changes over time-on-task (blocks 1-8) per age-group. Analysis of the factors time-on-task (block 1-8) and age-group (young, old) using a random mixed effects model (with randomised participant- and block-level effects) revealed a significant increase in the alpha-signal across blocks [t(32) = 3.06, ß = 0.10, p = 0.004] with the signal being elevated in the young group as compared to the older group [t(32) = -2.29, ß = -0.14, p = 0.03], but with no interaction [t(32) = -0.22, ß > -0.01, p = 0.83]. Note that directly examining the effects of age-group on the pre-stimulus, periodic component using cluster-based statistics (older vs younger participants) confirmed the age-effect in the alpha-band (alpha old < young), revealing one large negative, alpha-band cluster (highest cluster statistic = 9546, P = 0.001; see Fig 3.4B for cluster map), alongside a large positive cluster (cluster statistic = 8464, P = 0.001) in the adjacent beta band (14-30Hz). The latter showed elevated beta-activity in the old relative to the young group (see Fig 3.4B, spectrograms and cluster map).

Fig 3.4F illustrates the pre-stimulus alpha-signal that is sensitive to time-on-task (extracted from CP1) with regard to the co-variation with motivational manipulation, namely across block 8 and 9, separately for the motivated and non-motivated groups. Conducting a 2x2x2 ANOVA with the factors motivation group (motivated, non-motivated), age group (young, older) and block (block 8, motivational block 9) revealed no main effects of motivation on this alpha-signal [F(1, 26) = 1.00, p = 0.33, η^2 = 0.03], but an interaction between motivation x block (F(1, 26) = 5.00, p = 0.03, η^2 = 0.02). In addition, the young group had a consistently higher alpha-signal than the older group confirming the analysis above

[F(1, 26) = 12.94, $p = 0.001$, $\eta^2 = 0.31$], with no difference between blocks [F(1, 26) = 3.42, $p = 0.08$, $\eta^2 = 0.01$]. No other interaction was significant. Post-hoc analyses were conducted using paired t-tests to further explore the interaction of motivation group and block. These showed that the alpha power of the non-motivated group continued to increase between block 8 to 9 [t(17) = 2.48, $p = 0.02$], while the motivated group showed no further change in this signal [t(11) = 0.62, $p = 0.55$].

Analysis of the aperiodic component (exponent and intercept) using 2x2 ANOVAs with the factors time-on-task (block 1 vs 8) and age-groups (young, older) revealed significant group-effects for both the exponent (steeper exponents in the young group [F(1, 32) = 13.99, $p < 0.001$, $\eta^2 = 0.27$]) and the intercept (higher intercepts in the young group [F(1, 32) = 8.57, $p = 0.006$, $\eta^2 = 0.20$]) but no effects of time-on-task (exponent: [F(1, 32) = 0.46, $p = 0.50$, $\eta^2 = 0.003$], intercept: [F(1, 32) = 0.28, $p = 0.60$, $\eta^2 < 0.001$]) nor any interaction (exponent: [F(2, 32) = 0.68, $p = 0.42$, $\eta^2 = 0.004$], intercept: [F(2, 32) = 0.50, $p = 0.49$, $\eta^2 = 0.001$]).

In summary, these results reveal that periodic, pre-stimulus alpha-band activity shows a similar pattern for fatigue/mind wandering levels across experimental factors: centro-parietal alpha-power increases over time-on-task that are elevated in the younger as compared to the older participants, while at the same time being sensitive to the motivational manipulation. Thus, the pattern likely reflects attentional disengagement, reversible by re-motivation.

Post-stimulus (task-related) oscillatory activity: two beta-signals that relate distinctively to response strategy and motivational manipulation

As per the analysis of the pre-stimulus activity, we analysed post-stimulus oscillations in terms of effects of time-on-task first. We did this by identifying changes between experimental blocks 1 vs 8, running cluster-based statistics on the baseline-corrected TF transformed data. We then examined their co-variation with age and the motivational manipulation. In a second step, due to the absence of motivational effects in the above analysis, we then tested directly for the effects of the motivational manipulation in the post-stimulus window (using cluster-based statistics comparing block 8 versus the motivational block 9 as a function of motivation group).

Post-stimulus beta-activity changes with time-on-task reflect qualitative differences in response strategy

Cluster-based permutation statistics between blocks 1 and 8 on post-stimulus TF-data identified a positive cluster in the lower beta frequency range (cluster statistic = 4899, $p < 0.001$) occurring in a late post-stimulus window (500-1000ms; Fig 3.5A). The cluster is explained by a fronto-central beta-increase over time-on-task (detailed in Fig 3.5B).

To examine beta-changes across all experimental blocks 1-8, we extracted this beta-signal (14-24Hz: late time window significant in the cluster) from the electrode with the most prominent cluster t-statistic (C3) per block and age-group, over time and frequency bands as indicated in Fig 3.5D. A random mixed effects model with beta-power as the to-be-predicted variable confirmed its increase across time-on-task [$t(32) = 2.98$, $ß = 0.16$, $p = 0.01$] and revealed a higher value in the young participant group [$t(32) = -3.93$, $ß = -3.06$, $p < 0.001$], but no interaction [$t(32) = 0.15$, $ß = 0.01$, $p = 0.88$]. This indicates an overall linear increase of task-related beta-power across time-on-task that is independent of age group, while showing overall group differences. An inspection of the event-related beta-change (Fig 3.5B, line plot) provides evidence for a relationship to behavioural response patterns and hence response strategy across age-groups instead.

Inspection of Fig 3.5B (line plots) reveals a prominent beta desynchronisation around response onset (mean reaction times were 400-500ms), followed by a beta-rebound. The desynchronisation was much stronger in amplitude in the older than younger participants, whereas the beta-rebound showed an earlier latency in the younger compared to the older group, reflecting the differences in their reaction times (see above). Given this dynamic pattern and the fronto-central topography, we interpret this beta-signal to reflect differences in motor response strategies between the groups. To further inform this interpretation, we explored to what extent this signal could be driven by the motor response. We therefore re-analyzed the beta-signal but taking into account correct omission trials only (hence eliminating any contamination by motor execution). Given the low number of omission trials, we averaged the data across all blocks 1-8 (it was not possible to resolve blocks 1 and 8 separately). This analysis revealed the same pattern (comparing Figs 3.5C vs 3.5B), including in terms of age-group differences ($t(25) = -2.20$, $p = 0.04$), which therefore suggests that this beta-signal is more of a cognitive or motor control nature than linked to motor execution. Based on these findings, we interpret the stronger beta-desynchronization in the older as compared to the younger group to reflect deployment of more effort towards accurate motor control, while we interpret the shorter latency in beta-rebound in the young, as compared to the older group, to reflect the speeded response strategy.

To test whether the time-on-task related beta-signal also co-varied with the motivational manipulation, this signal was extracted in the electrode with the highest t-statistic (C3) also for the motivational block 9 and separately for the motivated and non-motivated groups, for comparison with block 8 (see Fig 3.5E). Using a 2x2x2 ANOVA comparing motivation group (motivated, non-motivated), age-group (younger, older), and block (block 8 vs motivational block 9), we observed an effect of motivation group [$F(1, 26) = 4.96$, $p = 0.04$, $\eta^2 = 0.14$] showing that the group randomly allocated into the motivational condition had an overall higher beta-signal (Fig 3.5E). There was no main effect of block [$F(1, 26) = 0.02$, $p = 0.89$, $\eta^2 < 0.001$] or age group [$F(1, 26) = 3.11$, $p = 0.09$, $\eta^2 = 0.09$], nor were there any significant interactions. This therefore indicates that in contrast to the pre-stimulus alpha-signal, this post-stimulus beta-signal is not amenable to manipulation by motivation.

Overall, these analyses suggest that the qualitative differences in response strategy (accurate vs fast) across the age-groups are reflected in a beta-signal of fronto-central topography, which in its rebound-component is modulated with time-on-task as well as reaction times (see analyses below).

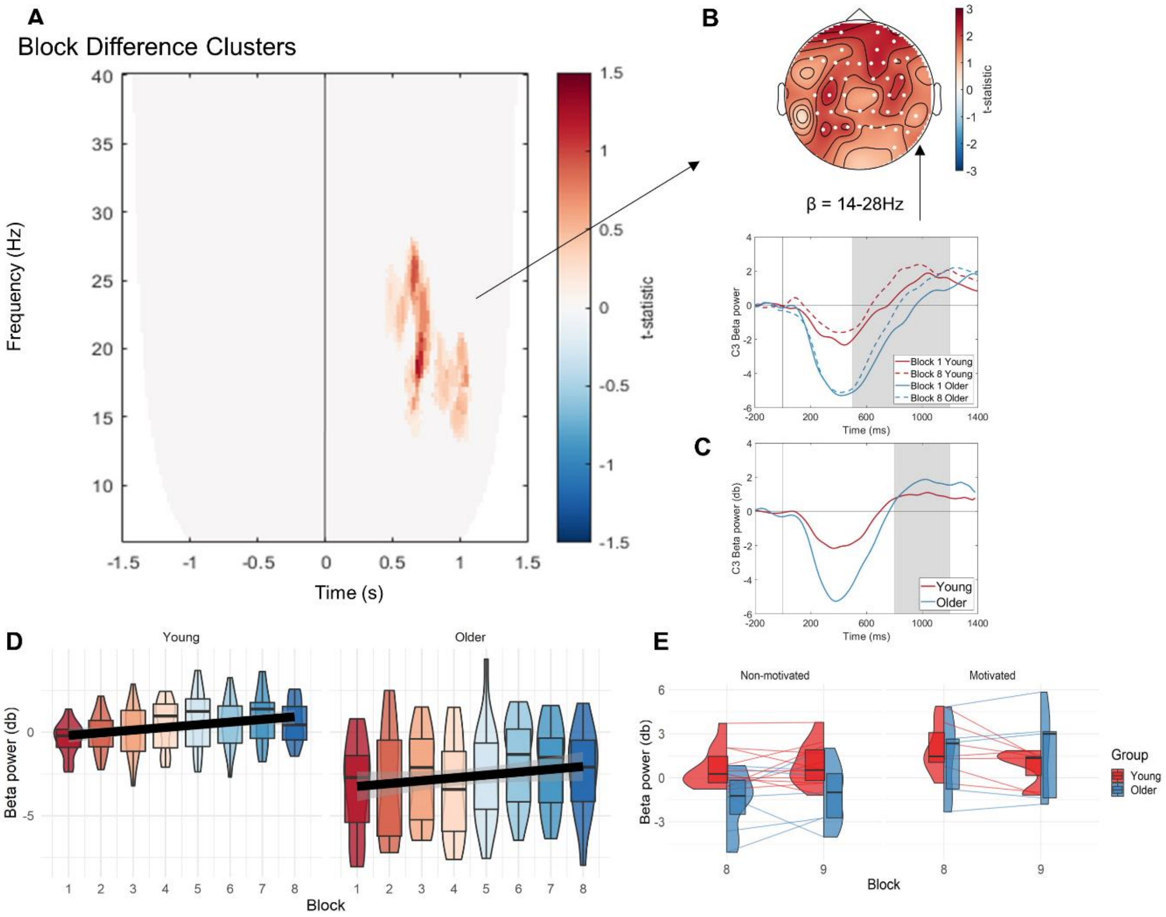

Fig 3.5 Time-on-task related oscillatory changes in the post-stimulus period. (A) Results of the cluster-based permutation test showing a time-on-task-related increase in the beta-band (14-24Hz) from block 1 to 8 in the later post-stimulus window (0.5-1s). (B) Topography of the time-on-task beta-change, indicating a fronto-central maxima. The line graph represents beta-changes across time-on-task and age-group, illustrating that the positive cluster denotes an increase in beta-activity over time (compare solid vs dashed lines). (C) PSD comparison of young and older participants in the same frequency band across correct omission trial window with inferential time period area indicated. (D) Effect of time-on-task across all experimental blocks 1-8 per age-group (young, older), showing an overall positive trend independently of group, but higher beta-power in the younger participants. (E) No effects of motivational manipulation on the beta-signal, with no differential increase from block 8 to 9 between motivated and non-motivated participants, across the young (red) or older (blue) age group. Participant-level changes are depicted alongside median values and quartile ranges.

Motivation effects on beta-activity

Because we did not observe the time-on-task related beta-pattern to be altered by motivational manipulation (as per above), we tested for effects of motivation in post-stimulus (task-related) activity directly through cluster-based permutation tests. We compared TF-differences between blocks 8 and 9 across the two motivational groups (motivated vs. non-motivated) collapsing across both age-groups (interaction of motivation x block in TF-space). The analysis revealed a broad, late beta-cluster (Fig 3.6A), showing a weaker left fronto-parietal beta-increase from block 8 to 9 in the motivated relative to the non-motivated group (statistic = 351.87, p = 0.002; see Fig 3.6B for topography and time course).

To examine whether this signal also modulates with time-on-task and/or age-group, we retrospectively extracted the motivational beta-signal (14-28Hz: in the relevant window) across all experimental blocks 1-8 and both age-groups from the electrode with the most prominent cluster t-statistic (AF3) in the test of motivation effects (Fig 3.6C). A linear model predicting this beta-power from across blocks and age groups showed no effect of either age [t(28) = -0.65, ß = -0.31, p = 0.52] or block [t(28) = 1.31, ß = 0.06, p = 0.20], nor their interaction [t(28) = 0.23, ß = 0.02, p = 0.82], indicating that this motivational beta-signal was unaffected by time-on task and age-group and hence distinct from the time-on-task beta-effect related to response strategy.

Finally, to test the beta-effects of motivation across all groups/conditions (Fig 3.6D), we run a 2x2x2 ANOVA with the factors motivation group (motivated, non-motivated), age-group (younger, older) and block (block 8, motivational block 9). The model revealed that the motivated group had higher beta-signals than the non-motivated group [F(1, 26) = 4.46, p = 0.045, η^2 = 0.12] and that there was a main effect of block [F(1, 26) = 21.36, $p < 0.001$, η^2 = 0.14] with a lower signal in block 9, but no effect of age [F(1, 26) = 1.71, p = 0.20, η^2 = 0.05]. The interaction between motivation and block was significant [F(2, 26) = 8.55, p = 0.007, η^2 = 0.06] independently of age-group (non-significant 3-way interaction motivation group x age group x block: F(3, 26) = 2.51, p = 0.13]). Post-hoc analysis exploring the interaction of motivation x block using dependent sample t-tests revealed that while the signal of the non-motivated group did not differ between the two blocks [t(17) = 1.94, p = 0.07], the motivated participants' beta synchronisation decreased [t(11) = 4.45, $p < 0.001$]. There was also a significant interaction between age and motivation [F(2, 26) = 5.28, p = 0.03, η^2 = 0.14] but this interaction was not further explored, as it almost certainly reflects a chance finding (despite random allocation in age and motivation groups). No other interaction was significant.

During the examination of the task-related signal, another cluster (statistic = 4577, P < 0.001) occurred in the early time window (0ms–450ms), indicating a decrease in the post-stimulus alpha oscillatory band with time-on-task. Its further investigation in connection with the fatigue-related P300 event related potential (ERP) component is described in Appendix 1.

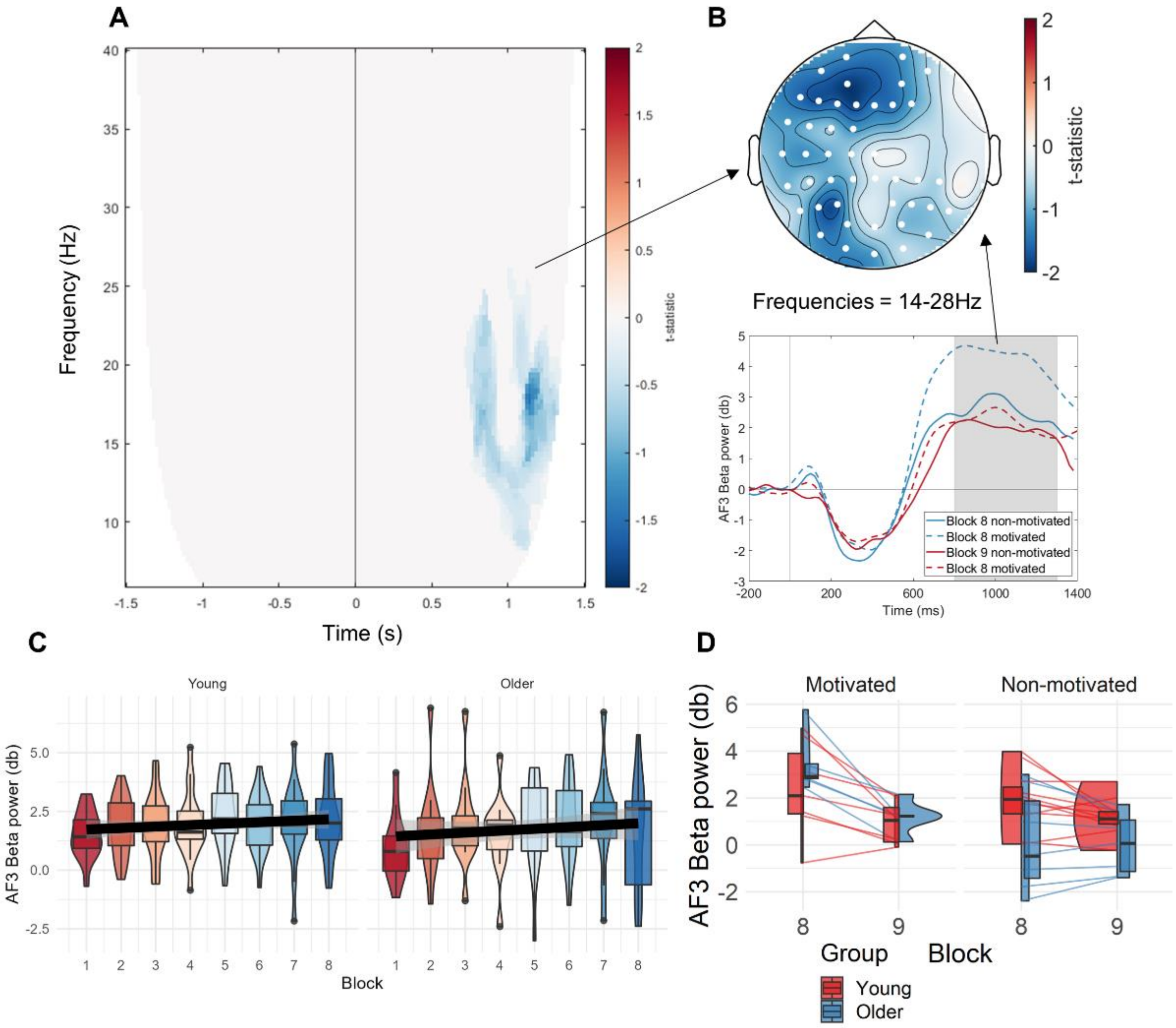

Fig 3.6 Motivation-related beta changes. (A) Results of the cluster-based permutation statistics testing the interaction motivation x block in TF-space (contrast of the difference signal of block (8 vs 9) between motivational groups). The results show a late (0.7 -1.2s) effect of motivational manipulation on beta activity (14 – 28Hz). (B) Topography and temporal dynamics of the motivation-related beta-change in the post-stimulus window indicating a left fronto-parietal decrease in beta-activity between block 8 to 9 in the highly motivated (dashed lines) but not the

non-motivated participants (solid lines). (C) Evolution of the motivational beta-signal over time-on-task (blocks 1-8) per age group (young, older). The plot shows that this beta-signal is stable over time-on-task. (D) Effects of the motivational manipulation on the beta-signal across all groups and relevant blocks, illustrating a larger beta-decrease from block 8 to 9 in the motivated relative to the non-motivated participants independent of age-group.

In summary, analyses of the post-stimulus oscillatory activity revealed two distinguishable beta-signatures: one that had a fronto-central topography and in its rebound-component was modulated with time-on-task, as a likely marker of response strategy, and another of fronto-parietal distribution modulated by motivation.

Relationship between EEG signals and behaviour

To detect links between behaviour, namely measures of subjective state fatigue, mind wandering and reaction time, and the neural markers of time-on-task, age effects and motivational manipulations (see frequency bands/electrodes identified in the above EEG analyses), we built multiple linear regression models predicting subjective and RT measures by neural signals with addition of the effect of age and their interaction. Single electrodes with the highest t-statistic resulting from permutation tests were extracted and changes in signal were compared to changes in subjective measures.

The model testing state fatigue (VAS) changes was not significant for its relationship to pre-stimulus alpha-changes (electrode CP1) [F(3,30) = 2.25, p = 0.10], or task-related beta-changes (electrode C3) as extracted in blocks 1 and 8 [F(3,30) = 0.78, p = 0.52]. Likewise, no effect was found for the relationship between mind wandering to pre-stimulus periodic alpha change [F(3, 30) = 1.73, p = 0.18], or task-related beta [F(3, 30) = 2.43, p = 0.09].

The model testing reaction time change was not significant for its relationship to pre-stimulus alpha-change (electrode CP1) [F (3,30) = 1.54, p = 0.22], but the model was significant for task-related beta-change (electrode C3) [F(3,30) = 8.84, p < 0.001]. There was no main effect of beta-signal (ß = 0.004, t = 0.22, p = 0.82), but a significant interaction between beta signal change and age (ß = -0.06, t = -3.09, p = 0.004). An inspection of Fig 3.7 reveals that the relationship between beta change and reaction time change was driven by the older adult group. Older adults who showed a greater decrease in reaction times, showed a greater increase in beta power. No effect was found for the relationship of error change to pre-stimulus periodic signal change [F(3, 30) = 0.19, p = 0.90], or task-related beta [F(3, 30) = 0.19, p = 0.91]. The relationship between behavioural change and motivational beta-signal difference between blocks 1 and 8 was not tested as the previous model showed no modulation of the signal with either age or time-on-task.

In summary, the post-stimulus beta-rebound was modulated with reaction times for older adults, giving further indication of post-stimulus beta as a likely marker of response strategy.

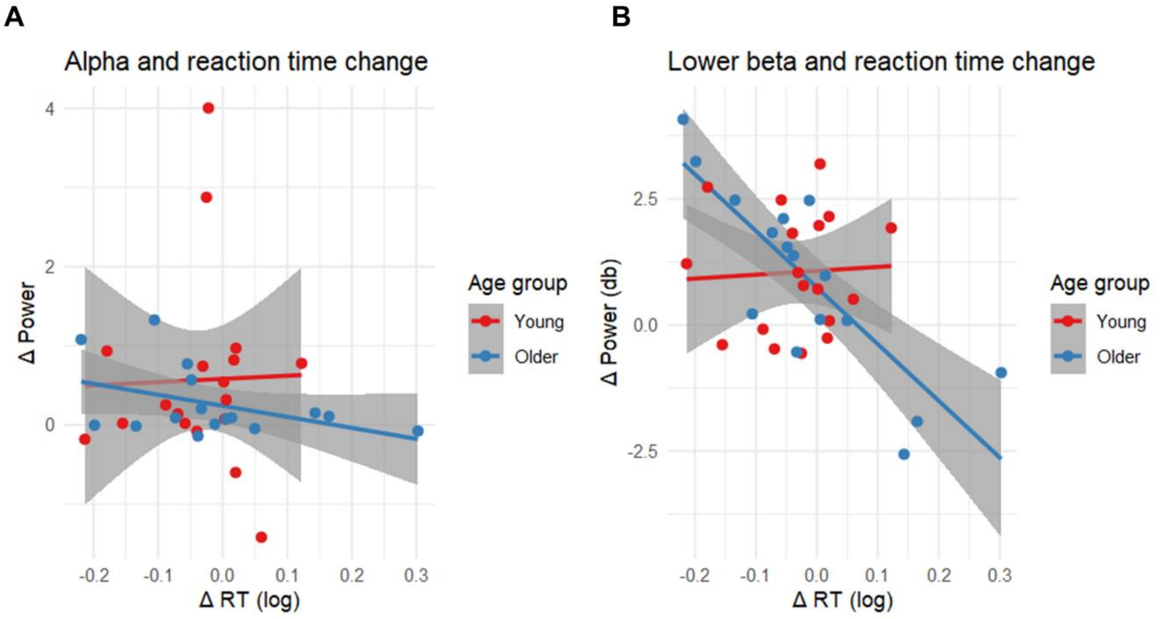

Fig 3.7 Brain and behaviour link. Relationship between the change in reaction times and (A) the change in alpha power over CP1, (B) change in lower beta power over C3 across the main experiment over time-on-task for both age groups.

Discussion

This study sought to identify neural patterns underlying vigilance, motivation and fatigue during sustained attention. Our results provide new evidence for two distinct oscillatory patterns associated with response strategy (post-stimulus fronto-central beta) and motivation (post-stimulus fronto-parietal beta). Contrary to our expectations, while the reported pre-stimulus alpha power rise mirrored the subjective rise in fatigue and mind wandering, we failed to find a significant correlation between these measures.

Pre-stimulus Alpha Oscillations

The task elicited a distinct linear increase in pre-stimulus alpha synchronisation over time. This time-on-task rise in alpha power reflects other research documenting time-related changes in EEG signal arising from experimental manipulations (Jacquet et al., 2021; G. Li et al., 2020; Tian et al., 2018) and adds to the existing body of literature highlighting detectable changes in alpha oscillations in relation to demanding tasks (Benwell et al., 2019; Huycke et al., 2021; Pershin et al., 2023). Unfortunately, our findings do not directly link these centro-parietal alpha-power increases to the observed general rise in subjective fatigue and mind-wandering. On the other hand, not only was there a significant rise in alpha power over time (blocks 1 to 8), but we also identified a greater elevation of the signal in the younger compared to the older participants. The signal then mirrored the reported fatigue/mind wandering scores which were not only elevated over time, but also higher in the younger compared to the older participants. Finally, the trajectory of rise in alpha power was impacted by participant motivation: while alpha power kept rising for the unmotivated participants during the final block (in line with the reaction times that also increased from block 8 to 9 in this group, indicative of fatigue), it levelled out for the motivated group (who were promised a monetary incentive if they outperformed others).

In light of the reported absence of a behavioural vigilance decrement, we propose that this pre-stimulus centro-parietal alpha increase during time-on-task that levels out with participant motivation comes short of a full link to subjective fatigue and may instead reflect a waning of attention (Babu et al., 2018; Klimesch, 2012; Macdonald et al., 2011), preceding a vigilance decrement.

Post-stimulus, time-on-task modulated beta-oscillation relate to response strategy

We also observed a time-on-task rise in post-stimulus fronto-central beta synchronisation which, in contrast to the rise in alpha power, was unaffected by motivational interference. This pattern followed the structure of a classic post-motor beta desynchronisation and rebound, i.e. the neural response related to preparation and/or execution of a motor response (Heinrichs-Graham et al., 2017; Parkes et al., 2006). In the present study, the beta desynchronisation was much stronger in the older compared to the younger group, whereas the beta-rebound latency was earlier in the younger group. Given this dynamic pattern, and the fronto-central topography, we interpret this beta-signal to reflect age differences in motor response strategy. More specifically, we think that these age (strategy) differences are of a cognitive or motor control (rather than motor execution) nature because we also found the same pattern for omission trials (which lacked a motor execution aspect). Our thinking is further underpinned by the significant relationship we found between beta signal change and age: older adults who showed a greater decrease in reaction time over time-on task, also showed a greater increase in beta power. This pattern was absent in the younger group. Overall, these analyses suggest that, across age groups, there are qualitive differences in response strategy (accurate vs fast), that are reflected in a beta signal of fronto-central topography: we interpret the stronger beta desynchronisation in the older, as compared to the younger group, to reflect a deployment of greater effort towards accurate motor control, with the shorter latency in the beta-rebound in the younger group, to reflect the speeded response strategy. These results further emphasise contrasts in age-specific response strategies reported previously (Dang et al., 2018; Lara et al., 2014; Statsenko et al., 2020; Vallesi et al., 2021), but more importantly, we now demonstrate that these qualitative strategic differences are underpinned by distinct beta oscillations (see Xifra-Porxas et al. (2019) for similar findings on grip strength).

Post-stimulus 'motivational' beta oscillation

In addition to the fronto-central beta-signature, we found another beta oscillation of fronto-parietal distribution that was independent of age-group but instead modulated by motivation. This signal was stable over time-on task, yet we found it to show a larger beta-decrease from block 8 to 9 in the motivated, relative to the non-motivated, participants. This decrease in beta power was coupled with a reaction time that levelled out in the motivated group (from block 8 to 9), while reaction times in the non-motivated group increased. Our findings thus show that the motivation manipulation was effective, similar to the results of Reteig et al. (2019) who showed a temporary increase in sustained attention task performance after an unexpected motivational manipulation. Most importantly, we show this motivational effect to be co-modulated with a beta decrease, whereas Reteig and colleagues failed to find any EEG markers linked to their motivation manipulation. Beta-oscillatory changes have previously been linked to motivational interventions (Wilhelm et al., 2022) and reactive to changes of internal state (Nickel et al., 2020), although there have been no previous reports on attentional motivation manipulations in human participants.

Our data thus best reflect the findings and interpretations of Stoll et al., (2016) who examined modulations of frontal beta in monkeys around spontaneous pauses in work. They found that after pauses, the beta power modulation would reset, and the cognitive control effect (task performance) was maintained. We report this signal resetting and maintenance of performance not for pauses in work, but instead for our motivation manipulation. In fact, in line with our data, Stoll and colleagues (2016) propose that frontal beta oscillations reflect multiple factors contributing to the regulation of cognitive control and that motivation parameters can act as modulators of cognitive control.

Limitations and future work

Our study reproduced many typical age related findings, including higher baseline mind wandering and lower reaction times (Diede et al., 2022; Fountain-Zaragoza et al., 2018; Learmonth et al., 2017), as well as strategy differences (Vallesi et al., 2021) prioritising speed over accuracy (Lara et al., 2014) in the younger over the older age group. We also found typical characteristics of ageing in the pre-stimulus oscillatory window regarding the structure of the aperiodic components of the signal in particular, with steeper exponents and higher intercepts for the younger compared to the older age groups (Cesnaite et al., 2023; Turner et al., 2023).

What was surprising was the absence of a decisive vigilance decrement, contrary to our hypothesis and in contrast to other work (Gartenberg et al., 2018; Kaufman et al., 2016; Pershin et al., 2023; Reteig et al., 2019; Walker & Trick, 2018). The speeding up of reaction times when taking participant-level randomised intercepts into account, replicates our own earlier behavioural findings (Hanzal et al., 2024b) with a small effect of task time on speed (blocks 1 to 8). Since the participant accuracy did not show a corresponding decline, this result cannot be interpreted as a vigilance decrement. Having consulted previous work (Reteig et al., 2019; Staub et al., 2014) where a decrement occurred at 20-35 minutes that continued being present in the following hour, we too expected a decline in our study, where the actual task took 45 minutes, and think that a longer experimental duration would have led to an eventual lapse of this maintained performance (Martínez-Pérez et al., 2023).

Unexpectedly, although the reported alpha rise over time was mirrored by a rise in subjective fatigue and mind-wandering (and these rises also closely reflected age (elevated tiredness in the younger) and motivation (reaction time rises in the non-motivated group (blocks 8 to 9) findings), we did not find a correlation between these reported alpha rises and the reported increases in fatigue and mind-wandering. It is possible that the subjective fatigue and mind wandering scales we used lacked sensitivity specific to the task and further work is needed here to elicit more robust participant responses, possibly a use of more frequent subjective probes (Weinstein, 2018).

Nonetheless, our findings are a first pointer of neural changes being more sensitive than performance decline, but further studies are needed to further firm up what centro-parietal alpha-power increases reflect. Alternative methods of delivering the motivational manipulation and subjective tracking of motivational mood states could also be sought to better decouple them from fatigue-related effects.

Conclusion

We report that undergoing 45 minutes of SART induced subjectively elevated fatigue and mind-wandering scores alongside a pre-stimulus centro-parietal alpha power rise. Post-stimulus activity revealed two distinguishable beta signatures: a fronto-central topography as a marker of behavioural strategy and a fronto-parietal distribution modulated by motivation. We suggest that these two signals reflect a motivational cognitive control mechanism behind resetting a performance decrement. Unfortunately, although the rises in pre-stimulus alpha oscillation mirrored the subjective fatigue and mind-wandering rises that occurred over time, these measures were not correlated, so this signal warrants further investigation.

Chapter 4: Age differences in motivation drive performance during the sustained attention to response task

Abstract

Young and older adults prioritise speed and accuracy differently during sustained attention tasks. While older adults generally show a preference of accuracy over speed, this is not always the case. The underlying factor behind this inconsistency may be motivational differences, with older participants compensating for a speed disadvantage with increased intrinsic motivation to perform well. We investigated this in a pre-registered study, using the Sustained Attention to Response Task (SART) in young (n = 25, mean age = 19) and older adults (n = 25, mean age = 69.5). We matched participant accuracy by titrating response window length. Both groups achieved similar performance and strategy during the titration, enabling a comparison without confounds resulting from differences in default age-specific strategies. All participants were then monetarily encouraged to perform better in terms of accuracy. Both groups responded with an adaptive strategy of slowed reaction times and enhanced accuracy, but the young participants improved much more, outperforming older adults, and reversing the speed-accuracy strategies that are typically observed. In addition, older participants reported higher baseline levels of motivation alongside a reduced motivation to alter performance for money. So, while the older participants could match young participant performance in titration due to their higher baseline motivational levels, the young participants improved much more than older adults in response to the monetary incentive. From these findings we argue that older adults are intrinsically motivated to do well on tasks whereas younger age groups perform optimally only after incentivisation.

Introduction

Age effects in sustained attention

The Sustained Attention to Response Task (SART; Robertson et al., 1997) has been widely used to study sustained attention in both clinical (van der Heide et al., 2015) and healthy populations (Lara et al., 2014). It is mainly used as a short probe of failures in attention to reflect lapses in vigilance, but has been increasingly used to investigate diverse factors influencing attentional responses in the healthy population. This has led to the identification of age-specific behavioural patterns during SART performance (Hanzal et al., 2024b; Vallesi et al., 2021). Older participants typically show higher accuracy on nogo trials, or trials when response is withheld (Staub et al., 2015), and have thus been reported as prioritising accuracy in their response (Vallesi et al., 2021; Wiemers & Redick, 2019). Conversely, their longer reaction times (Jackson & Balota, 2012; Vallesi et al., 2021) are often understood to reflect the general decline in sustained attention ability arising from ageing (Fortenbaugh et al., 2015). However, because this difference between young and older participants could simply reflect age-dependent strategic choices in task execution (an argument put forward previously (Fortenbaugh et al., 2015; S. Hsieh et al., 2015)), an interpretation of the observed performance differences in terms of an effect of ageing on attention is questionable. In a recent study (Hanzal et al., 2024a), although we replicated the age-dependent performance strategies (high accuracy and slow responses in older adults, low accuracy and high response speed in young adults), we did not find vigilance decrements (Gartenberg et al., 2018) that we expected to observe from time-on-task fatiguing mechanisms (Head & Helton, 2012; Roach et al., 2012) in either age group. We therefore highlighted the need to identify different factors leading to age-dependent differences in task performance (including strategy choices, motivation, resilience to fatigue), to better understand the general effects of ageing on sustained attention.

The default parameters of the SART (Robertson et al., 1997) provide the participant with an ambiguous choice of prioritising either speed or accuracy. The participant is incentivised to decide their own strategic priority, based on unmonitored internal processes (Blurton et al., 2023; Liesefeld & Janczyk, 2019).

A dichotomy in strategic response is thus enabled by a sufficiently long response window in the default task design. Group-specific strategies then emerge (Katsimpokis et al., 2020; Vallesi et al., 2021) because participants choose different points in the window to respond: Young participants typically react early in the response window, displaying faster reaction times (Staub et al., 2015). In contrast, older participants tend to more fully utilise the length of the window and in so doing, increase their accuracy (Brache et al., 2010; Jackson & Balota, 2012).

Previous studies have used modified versions of the SART to investigate various underlying mental processes that may influence performance (Z. Li et al., 2022; Rizzo et al., 2021; Seli et al., 2015) including manipulations of task complexity (Kool et al., 2010; Magnuson et al., 2021) to affect strategy choice. We follow this strand here by manipulating the speed-accuracy trade-off (Manohar et al., 2015; Wolf & Lappe, 2023) in the strategy choice between accuracy and reaction time. We achieve this by imposing a varied response window length, eliciting faster response times by necessity and thus reducing participant accuracy. In titrating (Learmonth et al., 2015; Manly et al., 1999; Martin et al., 2015) to a pre-defined accuracy constant we aimed to unify the strategy across both age groups and thus reveal underlying differences in the performance of each group. (Der & Deary, 2006; Gorus et al., 2006; Hübner et al., 2021; Smulders et al., 1999; Tun & Lachman, 2008).

Motivation

Researchers have already stated an effect of age on strategy choice as underpinned by differences in levels of baseline motivation. Definitions of motivation may vary, but are commonly linked to reward (Engelmann et al., 2009). Intrinsic motivation is generally characterised as an interest or enjoyment in the task stemming from the individual (Srivastava et al., 2011). Multiple studies describe older adults as highly intrinsically motivated participants (Carr et al., 2022; Hanzal et al., 2024a; A. D. Ryan & Campbell, 2021; Swirsky et al., 2023). Motivation has previously been noted to underlie the surprising behavioural advantage in older adults (Vallesi et al., 2021), biasing them towards a more motivationally-demanding accuracy strategy (Hübner et al., 2021). In other related investigations, older adults were noted to opt for a more self-driven inhibitory strategy, again leading to the pattern of longer reaction times and higher accuracy (Brache et al., 2010; Jackson & Balota, 2012). Others have shown older adults to be less prone to shift their strategy in response to further motivators due to ceiling motivation levels arising from their values (A. D. Ryan & Campbell, 2021). They are considered to experience higher rewarding value from the onset of the experiment, stemming from their beliefs of a benefit to society and a positive contribution in participation in research (Carr et al., 2022). In addition, older adults have been shown to have less sensitivity to reward and punishment, limiting alterations to their strategy (Ennis et al., 2013; Westbrook et al., 2013). It is even possible that older adults may experience a paradoxical worsening reaction to reward initiatives (Botvinick & Braver, 2015).

This increased baseline level of motivation in older adults can be contrasted with the bias present in a young student sample. Samples exclusively relying on a population of psychology students were previously criticised for low internal validity (Croucher et al., 2024). The monetary reward used as a means of sampling participants for experiments was suggested to carry a confounding effect (Hanel & Vione, 2016; Singer & Bossarte, 2006). Specifically, student participants have been noted to rely on a strategy of conservation of effort (Rodman et al., 2021), while also showing higher mind-wandering levels when compared to other samples (Staub et al., 2015). In this experiment, after titration, we introduce a surprise (monetary) motivational intervention to test for any resulting performance divergence between the age groups.

Fatigue

Fatigue is another factor considered to impede performance during sustained attention, with several studies reporting heightened levels of subjective fatigue accompanying time-on-task effects (Gartenberg et al., 2018; Kato et al., 2009; MacLean et al., 2009; Martínez-Pérez et al., 2023; Reteig et al., 2019; Walker & Trick, 2018). While some work has highlighted an effect of fatigue on behaviour, we failed to detect a reliable relationship with SART performance in our recent work (Hanzal et al., 2024a), amongst other investigators who also failed to find a reliable link (MacCoon et al., 2014; Schwid et al., 2003). It has been theorised that motivational effects may contribute to the assumed behavioural effect of fatigue (Gergelyfi et al., 2015; Hopstaken et al., 2015). The present study will thus also include a measure of recently experienced fatigue to re-test its possible impact on behaviour.

Study Rationale

In previous research, the introduction of an objective reward as a motivational manipulation led to both an increase in speed and accuracy, yet so far this has been tested only in a young, student sample (Engelmann et al., 2009; Manohar et al., 2015; Wolf & Lappe, 2023). It thus remains unclear how different age groups perform in response to a motivational initiative once their underlying strategy is unified, or in fact whether they differ in response to a manipulation of motivation. The precise relationship of motivational changes to age-specific performance in sustained attention is thus addressed in the present experimental design: we first aligned young and older participants to the same (higher accuracy over reaction time) strategy by titration of the task difficulty and then introduced a surprise monetary incentive. We predicted that inherent lower motivation would elicit a stronger motivating effect of the surprise motivational intervention, leading to a greater accuracy in the motivational block. We also predicted young participants to have lower starting levels of motivation and that their accuracy improvement would be greater after the surprise motivational intervention than that of the older age group.

Methods

Participants

The experimental design and hypotheses were pre-registered on the Open Science Framework (https://osf.io/pyzn7). The study was approved by the University of Glasgow College of Medical and Veterinary Life Sciences Ethics committee (Approval number: 200230387). All participant data was acquired between the dates 10th of October 2024 and 21st of November 2024. A total of 56 healthy adults were recruited between the ages of 18 and 96 from the university subject pool and local area and given monetary compensation for their time. Written consent was acquired from all participants. Participants were balanced for gender and were asked to report any existing medical conditions, eye-sight correction and medications which might impact their performance. Six participants were excluded throughout data collection: One participant reported an uncorrected visual deficiency in the left eye, as also detected by a visual field test. One participant was excluded for excessive caffeine use (2 units above recommended dosage). A further participant was excluded for reporting poor sleep (4 hours per day). Two participants were excluded for low MoCA scores (<24). Finally, a participant was excluded due to a possible technical fault, or inaccurate attendance to instructions (go accuracy lower than 80% throughout multiple blocks).

The final sample consisted of 50 participants (F = 28, M = 21, NB = 1) based on a power analysis of the sample needed to acquire an effect size of f = 0.2 in a 2x2 ANOVA within-between factor interaction. The participants were divided into a young (M = 25, F = 16, NB = 1, mean age = 19, SD = 1.38, range = 18-23) and older (F = 13, M = 12, NB = 0, mean age = 69.5, SD = 6.72, range = 60-85) age group. Five participants were left-handed, one was a smoker, all reported low to moderate caffeine consumption (estimated mean units per day = 1.09, SD = 1.05, range = 0-4), matching the maximum recommended daily dose of 400mg of caffeine (Mitchell et al., 2014). They also reported an average of 7.2 hours of sleep per day (SD = 1.04, range = 6-12). All young participants were enrolled university students. The participants were screened for cognitive difficulties using the Montreal Cognitive Assessment test (MoCA; (Nasreddine et al., 2005)), reflecting scores representative of a healthy population (Borland et al., 2017) in both young (mean score = 29.2, SD = 1.7, range = 25-31) and older adults (mean score = 27.7, SD = 1.65, range = 24-30). A Welch's t-test showed no difference between the groups in their MoCA scores, t(48) = -1.66, p = .099. Cut-offs for the groups were defined as 2SD below the mean (Borland et al., 2017), meaning all participants with MoCA below 24 were excluded. A short (4-minute) computerised visual screening assessment was administered at the beginning of the session to exclude potential visual pathologies. The task was adapted from a previous experiment on young and older groups (Hanzal et al., 2024a). A Welch's t-test identified no age-group differences in target detection within the visual regions where the SART stimuli were to be presented, t(48) = 1.57, p = .128.

Procedure

The experimental task and procedure are outlined in Fig 4.1. Participants provided basic demographic information and self-reported any known impediments to participation. After this, they first completed a measure of trait fatigue (MFI) and a brief adapted visual screening test (Hanzal et al., 2024a) targeting their central visual area to detect any impairments preventing them from participation. Participants proceeded to a brief training session to familiarise them with the SART. If they were unable to achieve the minimum required standard in the experiment during 2 mins of non-titrated SART (above chance accuracy), the training session was repeated. They then undertook one 5-minute baseline block of the SART matching our previous experiment (Hanzal et al., 2024a). The participants then carried out an adapted version of the task, designed for a titration-based investigation of performance decrements. They were instructed to be as accurate as possible, but to respond before the onset of the next trial. The difficulty levels of the task were manipulated through either an increase or decrease of the response window length by 50ms, based on the participant's accuracy in sets of 25 trials and determined by a target criterion of 92% accuracy. In total, participants carried out the titration procedure for 25 minutes, divided into 4 blocks with short breaks in between. They were not informed how many blocks of the task they were expected to complete in total. This procedure aimed to determine the response window length (300ms – 2500ms) at which the participant consistently achieved an overall accuracy close to 92%.

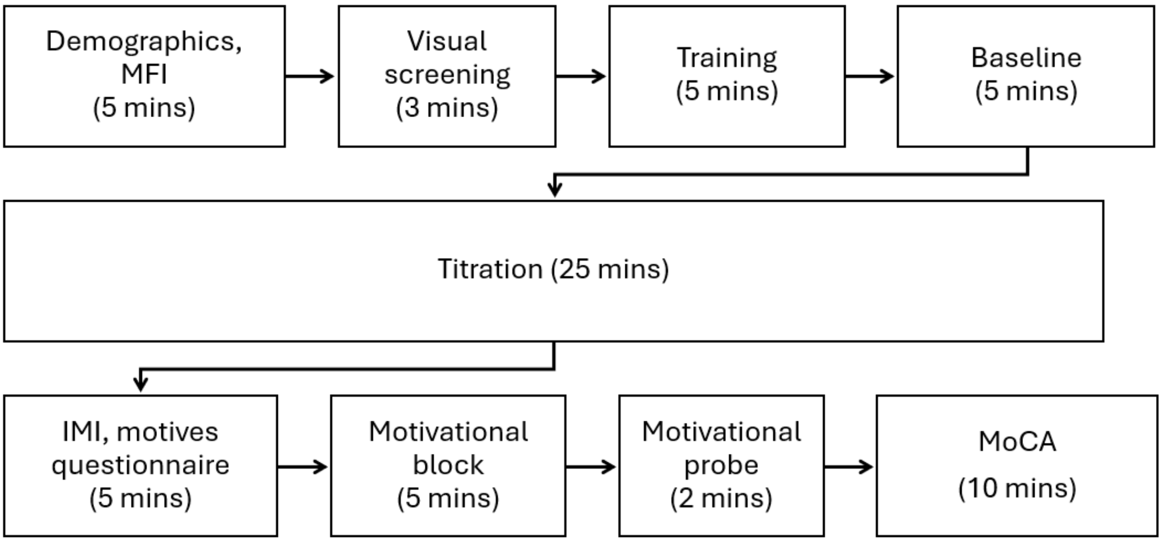

Fig 4.1 Experimental Procedure.

At the end of the titration, the participants were informed that the experiment was finished, and completed a subjective intrinsic motivation inventory (IMI; R. M. Ryan et al., 1983) and a brief adapted subjective measure to record specific motivations behind their experimentation. They then took a self-paced break. Then, all participants were informed about a further, unanticipated, block of the task presented at the same difficulty level as the last. They were likewise informed that if they achieved the highest improvement in accuracy, relative to all other participants in their age group, they would receive a prize of £50. The participants then carried out a final 5-minute block of the task, set to the difficulty level matching the average response window length of the last 125 trials at the end of the titration period, but with no further titration. At the end of the motivational block, they proceeded to fill in a single item measure (VAS-M) on perceived changes in their motivation as a result of the initiative. Before the end, they were screened for any cognitive impairments that could impact the experiment using the MoCA (Nasreddine et al., 2005) and then proceed to be debriefed. The overall duration of the experiment was 65 minutes.

Task

The participants underwent a modified version of the SART with varied levels of difficulty, implemented in PsychoPy, using custom Python scripts (Peirce et al., 2019). The task was displayed on a digital monitor (Dell Optiplex 9010), with a screen resolution of 1280x1024 pixels and a refresh rate of 60Hz. Participants were seated 60 cm from the screen, maintaining horizontal eye level with the centre of the display by the use of a chin rest. In each trial, the participants were instructed to fixate centrally on the fixation cross and attend to a stimulus presented at an angular distance of 1°, consisting of a number between 0-9 presented centrally for 150ms. The number then disappeared during the response window, which had a variable duration of 300-2500ms, before the next trial started. The response window length and the learning block response window lengths were set to 1000ms at the start of the experiment for all participants. The task was to respond using a spacebar press to all numbers that appeared (go trials), apart from the numbers 3 or 6, whilst withholding response to the appearance of numbers 3 and 6 (nogo trials). The numbers were pre-generated to be distributed randomly and represented in equal frequency. Based on the accuracy of the participant in a set of 25 trials, the subsequent set of trials had their response window length shortened or lengthened by 50ms to eventually achieve a desired equilibrium (92% accuracy for each participant). If accuracy on the previous block was lower than 92%, the subsequent block was made easier by lengthening the response window by 50ms. If accuracy was exactly 92%, the response window was kept constant. An accuracy of 92% was chosen to correspond to 60% nogo accuracy and 100% go accuracy (corresponding to 20% nogo trial rate), since go trial accuracy was expected to be at ceiling level for most participants (Hanzal et al., 2024b). An additional static fixation period of 6s was added between the sets of 25 trials. The difficulty of the motivational block was calculated to represent the average response window length, rounded to the nearest increment of 50ms in the last 125 trials of the titration, to reduce the effects of random fluctuations in accuracy.

Measures

The participants were asked to report their age, gender, number of hours of sleep in the past week and caffeine intake on the day as well as disclose known impediments to participation.

The Intrinsic Motivation Inventory (IMI) was used as a measure of subjective motivation (R. M. Ryan et al., 1983). It has been recently used for valuation of motivation and cognitive task performance (Cagna et al., 2024) and continues to show good reliability (Cronbach alpha > .7, (Monteiro et al., 2015)). It is a 7-point Likert scale that contains 45 items spread across 7 subscales. The three most relevant subscales were used: interest (7 items; e.g. 'I enjoyed doing this activity'), effort (5 items; e.g. 'I put a lot of effort into this') and value (7 items; e.g. 'I think this was an important activity') subscales. The experiment further used a motivation item question adapted from the use in our lab, probing participants for reasons for taking part in the experiment (8 options; e.g. 'To help the researchers make new scientific discoveries'). The participants were also probed on a visual analogue scale for motivation (VAS-M) with values 0-100 and a single question on the extent they felt motivated by the motivational intervention.

The Multidimensional Fatigue Inventory (MFI; Smets et al., 1995) was used to measure trait fatigue, and was comprised of 5 subscales with 4 items each (20 items in total) on a 5-point Likert scale. Previous work indicated a very good reliability of $\alpha = .84$ and showed a lack of floor and ceiling effects as well as item redundancy (Lin et al., 2009).

Results

All analyses were carried out in R (R Core Team, 2024) using the packages 'tidyverse' (Wickham et al., 2019), 'psych' and 'ez' (Lawrence, 2016). Packages used for graphical depiction were: 'ggpubr' (Kassambara, 2023), 'viridis' (Garnier et al., 2023) and 'Cairo' (Urbanek & Horner, 2023). Reaction times showed a heavy skew (1.33), and so were log-transformed for any further analysis. Any trials with a reaction time < 150ms were excluded from the analysis as likely to be representative of anticipation error (Hawkins et al., 2019).

Since each participant completed the task for a fixed duration of 25 minutes, the total trial numbers differed among the participants due to the variable response window lengths. A t-test on the total number of titration period trials in young (mean number of trials = 758, SD = 107, range = 550-912) and older adults (mean number of trials = 769, SD = 102, range = 550-1005) showed no differences between the groups, t(48) = -.361, p = .720. A t-test was also run on the average window length between the young (mean seconds = .882, SD = .214, range = .654-1.40) and older adults (mean seconds = .830, SD = .185, range = .525 – 1.37) in the whole titration period, also showing no between-group differences, t(48) = .921, p = .362.

Age-specific strategies

We first investigated differences among the age groups in the baseline block. A between groups t-test showed no differences between the two age groups on nogo accuracy in the baseline SART block, t(48) = -.200, p = .421, depicted in Fig 4.2A. A between groups t-test also showed no differences between the two age groups on reaction time in the baseline SART block, t(48) = -.128, p = .104, reflected in Fig 4.2B.

Additionally, to test age effects after titration, a two-sample t-test was run, testing the difference between young and older participants on experimental difficulty level (combined trial and presentation length) at the titrated window length. This again showed no differences between the groups, t(48) = .608, p = .273, as depicted in Fig 4.2C. The findings thus indicate that we did not replicate age-specific strategies in our sample, but that both groups had similar performance levels throughout the period prior to the motivational monetary manipulation.

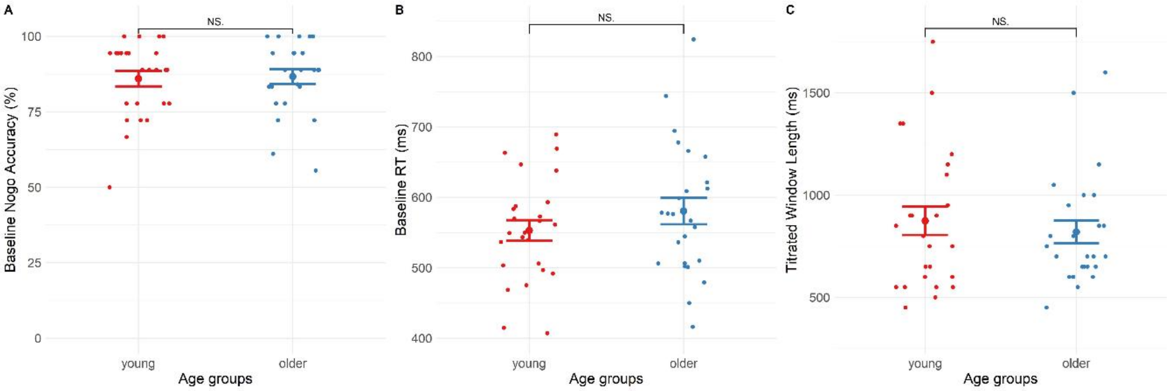

Fig 4.2 Age differences at baseline and after titration. Young participants did not differ from older participants in the baseline comparison block (5 minutes) either in nogo accuracy (A) or reaction times (B). Additionally, age groups (young and older) did not differ in their titrated window lengths at the end of titration (C).

Titration

We further tested the impact of the titration procedure on participant performance. Participants were split based on their initial median accuracy (93.78%). This resulted in two groups: those who better in accuracy than the average at baseline (mean accuracy = 95.20%, SD = .90%) and those who were worse in accuracy than the average (mean accuracy = 90.8%, SD = 2.34%). Then, the performance of both groups across the four titration blocks was modelled on several behavioural metrics.

A multiple linear regression [F(3, 196) = 17.98, R2 = .20, p < .001] showed that better performers at baseline had higher accuracy over all 4 blocks: t(46) = -6.19, p < .001. A main effect of titration block showed that overall accuracy decreased throughout the experiment, t(48) = -6.19, p < .001. There was an interaction between the effects of group and titration, t(48) = 5.08, p < .001. A series of post-hoc t-tests was conducted to outline the titration blocks where the groups differed. A t-test found a difference between the groups in block one, t(48) = 8.62, p < .001, but not in block two, t(48) = 1.28, p = .21, block three, t(48) = -.61, p = .54 or block four, t(48) = -.03, p = .98. The groups were thus no longer different in their overall accuracy by block two. Collectively, this indicates that the gap between the performers in overall accuracy decreased over time and disappeared, as seen in Fig 4.3A.

A multiple linear regression [F(3, 196) = 15.18, R2 = .18, p < .001] showed that better performers had higher nogo accuracy t(46) = -5.21, p < .001. A main effect of titration block showed that nogo accuracy decreased throughout the experiment, t(46) = -3.61, p < .001. There was an interaction between the effects of group and titration, t(46) = 3.20, p = .002. A series of post-hoc t-tests was conducted to test in which titration blocks the groups differed. A t-test found a difference between the groups in block one, t(48) = .6.47, p < .001 and block two, t(48) = 2.56, p = .02. No difference was found in block three, t(48) = 1.41, p = .16 and block four, t(48) = 1.3, p = .19. Collectively, this indicates that the gap between the performers in nogo accuracy decreased over time and disappeared, as seen in Fig 4.3B.

A multiple linear regression [F(3, 196) = 3.54, R2 = .04, p = .016] showed that better performers had higher reaction times t(46) = -2.52, p = .012. A main effect of titration block showed that reaction times generally decreased throughout the experiment, t(46) = -2.72, p = .007. There was no interaction between the effects of group and titration, t(46) = 1.96, p = 0.051. Collectively, this indicates that better performers preserved their slower reaction times throughout the titration period relative to worse performers, but both groups generally reduced their response times, as seen in Fig 4.3C.

A multiple linear regression [F(3, 196) = 34.65, R2 = .36, p < .001] showed no difference between the groups in their response window length: t(46) = 1.64, p = .10. A main effect of titration block showed that response window length decreased throughout the experiment, t(46) = -3.28, p = .001. There was an interaction between the effects of group and titration, t(46) = 2.52, p = .012. The interaction indicates that better performers gradually achieved more difficult response window lengths, with high performers reaching a relatively low response window length and low performers retaining a high response window length, as seen in Fig 4.3D.

Collectively, the testing of performance over time confirms that both groups of performers achieved an average of 92% accuracy at the end of the titration blocks. Good performers, in addition, reached a shorter response window length while matching the same accuracy level. The titration thus generally raised the difficulty of the task for high performers and maintained or reduced the difficulty for poorer performers. Alongside this, there was a limited effect on reaction times, with high performers preserving higher reaction times to maintain a more accurate strategy.

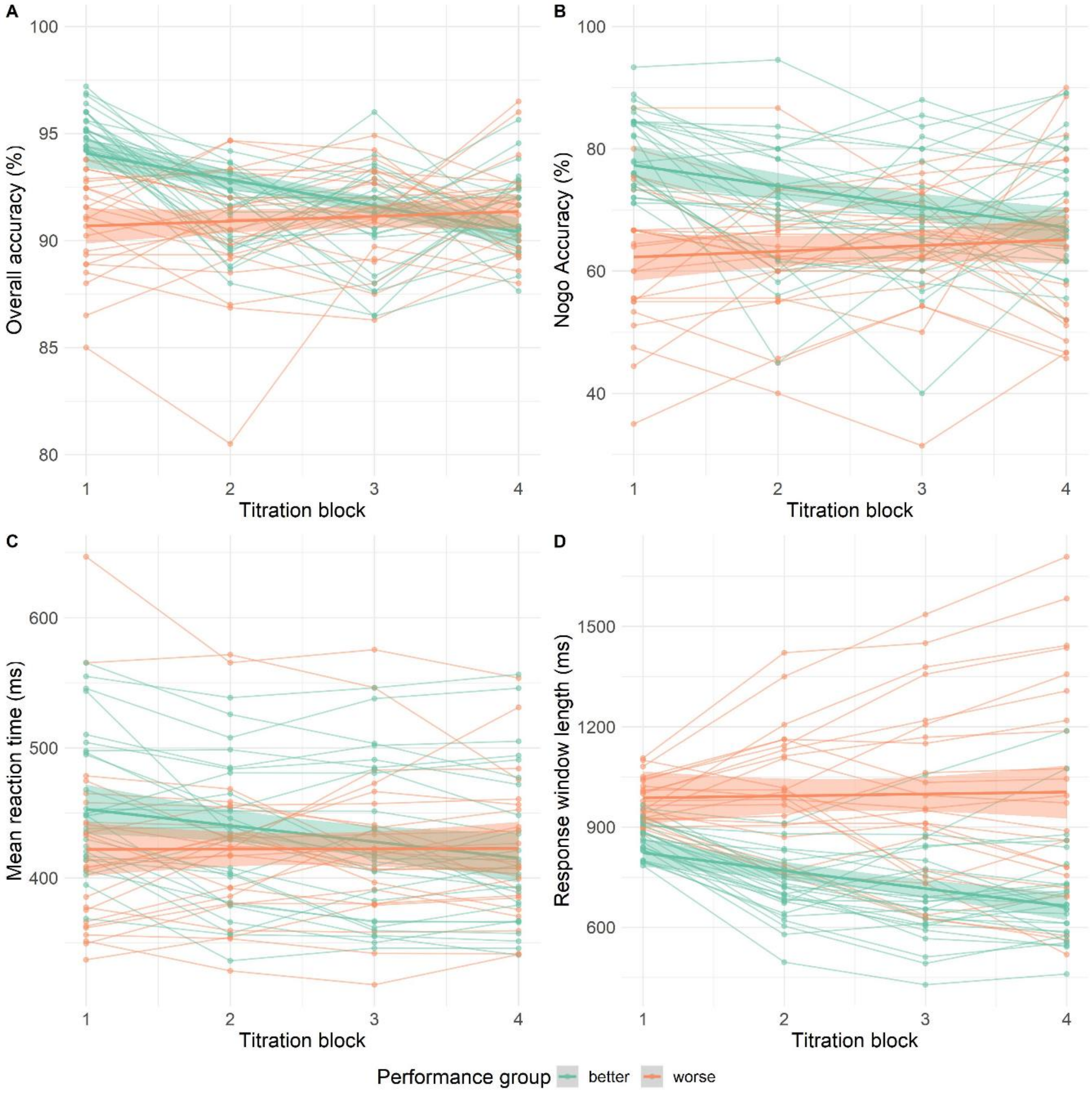

Fig 4.3 Median-split participant performance in titration over time. Participants were split into better (green) and worse (orange) performance groups based on their overall accuracy in titration block 1. The performance of each of these groups was then plotted across all four titration blocks in the metrics of overall accuracy (A), nogo accuracy (B), mean reaction time (C) and titrated response window length (D).

Motivational manipulation

The following analysis investigated the effects of the surprise motivational intervention. A 2x2 mixed ANOVA between age groups (young, older) and time points (last 125 trials of titration, whole motivational block) was run on overall accuracy. The resulting model showed no main effect of age, F(1, 48) = 2.50, p = .120, but that all participants were more accurate after the motivation, F(1, 48) = 48.27, p < .001. A significant interaction, F(1, 48) = 4.37, p = .042, showed that the young participants improved much more than the older adults, as depicted in Fig 4.4A. The motivational manipulation therefore worked to increase accuracy in both groups, but more so in the young group.

In addition, a 2x2 mixed ANOVA between age groups (young, older) and time points (last 125 trials of titration, whole motivational block) was run only on nogo accuracy, showing the same pattern, only more prominently. There was no main effect of age, F(1, 48) = .001, p = .974, but the participants were more accurate after the intervention, F(1, 48) = 39.33, p < .001. A significant interaction, F(1, 48) = 7.26, p < .001, showed that the young participants improved much more than older adults, as seen in Fig 4.4B. The descriptive difference in scale between nogo accuracy improvement and overall accuracy improvement shows that the difference in accuracy was driven by an improved withholding of responses in the nogo trials, rather than responding more accurately in the go trials.

In addition, A 2x2 mixed ANOVA between age groups (young, older) and time points (last 125 trials of titration, whole motivational block) was run for reaction times. There was no main effect of age, F(1, 48) = 2.98, p = .090, but the participants were slower after the motivational manipulation F(1, 48) = 7.12, p = .010, with no significant interaction, F(1, 48) = .216, p = .643, indicating a similar pattern of slowing in both age groups, as Fig 4.4C indicates.

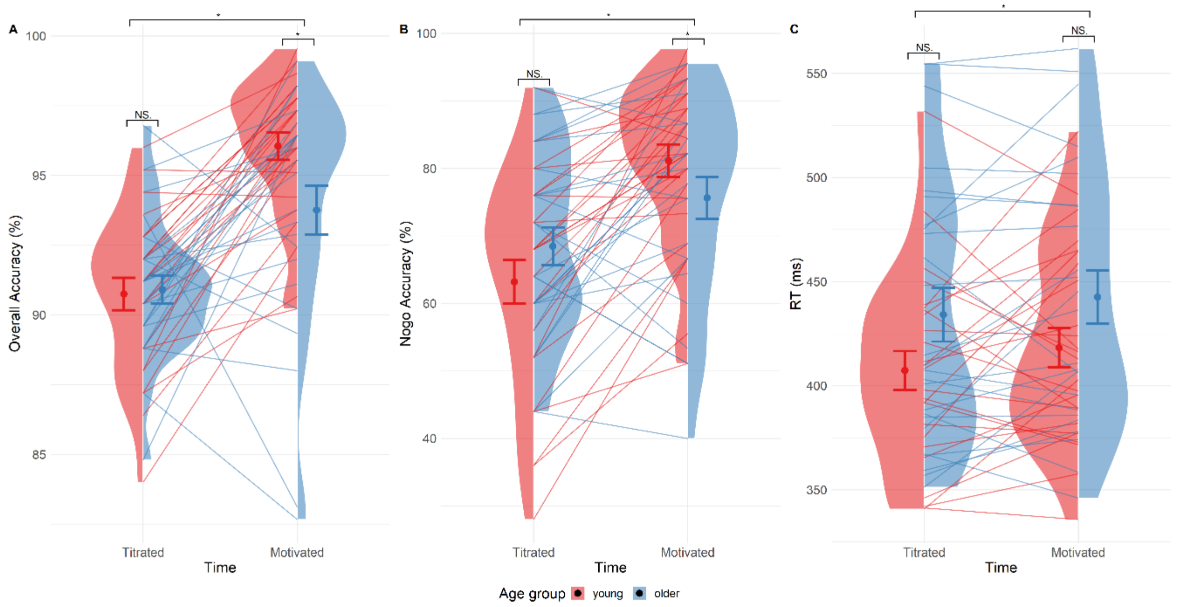

Fig 4.4 Performance difference after motivational manipulation. Plots comparing participant performance at the end of the titration period (last 125 trials of titrated block 4) with performance during the Motivational block. Young participants improved significantly more than older participants after the motivational manipulation both when measured in overall accuracy (A) and when focusing on nogo accuracy (B). Both groups generally increased their response time, yet no age differences were found (C).

Motivational differences

Next, we investigated the differences among age groups in the subjective perception of their motivation.

A Cronbach’s alpha was calculated for each of the subjective scales. IMI - interest showed alpha = .841, IMI - effort alpha = .765, IMI – value alpha = .821, indicating good to excellent reliability of the measures.

A between groups t-test was run, testing for differences between young and older participants on intrinsic motivation upon completion of the titration, for each of the three motivation sub-scales. Older participants had higher subjective motivation on IMI - interest, t(48) = -2.23, p = .015 (Fig 4.5A), and IMI - value, t(48) = -2.31, p = .013 (Fig 4.5B), but not on IMI - effort, t(48) = -.038, p = .485 (Fig 4.5C).

A t-test was run between the two age groups on post-motivational block change in motivation measured by the visual analogue scale (VAS-M). The young group was significantly more motivated by the monetary incentive compared to the older adults, t(48) = 6.40, p < .001, seen in Fig 4.5D.

A Pearson's chi-square test assessed the difference between the young and older participants in the distribution of their reported reasons for taking part in the experiment. The test did not show any differences between age groups, X(36) = 42, p = .227. Arguably, the findings were underpowered to adequately detect differences among the two age groups as out of the 8 reasons for participation, some cell observations in reasons for participation unexpectedly fell under 5 (McHugh, 2013). Nevertheless, the young participants were informatively much more motivated by money to participate (23 young vs 5 older).

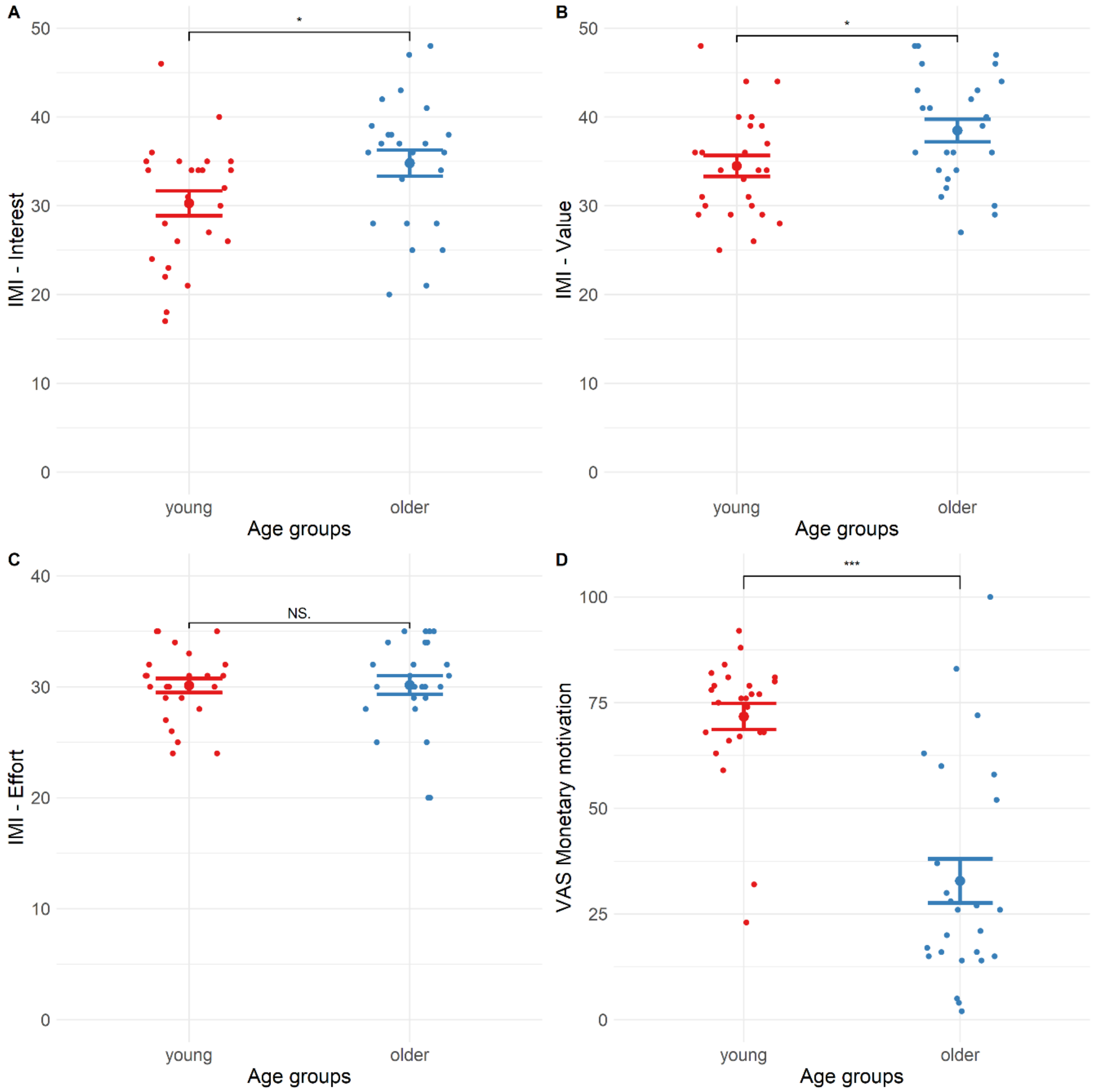

Fig 4.5 Age differences in motivation. Older participants had higher motivation to undertake the task based on IMI – Interest (A) and IMI – value (B), but not IMI – effort (C). The older participants were also less motivated by the intervention than younger participants (D).

Connection to fatigue

We also explored whether levels of motivation and subjective trait fatigue were associated with performance on the SART.

Cronbach's alpha was calculated for each of the subjective subscales of the multidimensional fatigue inventory. Most of the scales had good reliability: MFI - general fatigue had an alpha = .82, MFI - mental fatigue alpha = .843, MFI - physical fatigue alpha = .813, MFI - reduced activity alpha = .757, but MFI - reduced motivation only showed low alpha = .578.

Multiple linear regressions were run between the two age groups on subjective fatigue scores and titrated window length in the titration SART block, one for each subscale of MFI. No prediction of titrated window length or age group by fatigue was found for MFI scores overall, [F(3, 46) = .676, R^2 = 0.042, p = .571], MFI general fatigue [F(3, 46) = .399, R^2 = 0.025, p = .754], MFI physical fatigue [F(3, 46) = .453, R^2 = 0.029, p = .716], MFI mental fatigue [F(3, 46) = 1.018, R^2 = 0.062, p = .393], MFI reduced activity [F(3, 46) = .670, R^2 = 0.042, p = .575] or MFI reduced motivation [F(3, 46) = .592, R^2 = 0.037, p = .623].

A multiple linear regression tested the difference between the two age groups on the correlation between total subjective fatigue scores and total intrinsic motivation scores [F(3, 46) = 6.08, R2 = .284, p = .001]. Older adults were more motivated than young adults, t(46) = 3.09, p = .003, with no main effect of fatigue, t(46) = .669, p = .507 and with a significant interaction between age group and MFI total fatigue, t(46) = -2.78, p = .008. An inspection of a Fig 4.6 depicting the relationship shows that there was no relationship between motivation and fatigue in young participants, but older participants experienced more motivation if they also experienced being less fatigued.

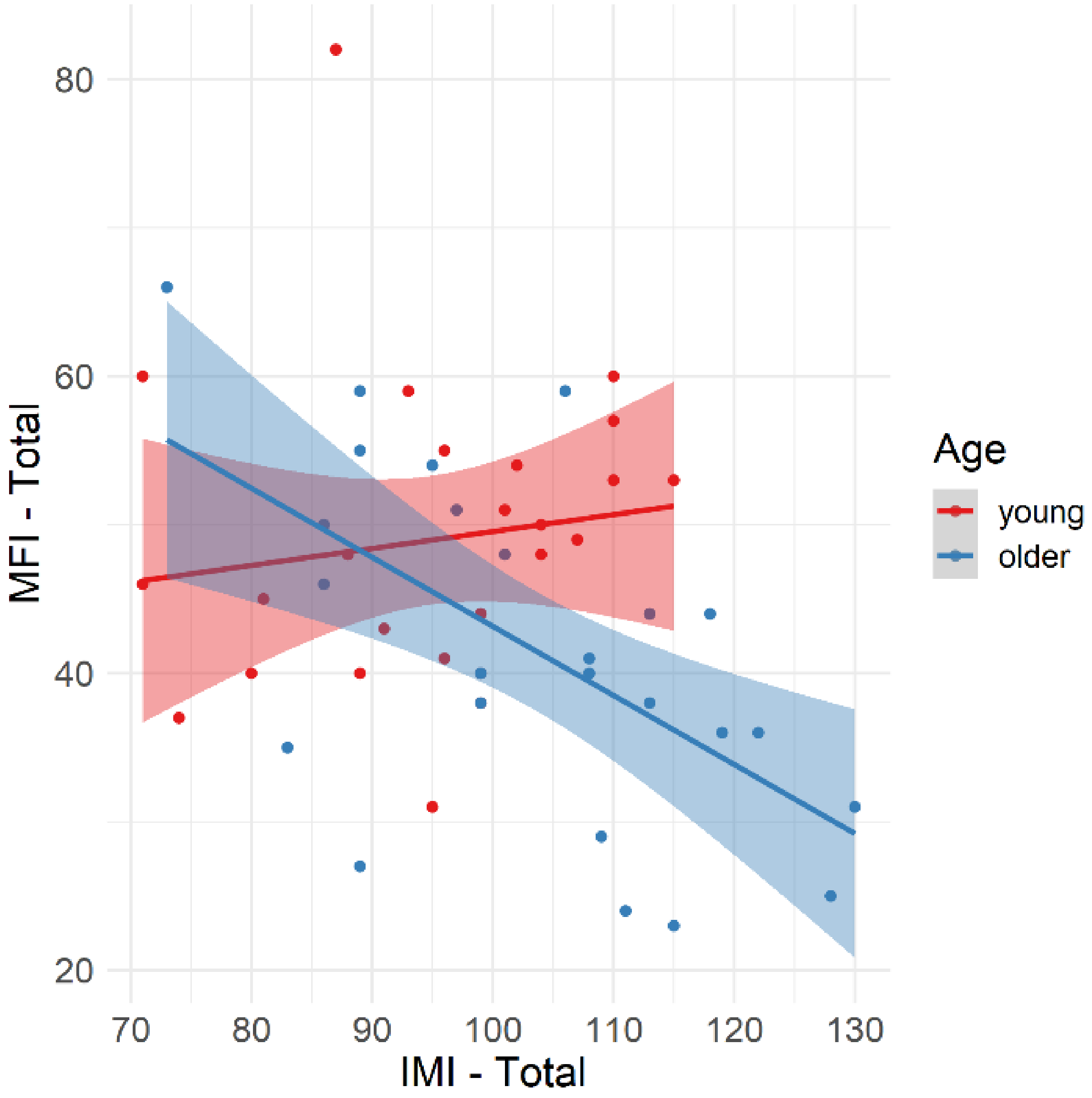

Fig 4.6 Age differences in the relationship of fatigue to motivation. Older participant total scores on the Multidimensional Fatigue Inventory (MFI) were associated with lower total scores on the Intrinsic Motivation Inventory (IMI), with no such relationship in young participants.

Discussion

This study examined how age, motivation, and fatigue influence strategy choice in the SART. To ensure comparable performance of both age groups, the response window was individually adjusted by titration to attain a shared accuracy of 92%. Notably, older participants reached the target accuracy without, as a group, requiring longer (and thus easier) response windows than the young adults. As a result, we did not replicate the prominent age effect of older adults being accurate but slower, and young adults being fast but inaccurate (Hanzal et al., 2024b; Vallesi et al., 2021). Nevertheless, the titration procedure still ensured that accuracy was matched before all participants were incentivised to perform better. This manipulation then successfully elicited an age effect: both age groups slowed their reaction times but improved in accuracy at different rates. Older adults showed less improvement than younger participants, who became much more accurate.

Both age groups initially reached a comparable level of task difficulty, as indicated by the similar response window lengths at the end of titration. During this phase, older adults also reported higher levels of subjective motivation, aligning with previous findings about their higher intrinsic motivation (Staub et al., 2014). We thus propose that their intrinsic higher motivation enabled this group of older adults to keep pace with the younger group up to the point of the motivational manipulation (Bourisly & Shuaib, 2018; Vallesi, 2016). Younger adults in turn were less motivated to do the task, which likely explains their (relatively) poorer performance prior to incentivisation and their greater ability to subsequently improve. In a related study, DeRight and Jorgensen (2015) investigated low effort in a sample of college students and also found a proportion of students with low effort, resulting in a surprising, subthreshold performance on key attentional and cognitive tasks. Dunn and colleagues (2019) reached a similar conclusion with a motivational imbalance in the student sample. The young participants in our study may be seen as exerting the minimum effort required to meet task demands, thereby adopting a strategy aimed at conserving energy (Botvinick & Braver, 2015; Gray et al., 2006; Shenhav et al., 2017) until there comes a point of renewed interest; in this case the interest is renewed by an extra monetary reward (Milyavskaya et al., 2021). This parsimonious strategy is arguably advantageous in light of the relatively low perceived value of the experiment, which then changes as a result of the motivation manipulation: our young participants strategically limited their effort during the titration and then improved heavily once motivated.

We thus highlight, for the first time in sustained attention research, motivation as the primary factor driving age-related differences in performance. The young participants reported strong reactivity to the motivational manipulation and showed greater improvement in accuracy than the older adults. Also, in contrast to some previous findings (Manohar et al., 2015; Wolf & Lappe, 2023), the young adults slowed in their reaction times in response to the motivation condition, but as a result gained a greater advantage in accuracy than the older group. In our experiment, the older sample did not alter their performance as much after the manipulation and reported a low perceived effect of the monetary initiative.

In the existing literature, diverse reasons are in discussion regarding the increased presence of intrinsic motivation in the older participants. It has been suggested that older adults seek to compensate for age-related slowing and so become more motivated to perform well (S. Hsieh et al., 2015; Jackson & Balota, 2012). This is then translated into a more demanding behavioural strategy. The account is based on reports of strong rapport between older adults and the researcher (Kylén et al., 2022; A. D. Ryan & Campbell, 2021) and a strong self-reported positive valuation of experimental participation associated with older adults (Barber, 2017). According to the socioemotional selectivity theory (Carstensen, 1993; A. D. Ryan & Campbell, 2021; Swirsky et al., 2023), older participants experience the positive value of participation as they are more attracted to short-term goals directly related to their experience during the experiment. They maximise the emotional well-being experienced in the present moment, gained from volunteering in scientific research (Wirth et al., 2023). Young participants conversely perceive time as a vast resource and so prioritise future-oriented goals, including advancing their future socio-economic status, and thus responding to monetary rewards. As a result, older adults may perceive participating in research itself as more rewarding than the financial compensation. This could further explain why the motivational manipulation only showed a limited improvement in older adults, who reported that the prospect of a future reward did not impact their already strong investment in the experiment. Their limited responsivity likewise aligns with a report of a smaller inclination of older adults to switch to a different behavioural strategy, contrasting with the ability of young people to more readily change task strategy (Harris et al., 2012).

None of these effects were connected to fatigue and there were no differences in trait fatigue between the groups, aside from a link between fatigue and motivation in the older group. We speculate that this could indicate fatigue as a component of motivation in the older group, but more research is needed to test this connection directly. Given this minimal link to fatigue, we propose that the motivational differences at baseline and in response to additional monetary manipulation underlie the observed age effect in sustained attention.

Limitations

It should be acknowledged that the study's recruitment approach was selective, thus making it potentially susceptible to bias in the form of higher socioeconomic status, health and educational levels relative to the typically ageing population. This was reflected in matched high educational attainment and MoCA scores of both age groups. Nevertheless, the conclusions regarding the older sample are aimed at populations typically participating in research. Older research participants may also differ from the typical population in their ability to access university-based research, and their interest in and awareness of opportunities to participate (Hjortskov et al., 2023). Future research may still consider ways to widen engagement, for example recruiting during public engagement events (Turner et al., 2023) may further aid the generalisability of the present findings. Our findings may also be amenable to replication in an online context (see our previous findings about strong age effects on sustained attention (Hanzal et al., 2024b)).

Overall, the subjective measures in this study reached a Cronbach's alpha of 0.7 only, thus not attaining the full reliability standard of 0.8 (Taber, 2018). One subscale of the MFI also had an unreliable score of 0.58. More rigorous testing of subjective motivational and fatigue states should be employed in future studies to consolidate the correspondence of subjective measures to behaviour.

Future Research

Our study raises the wider issue of the confounding effect of motivational factors in student samples commonly employed in experiments measuring performance. The present findings indicate that the choice of response strategy in young participants is dynamically affected by their level of motivation. Future studies, particularly those investigating the capacity of participants to perform at a certain level, should track motivational confounds. We thus show that on the SART, older participants were inherently motivated to do well, with only a little accuracy gain after the monetary incentive. In the case of this study, the commonly used young participant population was shown to generate suboptimal performance up to the point of the extra motivational manipulation. We thus propose that older adults can be seen as intrinsically motivated to do well on tasks, whereas younger age groups perform optimally only after incentivisation. The approach of factoring subjective motivation into the study design may be further utilised and expanded by the use of more precise measurements of motivation, including follow-up probes of participation motives (Soule et al., 2016) or frequent probes during the task (Reteig et al., 2019).

This experiment indirectly enriches the discussion of the theoretical underpinnings of vigilance decrements. Performance declines in sustained attention tasks have previously been associated with fatigue (Brosnan et al., 2022; Roach et al., 2012). Yet while vigilance decrements are sometimes known to occur after time-on-task (Reteig et al., 2019; A. S. Smit et al., 2004), this is not always the case (Ackerman et al., 2010; Ackerman & Kanfer, 2009; Dobryakova et al., 2013; Hanzal et al., 2024a; Nakagawa et al., 2013; Nieznański et al., 2020). The present findings indicate that the possible reason for this inconsistency is interference from an untracked underlying state of motivation driving strategy fluctuations, more so than that of fatigue.

Finally, this study showed that the effect of motivation can be studied by targeting different participant age groups. As age has been previously strongly associated with the difference in performance during sustained attention (Hanzal et al., 2024b; Vallesi et al., 2021), this experiment then supports a motivational account of sustained attention performance differences (DiMenichi & Tricomi, 2015;

Engelmann et al., 2009). It implies that vigilance decrements can be better understood by incorporating the factor of motivation (Arnau et al., 2017; Boehler et al., 2012; Boksem & Tops, 2008). It also contributes to a possible explanation of the mixed efficacy of attempts to improve performance in students (Schunk & DiBenedetto, 2021), pointing to the role of intrinsic motivation as an explanation.

Conclusion

This study investigated the impact of motivation on age differences in performance during sustained attention. We showed that young participants' performance in sustained attention was improved by interference with their motivation levels much more than in a sample of older adults. Older participants reported higher baseline levels of motivation alongside a reduced motivation to alter performance for money. So, while the older participants could match young participant performance in titration due to their higher baseline motivational levels, the young participants improved much more than older adults in response to the monetary incentive. From these findings, we argue that older adults are intrinsically motivated to do well on tasks whereas younger age groups perform optimally only after incentivisation. The findings show the need to track motivational factors in investigations into sustained attention.

Chapter 5: Discussion

Summary

In this thesis, I aimed to a) identify a link between subjective fatigue and behavioural and brain oscillation metrics related to the vigilance decline during sustained attention, and b) examine the role of age and motivation as further contributors. Three studies were conducted to test these connections, focusing on comparisons between young and older healthy participants.

In the discussion, I will examine the key findings from the three studies and draw conclusions related to the outlined goals. Furthermore, I will evaluate the relevance of these findings to future research while outlining the prospects of using the candidate patterns in neurofeedback. I will conclude that there is only a tenuous link between subjective fatigue and objective fatigue markers in the context of sustained attention. I suggest an alternative approach for future research that instead builds on the thesis's insights into the interplay of age and motivation in sustained attention.

Key findings

Subjective fatigue arises during sustained attention

One of the goals of the undertaken studies was to detect subjective fatigue during sustained attention. A rise in state subjective fatigue was then successfully found in both experiments in **Chapter 2** and **Chapter 3**. An auxiliary experiment in Appendix 2 further illustrated that this rise was not automatic but only occurred in connection with tiring tasks. This way, the studies confirmed the expectation that subjective fatigue arises during demanding tasks (Arnau et al., 2017; Behrens et al., 2023; Darnai et al., 2023; Massar et al., 2018; Wilhelm et al., 2022). The findings thus extend the literature on this effect to sustained attention (Brosnan et al., 2022; Pershin et al., 2023; Reteig et al., 2019), providing the most comprehensive survey to date of fatigue’s presence specifically during the SART.

The findings further illustrated the different relationships of state and trait (or prolonged[5]) fatigue to behaviour. **Chapter 2** suggested that short-term state fatigue was related to performance changes, more so than fatigue at the trait level, which, as also shown in **Chapter 4,** had no link to performance. Interestingly, state fatigue still arose without a decline in performance in **Chapter 3**, linking to several studies with similar outcomes (Ackerman et al., 2010; Ackerman & Kanfer, 2009; Dobryakova et al., 2013; Nakagawa et al., 2013; Nieznański et al., 2020; Wójcik & Nęcka, 2024). The described different outcomes for state and trait fatigue also connect with previous work identifying their distinctive correlates (Möller et al., 2019; Wylie et al., 2019, 2022). The findings collectively best match a recent account of introspective fatigue that emerges during demanding tasks yet is decoupled from performance decrements (Pessiglione et al., 2025).

Previous experimental studies have indicated age as a factor in subjective fatigue (Hinz et al., 2013; Vestergaard et al., 2009; Watt et al., 2000). However, the present investigation showed only weak age effects in reported fatigue and no difference in trait fatigue. If anything, older participants reported lower state fatigue at baseline prior to the experiment, both in **Chapter 2** and **Chapter 3**. This finding should be treated cautiously as state measures best capture relative changes rather than stable levels. Their timescale implies a greater degree of fluctuation, affected by multiple untracked factors (Earle et al., 2015; Herlambang et al., 2021; Tran et al., 2020), leading to low test-retest reliability. Nevertheless, it matches other findings where older participants were reported to show lower fatigue (Aggarwal et al., 2006; Engberg et al., 2017; Fuhrer & Wessely, 1995; Wylie et al., 2022). One possible explanation for the uneven levels of baseline state fatigue in older adults may be a sampling bias in the selection of healthier older participants, as discussed in **Chapter 1**. Additionally, older adults' subjective reports in **Chapter 4** showed a connection between the experiences of fatigue and intrinsic motivation. Motivational arousal has previously been suggested to arise during time-on-task (Brehm & Self, 1989), serving as feedback for the reassessment of task goals, possibly showing that this experience of fatigue

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[5] For more information, see Footnote 2 in Chapter 1.

is partly driven by higher motivation in older adults (Botvinick & Braver, 2015; Wilhelm et al., 2022), which I will discuss later.

Overall, the present investigation provides strong evidence for the onset of subjective fatigue during sustained attention. However, there were no substantial differences between levels of fatigue in different age groups. Consequently, any minimal age difference in fatigue was unlikely to have played the anticipated role in the other discussed age-related effects.

Oscillations may anticipate the vigilance decrement

The brief online experiment in **Chapter 2** showed a coupling of changes in experienced fatigue and accuracy in the SART. The finding then led to a prediction of a vigilance decrement in a longer version of the task. Yet, this unexpectedly failed to materialise in **Chapter 3**, despite matching the experimental length to previous investigations successfully inducing a decrement both in the SART (Lara et al., 2014) and in related tasks (Head & Helton, 2012; Kato et al., 2009; MacLean et al., 2009; Martínez-Pérez et al., 2023; Pattyn et al., 2008; Pershin et al., 2023). The null finding particularly contrasts with a notable example from research by Reteig et al. (2019), who observed and described a detailed decrement during a sustained attention task (frequent nogo trials) peaking 30 minutes into the task. Interestingly, Reteig’s study found an effect in a smaller sample (n = 21), but used a different paradigm with frequent nogo trials, as opposed to frequent go trials in the SART. Also, the experiment in **Chapter 2** had a much larger sample size, possibly contributing to the lack of effect in **Chapter 3**. Another likely influence on these results may be a possible contrast in ecological validity between online and in-person experimentation, a subject of debate (Bridges et al., 2020; Semmelmann & Weigelt, 2017) beyond the scope of this discussion.

Chapter 2 informed the key prediction in this thesis, that changes in relevant brain oscillatory patterns would accompany an exposure to a demanding task. This was rooted in known associations of brain dynamics with sustained attention (Barwick et al., 2012; Clayton et al., 2015; Jacquet et al., 2021; Sadaghiani & Kleinschmidt, 2016) and early indications in related research (Benwell et al., 2019; Reteig et al., 2019), as well as the emerging findings of Pershin et al. (2023), showing time-on-task increases in alpha and adjacent lower-frequency oscillations. Despite the absence of a vigilance decrement, **Chapter 3** still revealed two of the predicted brain oscillation patterns. The changes in both patterns further followed the expected direction of change, reflecting a disengagement with the task. These detected patterns were time-on-task rises in 1) pre-stimulus alpha synchronisation and 2) task-related beta synchronisation.

There is a lot of literature on the attentional role of pre-stimulus alpha oscillation (M. X. Cohen, 2011). Pre-stimulus alpha has been observed in anticipation of attentional reorienting (Bracco et al., 2018), and attentiveness to near-threshold visual stimuli is impacted by pre-stimulus alpha amplitude (Melcón et al., 2024). Pre-stimulus alpha phase predicted subjective awareness and objective performance in a luminance discrimination task (Benwell et al., 2017) and its ability to predict response probability has been used to show that it reflects the inhibition of attention (Zazio et al., 2020). It further reflects change from rest to task in the signal-affected stimulus-response processes of an auditory go-nogo task (Karamacoska et al., 2018). Ongoing pre-stimulus alpha oscillations trial-by-trial variations have also been linked to reported changes in attentional state (Macdonald et al., 2011). Some researchers have found changes in alpha oscillations to be independent of vigilance decrement: Resting-state alpha predicted tDCS gains on the SART, but without a link to vigilance decrements (Martínez-Pérez et al., 2023). Similarly, alpha decreased through a manipulation of attentional effort, but without a direct link to changes in reaction time (Byrne et al., 2020). Furthermore, manipulating motivation offset the rise in this pattern, highlighting a likely re-engagement with the task. Collectively, these findings point to an explanation of the detected rise in alpha synchronisation as a change in attentiveness to the task, even in the absence of any behavioural decrements.

An attentional component may also be found in the time-on-task increase in task-related beta synchronisation. Admittedly, the observed pattern follows the structure of the classical post-motor beta rebound (PMBR), the specific neural response concerned with the preparation (Darch et al., 2020; Swann et al., 2009) and/or execution of a motor response (Heinrichs-Graham et al., 2017; Parkes et al., 2006). Nonetheless, findings in rhesus monkeys (Stoll et al., 2016) highlighted a further role of these oscillations in cognitive or motor control. This was later seen in humans, where beta oscillations reflected control processes (Lundqvist et al., 2024) and were also directly proposed to indicate motor control during the SART (Mensen et al., 2022). Supporting this view, efforts to maintain vigilance have been associated with increased beta oscillation activity (A. Craig et al., 2012) and the oscillations were also linked to top-down attention (Riddle et al., 2019). Alike to the findings in **Chapter 3**, Pershin et al (2023) observed a temporal dimension to the beta oscillation and described its rises as reflective of a change in attentiveness. Furthermore, in **Chapter 3,** I found a minor link of the oscillation to performance; older adults who showed greater reductions in reaction times also exhibited greater increases in this beta power synchronisation. Thus, the present findings provide a sufficient basis for interpreting the presently detected beta oscillations as reflective of either motor or cognitive control changes, in this case accompanying an attentional task.

In summary, the two main oscillatory patterns detected in **Chapter 3** are generally consistent with an account of disengagement during sustained attention. This then matches the expectation set at the end of **Chapter 2**. Yet, as mentioned, there was little association between the patterns and behaviour, beyond a minor link of the task-related beta to changes in reaction times and age strategies. This account should thus be interpreted with some caution due to the absence of actual behavioural effects (Krakauer et al., 2017). More importantly, an interpretation of the decline as an attention-related process contrasts with an ambitious and spurious label of fatigue markers, as will now be discussed.

Elusive relation of oscillations to fatigue

In addition to a link to sustained attention, the oscillatory patterns described in **Chapter 3** resembled some previously identified markers of fatigue. They further coincided with an increase in subjective fatigue induced by time-on-task and their baseline levels also reflected baseline differences in state fatigue found between the age groups. However, correlations failed to establish a direct link between the patterns and the rise in subjective fatigue or performance decline. This lack of connection contrasts with the previous links found between fatigue and both pre-stimulus alpha (Aziezah et al., 2020; Bazanova & Vernon, 2014; Krigolson et al., 2021) and task-related beta (Krigolson et al., 2021; Pakenham et al., 2020). I also failed to find changes in the theta band, considered to be a part of a prospective fatigue marker (Arnau et al., 2021; Bazanova & Vernon, 2014; Krigolson et al., 2021; Talukdar et al., 2019), with frontal theta possibly one of the top candidates (Pessiglione et al., 2025).

Conceding that the patterns did not reflect fatigue, it may still be argued that the patterns indicated an onset of fatigue, since oscillations may carry multiple functional meanings (Beste et al., 2023; M. X. Cohen, 2011). However, my experiment did not provide enough evidence that fatigue was involved as a driver of any change in the pattern. There could be two reasons for this, namely that a) the pre-stimulus alpha synchronisation can only be changed by exclusively exogenous means and b) that the exact multi-component nature of the oscillation is not understood sufficiently to separate its fatigue-related component.

Other experiments have induced pre-stimulus alpha oscillation by using external stimuli instead of inducing fatigue. These findings include a study where laboratory room illumination level increased parietal EEG alpha activity in a sustained attention task, even affecting performance on the task (Ru et al., 2019) and spontaneous alpha increased in response to lower luminance on a critical flicker frequency task (Benedetto et al., 2018). Further findings have also suggested that cooler colours reduce alpha and increased reaction times (Min et al., 2013). Auditory influences on resting state alpha have likewise been noted both through music stimulation (Jäncke et al., 2015) and in phasic alerting (Wiegand et al., 2014, 2017). Another study suggested that as little as 50mg of caffeine exogenously suppresses EEG alpha power within 30 minutes of ingestion (Ajjimaporn et al., 2022).

The second reason for the unclarity about the alpha oscillatory change is that it is comprised of multiple, not fully understood components (Barzegaran et al., 2017). These include the known effects of other signals such as ERPs (Krigolson et al., 2021; Studenova et al., 2023), in addition to a plenitude of not fully explored biological components (Balestrieri et al., 2025; M. X. Cohen, 2011). This is especially relevant for explaining any age differences in the alpha synchronisation, which have previously been described as reflecting an uneven age-related decline of the different components (Knyazeva et al., 2018). Furthermore, Benwell et al.

(2019) reported that time-on-task also affects these components at different rates. Modelling work has likewise suggested that frequentist analysis of time-on-task effects may even introduce additional components as artefacts (Shinn, 2023). These reflections all suggest a presence of other components in the patterns and the limited understanding of their mechanisms alongside too many alternative explanations, preventing attributing them to fatigue.

In conclusion, I caution against interpreting the existing candidate oscillation patterns as markers of fatigue. **Chapter 3** showed that time-on-task changes in neural patterns do occur during demanding tasks, but their full functional meaning needs further investigation. Despite the co-occurrence of the candidate patterns with fatigue-associated events, the evidence for a strict, therapy-relevant link to fatigue remains inconclusive.

The role of age and motivation in sustained attention

The present studies found that participant motivation led to a distinct reduction in beta synchronisation (**Chapter 3**) and most notably drove the choice of task performance strategy (**Chapter 3, Chapter 4**). Concretely in **Chapter 4**, I showed that the choice of task strategy in the SART can be altered by manipulation of motivation both within participants through a monetary initiative and between participants by targeting a more motivated group (older adults). With regards to the older group, the chapters continued to replicate a strong age effect in behaviour: an advantage in accuracy (**Chapter 2, Chapter 3**), longer reaction times (**Chapter 2, Chapter 3**, **Chapter 4** tentatively – see Appendix 3) and ability to improve performance (**Chapter 4**). In addition, **Chapter 3** gave an indication and **Chapter 4** directly showed that this effect is driven by motivational differences.

In **Chapter 3**, I replicated the commonly known lower pre-stimulus alpha oscillation levels and the associated aperiodic components of older adults (Cesnaite et al., 2023; Turner et al., 2023). Likewise, I showed a beta oscillatory pattern, interpreted as reflective of a more committed baseline task strategy (Dang et al., 2018; Lara et al., 2014; Statsenko et al., 2020; Vallesi et al., 2021).

The account of higher intrinsic motivation in older adults provides a further perspective on the reasons for these oscillatory age contrasts.

In fact, a motivational account of age advantages in performance was highlighted in a recent meta-analysis investigating age effects in memory performance (Swirsky et al., 2023) and also discussed in **Chapter 1.** More specifically, motivation was found to have a particularly high impact on younger compared to older participants when the employed initiatives were financial (Bowen et al., 2020; Geddes et al., 2018). Older participants conversely gained more from a socioemotional reward (Friedman & Castel, 2013). Ryan and Campbell (2021) likewise suggested the nuance, discussing a partial preservation of ability in older age contingent on task goals. The findings of Chapter 4 matched this account since the older participants preferred the experiment's intrinsic value. This was reflected in their higher baseline motivation and performance, matching the young sample. They likewise showed a ceiling in motivation in their reduced reaction to a further monetary reward.

The present findings thus point to the socioemotional selectivity theory of increased motivation in older adults (Carstensen, 1993). According to this view, healthy older adults are intrinsically motivated to participate in research, a tendency attributed to their pronounced sensitivity to emotionally salient stimuli (Carr et al., 2022). According to the theory, they consider time to be a limited resource and thus seek positive and meaningful experiences in order to utilise it effectively[6]. Recruiting strategies for older participants rely on their increased reactivity to motives such as brain health advocacy, furthering of science and even an ability to draw increased entertainment value from experiments and socialisation with the researcher (Huxhold et al., 2022). The chance of proving retained cognitive health was also suggested to motivate better older adult performance. An opinion survey of 88 ageing researchers highlighted that older

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[6] Empirical findings have previously associated the salience of mortality with goal reorientation. Death awareness reoriented task-goals (Kosloff & Greenberg, 2009) and lead to diminished focus on finances in individuals with near-death experience (Kinnier et al., 2001). It incites a shift from the pursuit of material ends to an authentic engagement with life, as famously outlined in Martin Heidegger’s existentialist philosophy (Lavine, 1984, p. 232).

adults consistently showed higher concern with their performance and desire to prove their worth, explaining their increased baseline motivation levels (A. D. Ryan & Campbell, 2021). Older adults' motivation to partake in research thus sets them apart from the young adult sample who are otherwise prolific in general psychological research (Henrich et al., 2010). In contrast to older samples, young adults in a university environment already saturated with frequent cognitive testing through coursework seek no additional challenge to prove their performance ability (A. D. Ryan & Campbell, 2021) and have shown low effort, leading to suboptimal performance (DeRight & and Jorgensen, 2015).

In their meta-analysis, Swirsky et al. (2023) highlight that not all findings are consistent with the socioemotional account of age differences in motivation. Other proposed explanations are that high motivation may be driven by cultural or generational differences (Badham, 2024; Campbell et al., 2015; Van Rossem, 2021) or a purely biological mechanism arising from the ageing processes (Bourisly & Shuaib, 2018; Vallesi, 2016). These alternative explanations for the age effect were not explored in the present thesis and may instead be tested in future research.

While the interplay of motivation and age effects is now widely discussed in the working memory literature, I now highlight this role of motivation as a driver of the age effect in sustained attention. Based on this thesis, future research should consider motivation as a strong co-variate in cross-sectional studies focusing on young and older samples in sustained attention and other paradigms.

Limitations and future directions

Investigating motivational and age effects

Research on sustained attention across age groups can gain from the approaches presented here, provided their key limitations are carefully considered. The approach used in the present work was a within-subject manipulation of motivation, leading to a robust change in both subjective and objective measures in **Chapter 4**. The design of motivational manipulations still requires careful consideration, though, as their effects remain inconsistent (Wójcik & Nęcka, 2024). Although **Chapter 3** included a motivational manipulation with a control condition, which was a valuable addition, but lead to a lowered statistical power in return. On reflection, the design of Chapter 3 was suboptimal in incorporating too many variables (age, fatigue, motivation, multiple EEG analytical approaches). A future investigation should consider the complexity of the interaction of age and motivation with any additional factors in light of the available sample size. As a suggestion for an interesting expansion of the design, Ryan and Campbell (2021) have implied that extreme motivational initiatives would be as effective in older as in young participants. This is a promising, but untested feature for consideration in future work.

Chapter 3 and **Chapter 4** were carried out in a traditional laboratory context. This environment may be an exogenous influence on the perceived value of the experiment, as discussed in **Chapter 1**. Conducting naturalistic experimentation may help to reduce this effect. One option would be testing of participants in an environment lacking implicit motivational cues, such as at home or through more familiar tasks (Hockey, 2013, Chapter 5). Some pioneering work has suggested such effects when testing executive control of older adults (Campbell et al., 2015). Recording participant data through public engagement may also be an option to reach more diverse samples outside of the laboratory environment (Turner et al., 2023). While online experiments also give access to more diverse samples, the preserved behavioural age effect described in **Chapter 2** warns that online research may not reduce the motivation inherent in the testing of older adults.

In an attempt to simulate a false end to the experiment in **Chapter 3**, both pre- and post-state measures of fatigue were administered prior to the motivational manipulation. Retrospectively, an additional probe of mood states after the manipulation would have benefited the subsequent attempt to differentiate between changes in motivation and fatigue, later emerging in **Chapter 4**. Capturing introspective motivation and fatigue remains a notable challenge for research (Pessiglione et al., 2025). Here, frequent probes were avoided due to their additional effects on behaviour (Seli, Carriere, et al., 2013; Wiemers & Redick, 2019), but relying solely on pre- and post-experimental subjective measures still leaves considerable room for improvement.

The emergence of the beta oscillatory pattern related to motivational effects in **Chapter 3** merits follow-up in future work. However, the current approach came across a lot of limitations that future research should consider. Significant changes would need to be made to the paradigm investigating the connection of brain function to the motivational effect: Here the designs of the SART trials in **Chapter 3** and **Chapter 4** did not align. The short trial length of the SART version in **Chapter 4** would interfere with processing EEG signal trial-by-trial. The dynamic changes in task parameters arising from the titration may further impede statistical power. The motivational section of **Chapter 3** had a control condition, while the experiment in **Chapter 4** featured the same manipulation in all participants. Future research should formulate a new design addressing these inconsistencies and so bridge the gap in knowledge about brain and behaviour links in motivated sustained attention performance. Future work may also consider complex, naturalistic conditions (Welke & Vessel, 2022) or standardised task batteries (Hassan et al., 2024). Another alternative would be to more concretely isolate brain areas associated with the pattern via the use of a combined EEG-fMRI approach (Y. Guo et al., 2023).

Continued search for biomarkers of fatigue

Since its conception, EEG has been recognised for its potential to monitor brain signal in real time and detect its disturbances (Loomis et al., 1938). On the individual level, EEG has been used to detect sleep pathology (Light et al., 2018; Putilov & Donskaya, 2015) and epileptic seizures (Alvarez & Rossetti, 2015). Relating to the success of these EEG applications, research efforts have focused on the early detection of fatigue (Correa et al., 2013; Lin et al., 2019; Sun et al., 2014). Knowledge of reliable group-level markers of fatigue has been proposed to revolutionise areas such as assisted driving (Correa et al., 2013; Xu et al., 2018), technical work (Bernhardt et al., 2019), piloting (Roach et al., 2012) or, in the long term, clinical diagnosis (Othmani et al., 2023) and treatment using neurofeedback.

Despite these hopes, the work in this thesis highlights the ongoing gap in the knowledge of group-level fatigue markers. The present investigation did not find a link between known candidate brain patterns and subjective or objective measures of fatigue. While it is important to recognize the limitations of the thesis's empirical chapters, they still highlight the ongoing challenge in identifying concrete EEG markers in neurofeedback. As I discussed in **Chapter 1**, research findings point to an effect of neurofeedback, but targeting specific frequencies does not commonly impact their associated processes (Hesam-Shariati et al., 2022). Neurofeedback either only induces changes in the targeted EEG bands (He et al., 2020), or at times general behavioural improvements (Chiasson et al., 2023). In contrast, only a direct link of a targeted marker to a behavioural outcome can lead to reliable therapeutic treatments (Barack et al., 2022).

Ongoing efforts to enhance neurofeedback research standards aim to clarify its effect size. Suggestions for improvements include pre-registration of research questions, increasing sample size through open science projects, developing better control measures and control groups, using tightly defined protocols and defining clear outcome measures (Ros et al., 2020; Sorger et al., 2019; Taschereau-Dumouchel et al., 2022). In future research, control conditions should be chosen very carefully to bridge the gap between the targeted markers and the change in the specified mental process. To date, the ability to successfully target fatigue with neurofeedback remains an experimental and tentative possibility. Thus neurofeedback should continue to be seen as having, at best, limited effects in the treatment of fatigue even if targeting its commonly associated frequency bands.

On the other hand, individually-tuned algorithms may prove to be a sounder long-run approach to neural interventions. Existing systems reach better detection ability by calibration to patterns specific to each individual, as seen in the current use of deep learning models (H. Li et al., 2022) or BCI systems (dos Santos et al., 2023; Karim et al., 2023; Wang et al., 2024). Notably, the features used by the algorithms extend far beyond canonical frequency bands. This also parallels calls to expand the understanding of the oscillations' functional role beyond pre-defined bands (Balestrieri et al., 2025). With recent developments in the utilisation of additional features of the signal, such as the aperiodic components (Donoghue et al., 2022) also analysed in this thesis, the future holds many interesting avenues for detecting fatigue from brain signals, beyond neurofeedback.

This invites a broader reflection on the effort to establish EEG markers of pathology. While oscillations are widely utilised as measurements of mental processes, their role as a causal condition of behaviour (Barack et al., 2022; M. X. Cohen, 2011) remains theoretically disputed (Barack et al., 2022; van Bree et al., 2025). Limited advances in establishing strict causal relationships between oscillations and behaviour contrast with more successful findings from other areas of neuroscience focusing on the causal effect of single neurons (Stiefel & Ermentrout, 2016). These studies provide much stronger evidence that neural activity is a causal driver of broader biological processes (Esghaei & Daliri, 2014; Tremblay et al., 2015), and have led to effective interventions, as seen in highly localised deep brain stimulation (Meyer et al., 2024). However, the success of such approaches is largely confined to the level of single neurons (Haider et al., 2016; Okun et al., 2010). Although oscillations emerge from neural activity, research has still not fully mapped how an oscillation scales from single-cell to system level (M. X. Cohen, 2017; Stiefel & Ermentrout, 2016). In turn, theorists disagree about the degree of generalisability of a causal claim from Local Field Potential (LFP) to Global Field Potential (GFP), such as EEG oscillations. Larger-scale causal inferences from lesion studies offer valuable insights into bridging the gap between local and global effects, but are also limited by confounds, such as neuroanatomical damage (M. X. Cohen, 2011). As a result, most GFP studies are then constrained to proposing associative, rather than causal, links (Krakauer et al., 2017). Yet, establishing oscillations as causal conditions of behaviour is essential if they are to be considered true markers, as a marker must reliably indicate a change in the process it signifies. This is inconsistent with my key findings in **Chapter 3**, where the candidate signals appeared independent from subjective (and objective) fatigue. The present findings therefore cannot support more than an epiphenomenal relationship between candidate oscillatory markers and fatigue. Here, epiphenomenal refers to oscillations acting as passive reflections of core causal processes in the brain (Barack & Krakauer, 2021; H. Smit & Hacker, 2014). Accordingly, I encourage continued exploration of EEG signal dynamics as part of the broader scientific effort to map brain function (M. X. Cohen, 2017).

Covid

The direction of this dissertation was affected by the emergence of the Covid-19 pandemic. This had a decisive influence on data collection and diverted me from the originally envisioned samples. The first behavioural study had to be moved online due to the inability to test face-to-face. This, becoming **Chapter 2**, revealed a strong age effect, which was further utilised as a means to shift focus from an envisioned clinical sample (post-stroke fatigue patients) to older adult (control) groups. Despite this, data collection for the samples, particularly the older adults in **Chapters 3**, was still affected by additional Covid restrictions and the need to rebuild the School's collapsed older adult participant pool. Despite this, re-focusing the thesis brought to light novel findings relating to age and motivation, which still allowed a discussion of the original aim of informing neurofeedback alongside considering the underlying impacts of motivation.

Conclusion

Task performance and brain activity patterns were previously suggested as indicators of fatigue, leading to their use as targets in neurofeedback interventions. The experiments in this thesis sought to clarify the extent of this connection. The resulting tests failed to find a strong link during sustained attention. While I identified a prospective coupling of fatigue to a vigilance decrement in **Chapter 2**, I also found a strong connection to another, better-known factor in sustained attention: age. Further testing of a prospective decrement over a more extended time period in **Chapter 3** revealed its independence from patterns of brain activity typically associated with fatigue, namely a rise in pre-stimulus alpha synchronisation and task-related lower beta synchronisation. The changes instead corresponded to age and motivational effects during the sustained attention task, rather than to subjectively reported rises in fatigue. The final experiment in **Chapter 4** confirmed that motivation, rather than fatigue, drove changes in task performance. I conclude that the account of fatigue as a dynamic subjective time-on-task rise coupled with readily available metrics is simplistic (as per **Chapter 3** and **Chapter 4**) and requires further understanding and continued development of adequate research designs before conversion into an applicable neurofeedback intervention. The experiments instead highlight motivational and age-related drivers of performance and associated oscillatory signal change during sustained attention as a topic for prospective research.

Accompanying Material

Appendix 1

Additional analyses pertaining to **Chapter 3.**

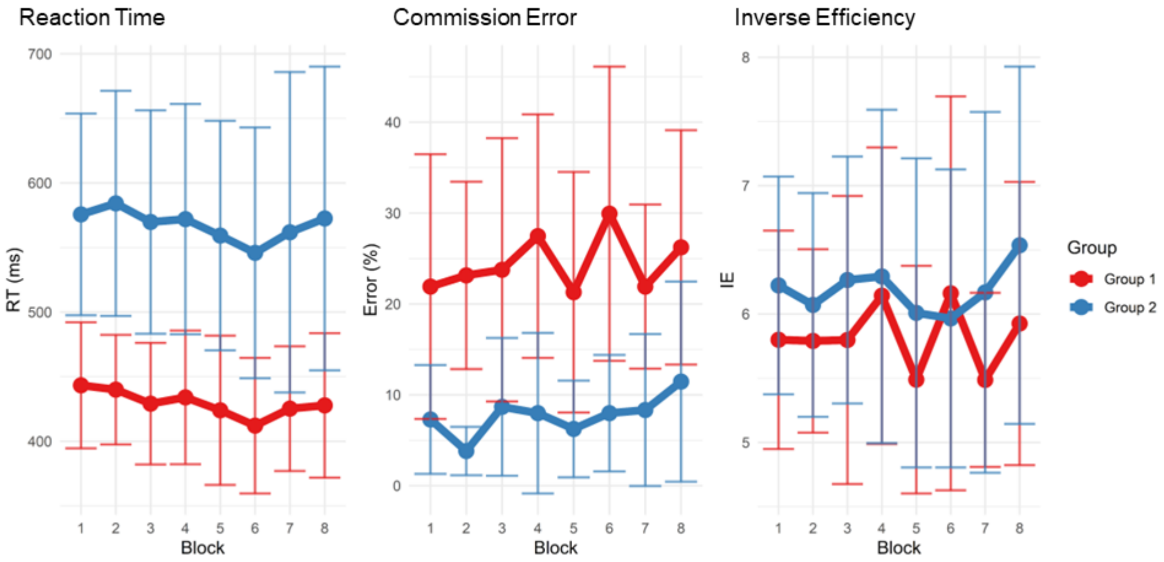
Speed-accuracy trade-off

Analysing age and time differences in performance of both age groups revealed a pattern of high reaction times and low commission error in older adults, with the opposite pattern of low reaction times and high commission error in young participants. Due to their inverse nature, an exploratory analysis was undertaken to compare these alongside a single measure. Previous findings investigating speed-accuracy trade-offs between accuracy and reaction time used the metric of inverse efficiency to calculate a single performance metric reflective of their mutual relationship (Bruyer & Brysbaert, 2011; Statsenko et al., 2020).

To obtain block-level inverse efficiency scores, log-transformed reaction times were averaged across each participant. Subsequently, these averages were divided by commission accuracy, determined by subtracting commission error from 1.

A two-way ANOVA was conducted to examine the effects of block (first, last), group (1 = young, 2 = older) and their interaction on inverse efficiency. The results showed no significant main effect of block, $F(1, 32) = 1.08$, $p = 0.307$, $\eta^2 = 0.011$ and newly, the main effect of group was now not significant, $F(1, 32) = 2.91$, $p = 0.097$, $\eta^2 = 0.058$. The interaction between group and block was also not significant, $F(2, 32) = 0.20$, $p = 0.655$, $\eta^2 = 0.002$. Collectively, the results in performance alongside the original findings are depicted in Supplementary Fig 2.

While the index of inverse efficiency was not pre-registered, its notable stability in both age groups further complements the findings about their different behavioural strategy. It signifies that both groups were similarly efficient, but had a different emphasis in their approach to the task. It also corresponds to the lack of group differences in subjective change, showing a similar efficiency over time.



Supplementary Fig 1 Mean reaction time, commission error and inverse efficiency in both experimental groups. (1 = young, red, 2 = older, blue) across 8 blocks with standard deviation bars.

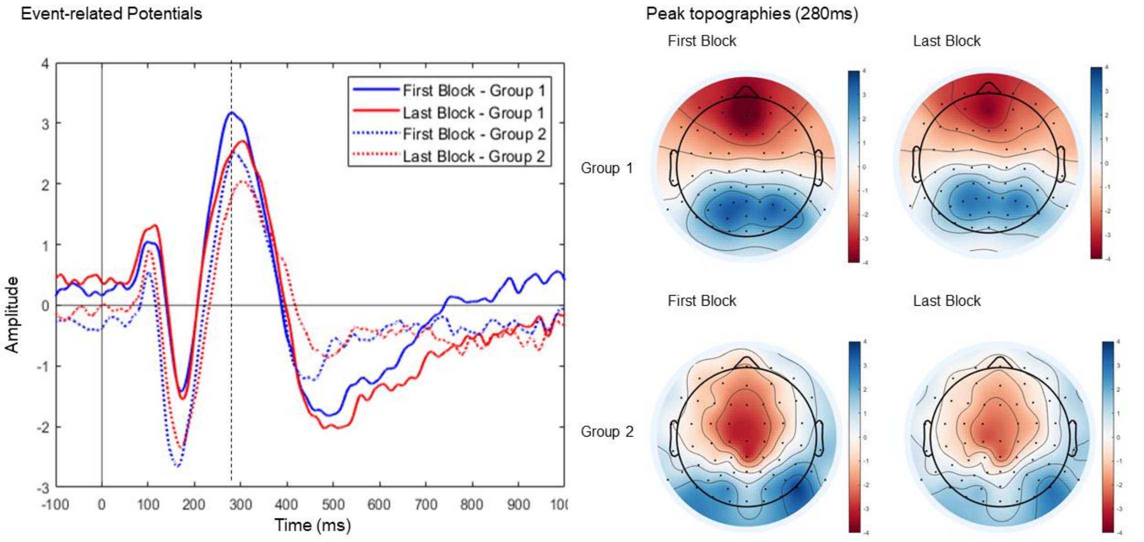
ERP analyses

As a detected cluster reflected early task-related alpha desynchronisation, it was further investigated for its possible connection to the P300 ERP component (Picton, 1992; Studenova et al., 2023). Aside from oscillations, changes in the P300 ERP component have been associated with subjective fatigue (Krigolson et al., 2021), as well as time-on-task in sustained attention paradigms (Z. Guo et al., 2016; Hart et al., 2012), and ageing (Kaufman et al., 2016). We thus mapped the P300 ERP-changes across the factors of interest (time-on-task, fatigue, the motivational manipulation), as well as age group.

ERPs from the same time window of the signal coming from the highest un-lateralised electrode, detected as significant by the cluster permutation (Fz), were compared in their group peak maxima. A 2x2 ANOVA was conducted to examine the effects of block (1, 8) and group (younger, older), and their interaction on the baseline-corrected signal. The resulting model was not significant, F(3, 56) =0.56, p = 0.65. Furthermore, the same signal was also traced into the motivational condition, compared in a 2x2 ANOVA collapsed across age, examining the effect of block (8, 9) and motivation (non-motivated, motivated).

The resulting model was significant F(3, 56) = 3.47, p = 0.02. There was no effect of block (ß = -0.21, t = -0.40, p = 0.69), but the non-motivated group had a higher P300 amplitude (ß = -1.24, t = -2.06, p = 0.04), with no interaction (ß = -0.19, t = -0.23, p = 0.82). A test was also run to detect an effect of trial type (commission, omission) and age group (young, older) on the P300 amplitude. The overall model was significant F(3, 64) = 7.70, p < 0.001. The test revealed no effect of trial type (ß = -0.16, t = -0.22, p = 0.83), a higher P300 amplitude in young participants (ß = 2.41, t = 3.31 p = 0.002) and no interaction (ß = 0.13, t = 0.13, p = 0.90). The findings are presented in Supplementary Fig 1.

Regarding the P300, the analysis only found a robust effect of age on P300 amplitudes. P300 was higher in the younger compared to the older age group, as consistent with much ageing literature (Tsolaki et al., 2015). Yet we failed to detect the established task-related pattern of an occipito-parietal P300 amplitude decrease, associated with either effortful processing (Hart et al., 2012) or fatigue (Egner & Gruzelier, 2004; Hart et al., 2012; Krigolson et al., 2021; Kustubayeva et al., 2022).



Supplementary Fig 2 Effect of time and group on the Fz P300 ERP across time (ms). Showing the difference between the first and last block (blue, red) and groups (1 = young, solid line, 2 = older, dashed) as well as the associated topographies. The dashed line indicates the inferentially tested latency.

Covid analysis

The sample contained 10 participants (of 40) who reported testing positive for Covid-19 in the past 3 months. In keeping true to a pre-registered aim of the study, we tested the effect of the recent experience of Covid on the key subjective and behavioural measures. A Wilcoxon rank sum exact test was run due to disbalanced group sizes.

Recent experience of Covid did not predict a difference in participant reaction times, $W = 146$, $p = 0.09$, participant nogo accuracy, $W = 58$, $p = 0.07$, baseline state fatigue, $W = 73$, $p = 0.22$ or baseline state mind wandering, $W = 158$, $p = 0.81$.

Appendix 2

Subjective mental state and fatigue, an investigation into possible paradoxical effects.

Background

In past experiments, fatigue has been induced via demanding tasks (Z. Guo et al., 2016). Nonetheless, a change in state may still arise during experimentation, even in the absence of demanding tasks, if participants adjust their performance in response to perceived expectations, described as demand characteristics (McCambridge et al., 2012). Pessiglione et al. (2025) also recently underlined unreliable introspection of fatigue state. As a result, a concern with the measurement of subjective state change in our own experiment (Hanzal et al., 2024a) led to a separate confirmation test of task-specificity of rises in subjective fatigue.

Based on our previous data and anecdotal findings, there was some indication that even a non-fatiguing task will elicit a detectable change in state fatigue levels compared to baseline. A reliable rise in subjective state fatigue should be task-specific (Behrens et al., 2023), as opposed to being induced by the experience of being experimented upon alone. We thus tested the effect of a simple task of watching entertaining videos in a laboratory environment on the report of fatigue.

Methods

The study was pre-registered on OSF (https://osf.io/fybc9). To achieve a minimal informative sample, an inclusion of 12 eligible participants was determined by a power calculation using the ‘pwr’ R (R Core Team, 2013) package to allow the detection of a large effect d = 0.8 with a one-sided hypothesis (J. Cohen, 2009). A large effect was based on a related pilot finding (Hanzal et al., 2023), where an undemanding 50-minute-long task of watching a documentary showed a difference between initial and final state fatigue levels greater than one standard deviation in overall state change.

To pick appropriate non-fatiguing stimuli, three entertaining Youtube videos (Wurtz, 2017; PBS Idea Channel, 2017; Vsauce, 2015) were chosen to be displayed to the participants, following a previous similarly conceived controlled condition (Hanzal et al., 2023; O'Keeffe et al., 2020). The videos totalled 50 minutes and 28 seconds in duration. All were popular (Silvianetri et al., 2022) informative videos about scientific concepts meant to engage the participants. In addition, the participants were administered the Visual Analog Scale (VAS) for fatigue (Lee et al., 1991) before and after watching the videos. Then, the participants were partly debriefed using the following text:

'Thank you very much for your participation! In order to collect valid data, we could not be explicit about the focus of this study. This was unavoidable, so below is the information regarding the study. Please read it carefully.

The experiment's aim was to investigate "demand characteristics", or the experience of taking part in an experiment and its impact on subjective mental states. We administered you an identical questionnaire measuring momentary fatigue levels before and after the experiment. The experiment was not particularly fatiguing, so any experienced rise in subjective fatigue levels may have been due to performance expectations.

If you became suspicious of the nature of the experiment, you are still fully entitled to the payment, but we will not consider your data in the main analysis.'

They were then probed by two further questions to confirm suspicion:

Did you suspect this to be the case?

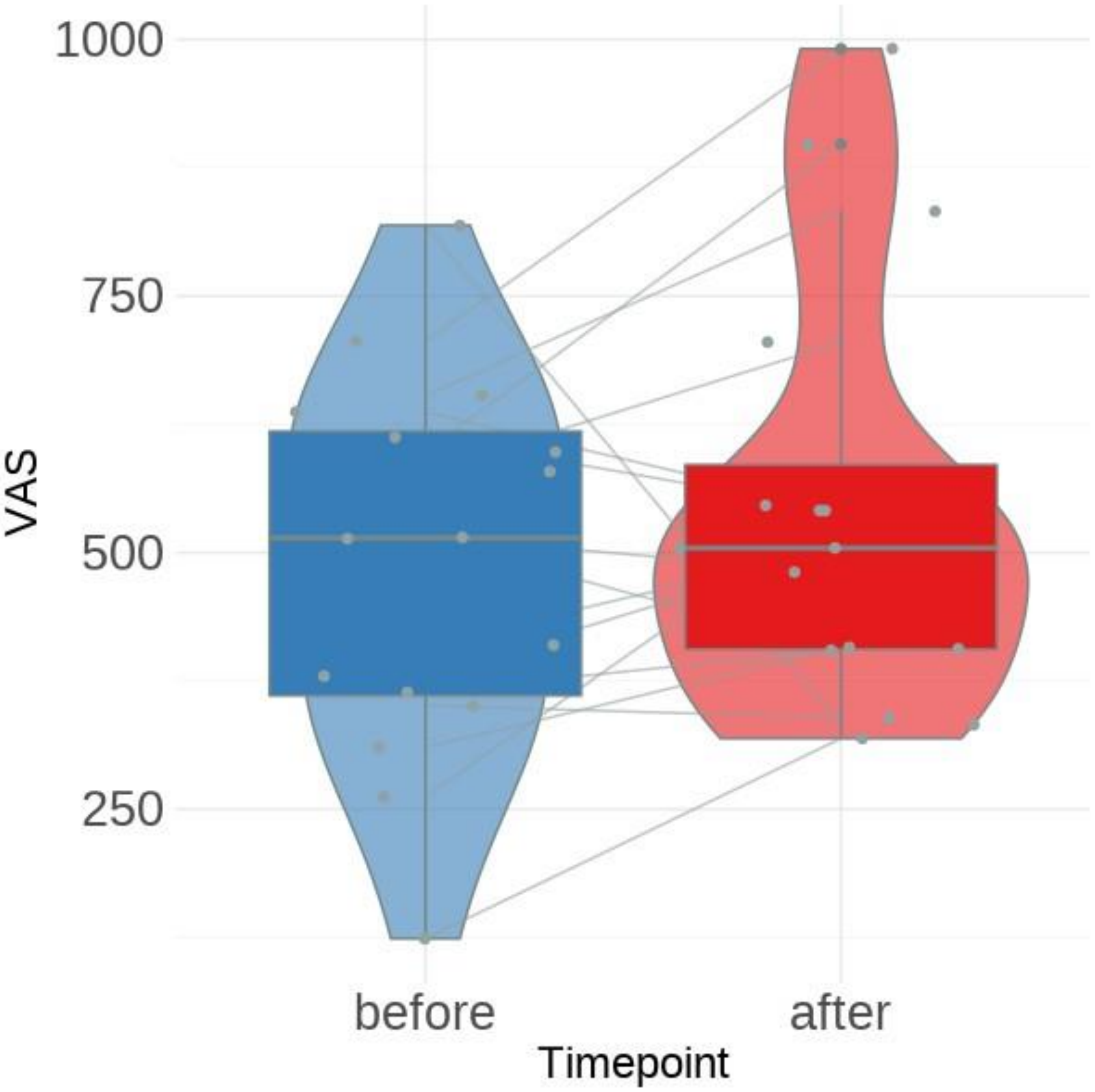
Please describe what you thought this experiment was about:

Participants then received full debrief and compensation for their participation, similarly to the experiment in **Chapter 3**. If they showed any suspicion of bias as detected in the answers to the follow-up questions, their data was excluded from the analysis.

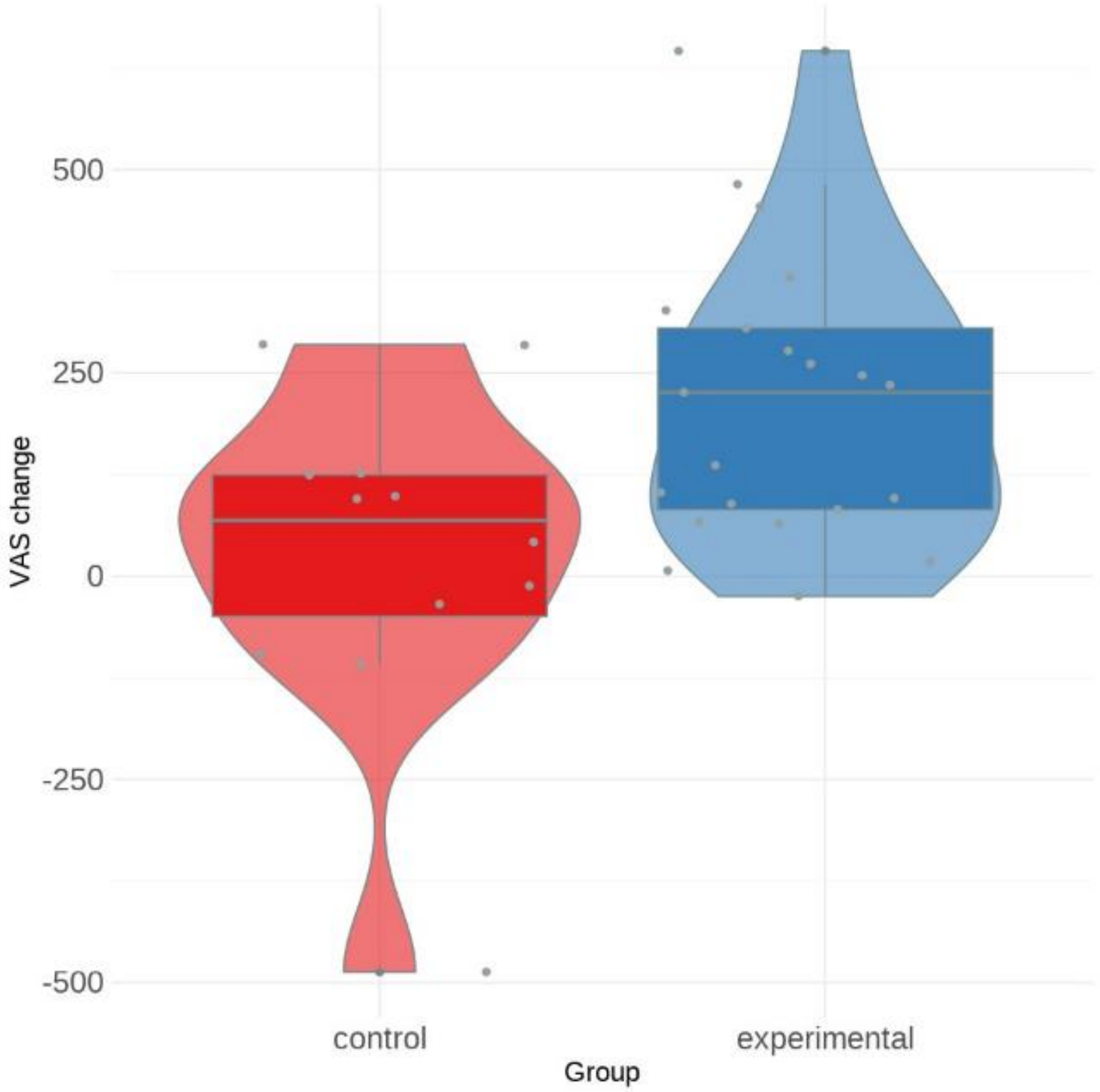
Results

16 participants in total were recruited. Later, 4 were excluded based on screening for demand characteristics (2 declared these, 2 based on their qualitative report), nevertheless, re-runs of the main tests including these participants lead to the same results. The VAS change scores before and after the experiment were not significantly different based on a Welch one sample t-test, t(22) = 0.36, p = 0.36, even when including participants suspicious of their own demand characteristics, t(30) = 0.83, p = 0.21, indicating that the experiment did not induce subjective fatigue change. The test is depicted in Supplementary Fig 3.

A comparison of VAS change in this subjective scale sensitivity study and the VAS change in the participant sample from **Chapter 3** showed a notable difference, t(50) = 8.10, p = 0.006, with participants in **Chapter 3** showing much higher levels of VAS change. The effect was present even with the inclusion of participants suspicious of their own demand characteristics, t(54) = 6.58, p = 0.01. Or with the exclusion of older adult participants in **Chapter 3** from the comparison, t(30) = 7.6, p = 0.01. The difference between the experiments is depicted in Supplementary Fig 4.



Supplementary Fig 3 Stable pre- and post- fatigue levels in an easy task. (the comparison here includes all 16 participants).



Supplementary Fig 4 Changes in fatigue in two experimental groups. The young participants in the control experiment (control, red) showed practically no change, even in those with demand characteristics detected. In contrast, the young participants (experimental, blue) in the EEG experiment (Chapter 3) had a general increase in fatigue over a time window of the same length.

Conclusion

In summary, as opposed to the results regarding a rise in subjective fatigue in **Chapter 3**, a matched group of participants in a non-fatiguing task did not show a significant rise in subjective fatigue levels, even when controlling for the influence of demand characteristics. The findings help to illustrate the specificity of the detected rise in subjective fatigue to tasks more demanding than an easy control condition undertaken in a laboratory environment.

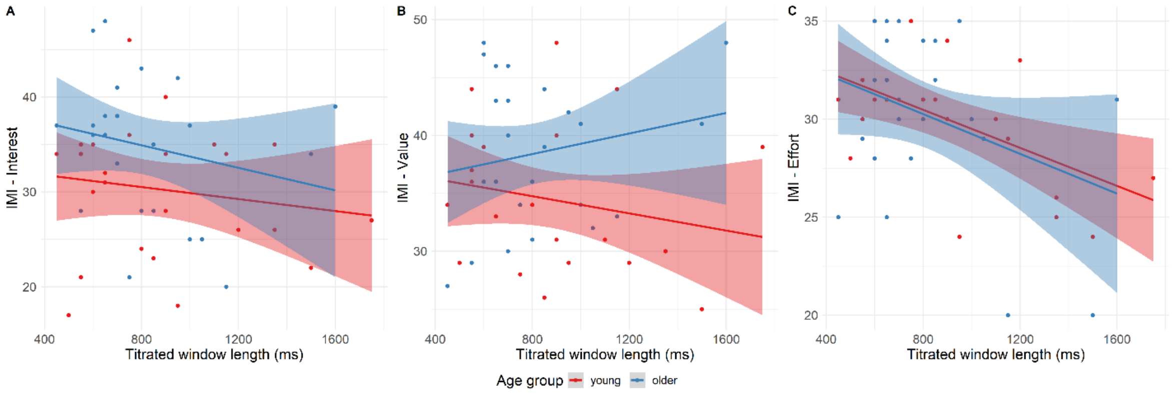
Appendix 3

Exploratory analyses of non-pre-registered relationships in **Chapter 4.** Further clarified links between performance and motivation in the two age groups.

Motivation and performance in the titration blocks

We additionally investigated whether the achieved titrated window length at the end of the titration period was predicted by baseline motivation, as measured by the IMI subscales. A multiple linear regression showed no relationship of IMI - interest and age to titrated window length [F(3, 46) = .48, R2 = .043, p = .571], as per Supplementary Fig 5A. Likewise, a multiple linear regression showed no relationship of IMI - value and age to titrated window length [F(3, 46) = .824, R2 = .051, p = .487], as per Supplementary Fig 5C. However, a multiple linear regression showed a relationship of IMI - effort and age to titrated window length [F(3, 46) = 4.37, R2 = .222, p = .009]. As indicated in a previous test, there was no main effect of age, t(46) = -1.625, p = .111, but a clear negative relationship with IMI - effort, t(46) = -3.17, p = .003, and no interaction, t(46) = 1.56, p = .126. This indicated that all participants who experienced more effort also achieved a shorter (and more difficult) titrated window length. This relationship is depicted in Supplementary Fig 5B.

Similar effects were found with overall accuracy and nogo accuracy, but are omitted for brevity.



Supplementary Fig 5 Relationship of age and motivational improvement during titration. Multiple linear regression testing the difference between age groups (young, older) in the relationship between the achieved titrated window length (ms) and motivational subscales. The plots show no relationship for IMI – Interest (A) and IMI – Value (B), but show that both groups achieved faster titrated window length with higher ratings of IMI – Effort (C).

Age-specific strategies during titration

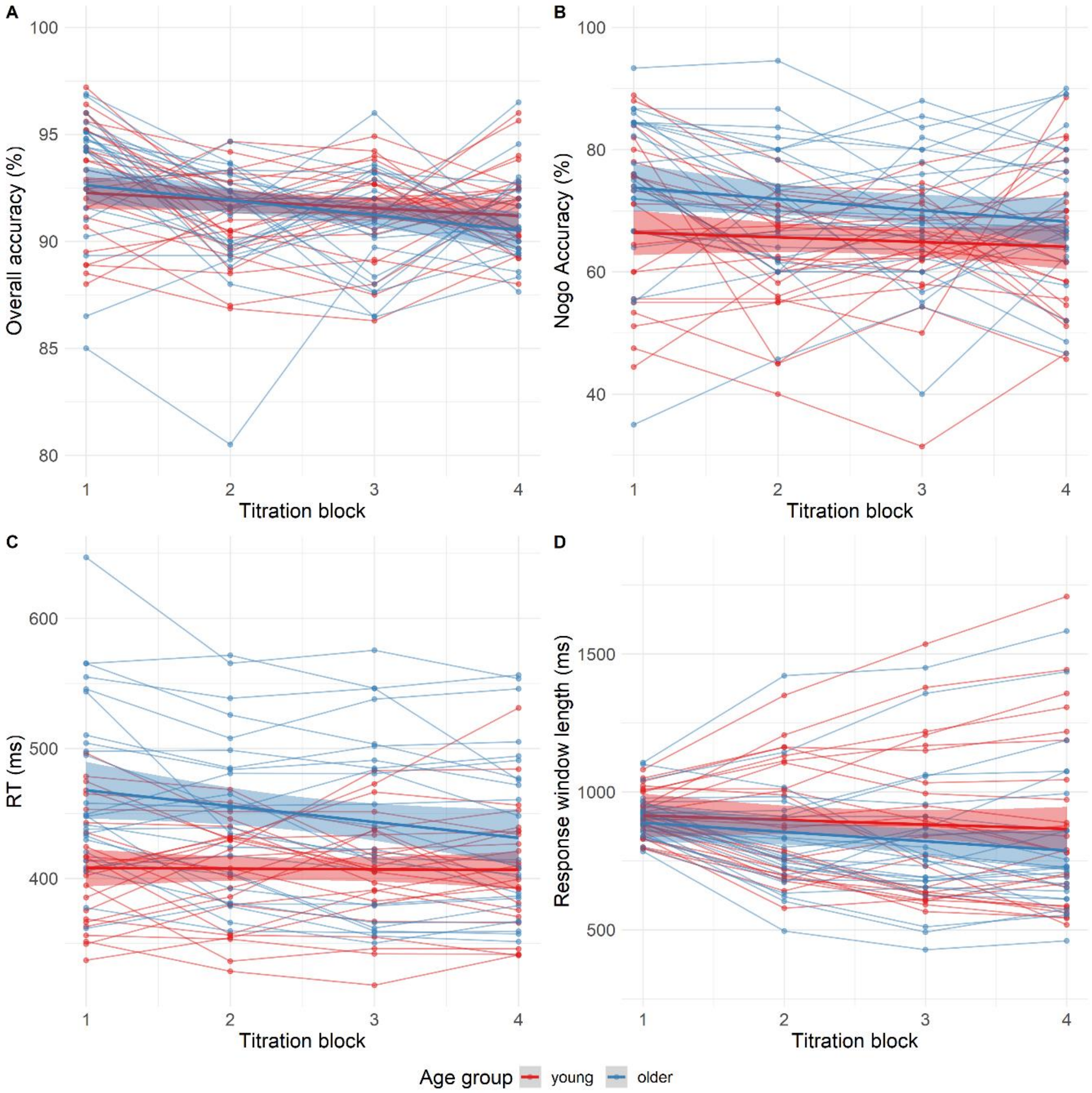
Because the age groups showed no differences at baseline, they were compared across the entire titration period across its four blocks to incorporate further trials and increase statistical power. Young adults had overall faster response reaction times over the titration period (mean = 406.12ms, SD = 104.78ms) than older adults (444.78ms, SD = 120.27ms). Nogo accuracy over the titration period of the young (mean = 65%, SD = 8.04%) participants was marginally lower than older participants (mean = 70.90%, SD = 10.10%).

A multiple linear regression [F(3, 196) = 4.27, R2 = .047, p = .006] showed no effect of age on overall accuracy, t(46) =.82, p = .415, as well as no effect of time, t(46) = -1.62, p = .108 and no interaction, t(46) = -1.10, p = .275, see Supplementary Fig 6A.

A multiple linear regression [F(3, 196) = 5.48, R2 = .078, p = .001] showed that older adults had higher nogo accuracy t(46) = 2.14, p = .034, but there was no effect of time, t(46) = -.752, p = .453 and no interaction, t(46) = -.752, p = .453, see Supplementary Fig 6B.

A multiple linear regression [F(3, 196) = 12.12, R2 = .157, p < .001] only showed that older adults had higher reaction times overall, t(46) = 3.67, p < .001, but that there was no effect of time, t(46) = -.298, p = .766 and no interaction, t(46) = -1.58, p = .116, see Supplementary Fig 6C.

A multiple linear regression for the effect of age groups and time on response window length was not significant [F(3, 196) = 2.034, R2 = .030, p = .110] but Fig 6D still descriptively suggests that participants in both age groups followed diverse courses over the titration period.



Supplementary Fig 6 Age-specific behavioural differences. Considering the titration period (25 minutes), the two age groups (young and older) did not differ in their overall accuracy (A). But older participants were more accurate on nogo trials (B) and slower (C), without time-on-task effects (differences between blocks 1-4). The groups did not differ in their titrated window lengths (D), although there was high variability in the titrated window lengths.

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