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Dynamic oscillatory networks predict individual differences in cognition

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Abstract

Humans have evolved great cognitive abilities that let them perceive, remember, and utilize the rich information they are surrounded with. Cognition can be divided into memory-related processes, which encode and maintain sensory information, and the executive functions, which control the mind's access to this information in a goal-driven manner. Previous research has associated cognitive functions with various changes in rhythmic neuronal oscillations that provide a mechanism for regulation and temporal coordination of information processing across local and large-scale neuronal populations. However, there is a limited understanding of how individual and moment-to-moment variability in spatio-temporal patterns of neural oscillations might predict performance variability in cognitive tasks. In my thesis, I investigated oscillatory mechanisms underlying the variability in visual working memory capacity and cognitive flexibility to show how these dynamics relate to behavioral differences between individuals, using electroencephalography (EEG) and magnetoencephalography (MEG).

In Study I, we asked whether local neuronal oscillations and their large-scale network interactions predict the bilateral field advantage (BFA) in a visual working memory (VWM) task. VWM has a very limited maximum capacity, but this capacity can be larger if stimuli are presented bilaterally, leading to preserved task performance. In Study I, we investigated if spatio-temporal patterns of oscillatory modulations explain this BFA. We recorded brain activity with high-density EEG of subjects (n = 26, 14 males) performing a VWM task with uni- and bilateral visual stimuli. We found that the BFA was associated with early suppression of low-alpha to low-beta band amplitudes, and a subsequent increase in high-alpha and low-beta amplitudes. Additionally, we found a concurrent load-dependent interareal synchronization in the high-alpha band that connected prefrontal and posterior brain areas across the left and right hemispheres. The strength of these changes in oscillations correlated with better performance across the study cohort. In Study I, we therefore demonstrated that the electrophysiological basis of the BFA in VWM is both found locally and in interactions across the cortex, revealing differences in attentional deployment and enhanced interareal integration.

In Study II, we asked whether oscillatory mechanisms could explain individual variability in endogenous cognitive flexibility. To assess the neural mechanisms of un-cued endogenous task switching, we recorded MEG while subjects (n = 26, 15 males) performed the Wisconsin Card Sorting Test (WCST). In the WCST, participants need to sort cards by a changing and not explicitly instructed rule, requiring the ability to rapidly adapt behavior based on feedback and memory. We analyzed the dynamic oscillatory modulations associated with feedback-driven cognitive flexibility and the factors that underlie individual task-switching performance. We then implemented a sequential learning model to identify the impact of feedback sensitivity on oscillation dynamics and performance. Faster and more accurate task

switching was predicted by gamma band amplitude increases together with parietal alpha and beta band suppression following feedback. Additionally, sustained alpha desynchronization correlated with higher learning speed. These brain-behavior relationships were mediated by feedback responsivity, so that higher sensitivity to positive feedback explained modulations in the alpha- and beta-band amplitudes as well as theta and alpha phase synchronization, whereas sensitivity to negative feedback was mainly associated with larger gamma amplitudes. Lastly, we found increased theta-gamma phase amplitude coupling during switch trials to be associated with better performance. Our results from Study II demonstrate that un-cued task switching is characterized by local amplitude changes in the prefrontal and parietal cortex in all frequency bands, fronto-parietal alpha desynchronization and inter-areal theta band synchronization, depending on the individual's reactivity to different types of feedback, and further revealed the role of theta-gamma phase amplitude coupling in cognitive flexibility.

In these two PhD studies, I provide novel insights about the functional significance of neuronal oscillations for human cognition via tuning of local neuronal processing and modulation of the long-range information transfer between distal cortical regions. I also demonstrate the role of these dynamic changes in interindividual differences in VWM (Study I) and cognitive flexibility (Study II). Together, these findings improve our understanding of the complex and dynamic changes in brain activity that characterize human cognition.

List of original publications

This thesis is based on the following publications:

I. **Sattelberger, J.**, Haque, H., Juvonen, J. J., Siebenhühner, F., Palva, J. M., & Palva, S. (2024). Local and interareal alpha and low-beta band oscillation dynamics underlie the bilateral field advantage in visual working memory. *Cerebral Cortex*, 34(11), bhae448.

II. **Sattelberger, J.**, Haque, H., Mengxing, L., Simola, J., Palva, J. M., Halassa, M. & Palva, S. (2025). Neuronal oscillations underlie the preparative task switching in the Wisconsin card sorting test. *BioRxiv,* https://doi.org/10.1101/2025.05.19.654819.

Author's contributions:

I. This study was planned and designed by me together with Hamed Haque and Satu Palva. I finalized this study's experimental set-up in the EEG laboratory with Joonas Juvonen and then developed the psychological experiment. All EEG and MRI data from the participants (N=26) were recorded by me. I, together with Felix Siebenhühner and Joonas Juvonen, developed the Python code for the analysis of the EEG dataset. I then carried out the formal EEG data analysis including preprocessing, estimation of the functional metrics, statistical analysis, and visualization of the results. Further, I processed the MRI data of all subjects and analyzed the behavioral data statistically. I and Satu Palva wrote the manuscript together with the other co-authors and took care of the revision after peer review.

II. This study was conceptualized by me, Hamed Haque, Michael Halassa and Satu Palva. I performed the formal analysis of the MEG data including estimation of functional metrics, statistical analysis and visualization of the results. I carried out the behavioral analysis together with Mengxing Liu. I and Satu Palva wrote the manuscript together with the other co-authors.

The publications are referred to in the text by their roman numerals.

Abbreviations

ANOVA	Analyses of variance
BEM	Boundary element method
BFA	Bilateral field advantage
CT	Control network
DA	Dorsal attention network
EEG	Electroencephalography
fMRI	Functional magnetic resonance imaging
FP	Frontoparietal network
GS	Graph strength
HRs	Hit rates
iPLV	Imaginary phase locking value
IPL	Inferior parietal lobule
Lim	Limbic network
MEG	Magnetoencephalography
MNE	Minimum norm estimates
MRI	Magnetic resonance imaging
NCM	Noise covariance matrix
PAC	Phase amplitude coupling
PFC	Prefrontal cortex
PLV	Phase locking value
PPC	Posterior parietal cortex
RTs	Reaction times
S1	Sample stimulus
S2	Target stimulus
SM	Somatomotor network
TF	Time-frequency
TFR	Time-frequency representation
TP	Temporoparietal network
VA	Ventral attention network
Vis	Visual network
VWM	Visual working memory
WCST	Wisconsin Card Sorting Test
WM	Working memory

1 Introduction

The cognitive functions of the human mind have long interested philosophers and researchers. Already Aristotle (384-322 BC) conducted studies of the “rational soul” which he believed to set humans apart from all other living beings and to include two components: an information storage of all acquired concepts and an active agent that selects and combines ideas from this storage (Aristotle, ca. 350BC/1931). Since then, curiosity about the biological mechanisms of cognitions and the origin of individual differences has not ceased. Surprisingly, Aristotle’s definition of the rational mind is not too different from the modern understanding of interacting yet compartmentalized cognitive abilities, divided into memory processes and cognitive control functions. For example, consider going to the supermarket to buy snacks and drinks for a party in the evening. As you are scanning the alcohol aisle for your favorite bottle of prosecco, you suddenly get a call from another friend who tells you that they will be able to come as well and that they would like to drink apple juice later. You therefore head to the next section to get the juice. In this example, you need to take in relevant information and retain it over a short period of time, e.g., your friend telling you their beverage request on the phone, while you also change your goal and adapt your search behavior, e.g., as you change the aisle to look for apple juice instead of prosecco.

The currently predominating model of working memory in cognitive psychology by Baddeley and Hitch (1974), incorporates both of these functions and like Aristotle, still postulates one central executive that controls information access and sets goals, but it divides the sensory information storage into specific storages for visual features and auditory information next to the episodic buffer that upholds short sequences of combined sensory input and long-term memories. While this multicomponent model has received vast support from experimental studies, nobody has been able to identify a specific location in the brain that would exclusively house any of these components. In turn, evidence suggests that cognitive functions are enabled through networks of fast, functional connections between multiple brain areas. These networks can be precisely studied with neuroimaging methods that reveal the electrical activity of the brain.

In 1924, Hans Berger was the first to record the ongoing electrical activity of the human brain from the scalp, a technique he called electroencephalography (EEG). In the analysis of this recording, he also discovered the alpha rhythm (ca. 8 to 12 Hz) that occurs ubiquitously across the human brain (Berger, 1929) and which has since been connected to a plethora of cognitive functions as explained in later sections of this thesis. Almost exactly 100 years later, measuring these cortical electric rhythms scientifically called neuronal oscillations with EEG or magnetoencephalography (MEG) remains the gold standard to obtain the whole-brain activity with the highest temporal resolution. In combination with structural magnetic resonance images (MRI) yielding detailed anatomical brain scans and modern, powerful

computational resources, it has become possible to model the individual patterns in local cortical signal changes and their inter-areal functional connections.

For this dissertation, I used these techniques to address current knowledge gaps in the specific roles of oscillatory modulations across the brain areas in human cognition and how they differ between individuals. This thesis therefore explores how fast oscillatory networks arise and change dynamically to adjust for different cognitive task needs and furthermore argues that these dynamics can account for individual differences in behavioral performance.

2 Literature review

2.1 Cognitive functions and the brain

The American Psychological Association defines cognition as entailing “all forms of knowing and awareness, such as perceiving, conceiving, remembering, reasoning, judging, imagining, and problem solving.” (n. d.).

From this definition, two main aspects of cognition can be identified, namely, memory-related processes that encompass all necessary subprocesses related to encoding and maintaining sensory information and the executive functions that access the information in order to retrieve, manipulate and apply the information according to a currently set goal. While there is an ongoing debate about the definitions and interactions of attention, short- and long-term memory storage and cognitive control, they are undoubtedly intertwined and as cognitive functions, support one another. The multi-component model of working memory (WM) integrates memory and control functions into a common framework where the central executive regulates information access and sets goals, and visual and auditory information are stored in the visuospatial sketchpad and the phonological loop, respectively (Baddeley, 2012; Baddeley & Hitch, 1974). Additionally, the episodic buffer combines the multimodal sensory input into short sequences or chunks and interacts with long-term memory. Since then, many other models of working memory have been proposed (Van Ede & Nobre, 2023), including those considering WM an activated state of long-term memory (Cowan, 1999; Oberauer, 2002), but also neurobiological models where WM is based on hierarchical information processing (e.g., Hasson et al., 2015), neuronal short-term plasticity (Jääskeläinen et al., 2011) or neuronal spiking (Miller et al., 2018). Nonetheless, Baddeley’s model remains one of the most relevant theoretical frameworks for WM research due to its compartmentalization of cognitive subfunctions, making it highly useful for psychophysical experiments.

In the original model of WM, the central executive is defined as a not further classified attention control system (Baddeley, 2012) but other accounts have recognized cognitive control as a complex, multi-componential construct itself (Badre, 2011; G. Gratton et al., 2018; Miyake & Friedman, 2012; Satpute et al., 2014) that describes the ability of humans to generate and maintain task-relevant goals while also suppressing task-irrelevant goals (C. Gratton et al., 2018). The executive functions of cognitive control can be further divided into updating of WM, inhibition of task-irrelevant stimuli, and cognitive flexibility which encompasses the ability to quickly switch behavior to a changing task environment (Miyake & Friedman, 2012; Miyake et al., 2000). As such, the cognitive control functions can also be understood as mechanisms of selective attention (Desimone & Duncan, 1995) that shape how sensory input information is encoded and maintained.

Together, WM and cognitive control regulate the conscious information exchange of the mind with the surroundings. In a world bursting with information, it is necessary to control exactly which input matches our current goal in order to process it efficiently. Consequently, WM is considered as the core cognitive mechanism of intelligence (Colom et al., 2008; Hagemann et al., 2023; Kyllonen, 2002; Kyllonen & Christal, 1990). Despite its importance for cognitive functioning, visual working memory (VWM) capacity is severely limited to 3 ± 1 concurrent objects even in healthy young adults (Cowan et al., 2005; Luck & Vogel, 2013; Park et al., 2007), posing severe restrictions on the amount of visual content that can be remembered simultaneously. However, the VWM capacity has been found to vary largely between individuals and to depend on the experimental task (Luck & Vogel, 2013). This has led to a debate whether individual VWM capacities result from a varying number of limited, fixed mental "memory slots" (Luck & Vogel, 1997; Vogel et al., 2001; Xu & Chun, 2006) or from the size of a VWM "resource pool" that can be distributed across memory objects more flexibly, so that either few and precise or relatively more and vague representations can be maintained (Alvarez & Cavanagh, 2004a; Bays et al., 2009; Bays & Husain, 2008; Wilken & Ma, 2004). Individual capacity limits can therefore be explained as either running out of slots or as insufficient resources allocated to the memory items to retrieve them reliably (D'Esposito & Postle, 2015; Luck & Vogel, 2013; Ma et al., 2014). Intriguingly, these capacity limits have been found to be larger in VWM tasks with bilaterally presented stimuli, introducing a bilateral field advantage (BFA) (Delvenne, 2005; Galeano Weber et al., 2020; Umemoto et al., 2010; Zhang et al., 2018). Similarly, individuals vary in their task-dependent cognitive control capabilities (Braver, 2012; Darda et al., 2020; Jurado & Rosselli, 2007), resulting in fewer errors and lower switching costs where cognitive flexibility is required.

Earlier research often used functional MRI (fMRI) or sensor-level EEG to try to find the brain areas crucial to the subfunctions of VWM and cognitive control resulting in the identification of three main sites. While the maintenance of perceived objects is generally localized with fMRI to the visual cortex (Emrich et al., 2013; Kravitz et al., 2013; Riggall & Postle, 2012), central executive control of task-dependent top-down goals has been shown to be localized to the prefrontal cortex (PFC) (Markowitz et al., 2015; Rowe et al., 2000; Sreenivasan et al., 2014). Memory retrieval, in contrast, has been associated with the posterior parietal cortex (PPC) (Jones & Berryhill, 2012; Munk et al., 2002). However, while this approach serves well to localize functional units, it cannot explain how their segregated activity is integrated across time and space to enable coherent cognitive functions. The need to understand the nature of this integration is highlighted by findings that a lesion in one single area does not necessarily lead to disruption in the respective cognitive function (e.g., in the WCST). Additionally, multimodal WM and cognitive control functions are known to activate many cortical areas at once. Therefore, it has remained unclear which neuronal mechanisms might underlie VWM and cognitive control capacity limits, and specifically, their temporal dynamics. In the next sections, I will explain how this research question can be addressed using combined neuroimaging methods and cognitive experiments.

2.2 Neuronal oscillations

What can neuronal oscillations tell us about cognition and why? To answer this question, it is necessary to understand how neuronal oscillations are generated by the brain. The human brain has been estimated to consist of roughly 80 to 100 billion neurons forming over 100 trillion synapses (Goriely, 2025; Herculano-Houzel, 2009). Information transmission within neurons happens via the formation of an action potential, that is a rapid electric discharge of the cell membrane, that travels along the axon up to the synaptic terminal, where the neuron connects to other neurons through mostly chemical and some electrical synapses. In chemical synapses, the arriving electric signal triggers the release of neurotransmitters which after passing the synaptic cleft bind to the receptors of the receiving neuron, leading to a postsynaptic voltage difference in the receiving neuron's dendrite. In electrical synapses, the electric signal passes the cleft directly. The sum of all postsynaptic potentials across the receiving neuron's dendrites determines whether a new action potential is formed.

However, single neurons rarely fire alone. If large populations of neurons (thousands to millions) fire and rest simultaneously, their cumulative postsynaptic potentials give rise to large-scale neuronal oscillations that, depending on the type of neurons and stimulus, occur in frequencies between 0.1 Hz and up to at least 600 Hz (Buzsaki & Draguhn, 2004). Generally, neuronal oscillations have been considered to be generated by interactions between excitatory pyramidal neurons and inhibitory interneurons or by inhibitory neurons only (Bosman et al., 2014; Buzsáki, 2009). The UP- and DOWN-states within an oscillatory cycle are thus thought to reflect neuronal excitability and inhibition, respectively. Consequently, neuronal oscillations are not a mere epiphenomenon of many concurrent postsynaptic potentials: Local entrainment of firing patterns serves as reinforcement of excitatory signal pathways (Buzsáki, 2006; Buzsaki & Draguhn, 2004). An excitatory neuron firing at the same time that other neurons are excitable is therefore more likely to have its signal propagated. The larger the local population of neurons with postsynaptic potentials is and the closer in time these potentials arise, the bigger the peak oscillation amplitude we can observe when recording the large-scale electric activity of the brain (Schroeder et al., 2008). Oscillations are also described by their phase marking the elapsed time within the cycle and by their frequency which is the number of completed cycles per second.

Even different local populations of neurons in distant parts of the brain don't always fire in isolation. In an early experiment, it was observed that the neuronal oscillations of cats' visual cortices synchronized across two recording sites as the cats were watching a moving bar (Singer, 1999). From this arose the idea that transmission of information between neural populations is facilitated through the synchronization of their oscillations (Azouz & Gray, 2003; Singer, 1999, 2009). Accordingly, the concept of communication-through-coherence posits that populations with a constant phase relationship sustain a constant spike time relationship, allowing effective information transfer between them (Fries, 2005; Fries, 2015). By having common windows of excitability, neural populations can form a network in which the postsynaptic potential consistently forms at an advantageous time to evoke a subsequent

action potential. Synchronized networks of different cortical areas have since been found to weaken or strengthen in humans performing various cognitive tasks (Palva & Palva, 2012; Petersen & Sporns, 2015; Singer, 1999, 2009; Vinck et al., 2023).

Lastly, another way of integrating cortically distal and spectrally separated information processing is through cross-frequency interactions. While phase synchronization within frequency bands can achieve spatial integration, it does not explain how networks of different frequencies can interact for information integration. Instead, these interactions have been suggested to be mediated by phase-amplitude coupling (PAC), also sometimes called "nested oscillations" (Axmacher et al., 2010; Bahramisharif et al., 2018; Canolty et al., 2006; Cohen et al., 2009; Cohen et al., 2008; Keitel et al., 2018; Lakatos et al., 2013; Lakatos et al., 2005; Park et al., 2016; Roux & Uhlhaas, 2014; Vanhatalo et al., 2004). Modulation of amplitude peaks of a faster oscillation by the phase of the slow oscillation allows for temporal integration of information distributed across frequencies. Accordingly, both local and inter-areal PAC has been shown to play a crucial role in various cognitive functions (Ursino & Pirazzini, 2024), including visual attention and working memory (Bahramisharif et al., 2018; Brooks et al., 2020; Lisman & Jensen, 2013; Siebenhühner et al., 2020) as well as tasks requiring cognitive control (Cansler et al., 2023; Chen et al., 2022; Esghaei et al., 2022; Papaioannou et al., 2022).

All these dynamics of neuronal oscillations can be measured non-invasively with EEG or MEG which pick up the electromagnetic fields and currents generated primarily by coherent postsynaptic currents in large sheets of co-linearly oriented pyramidal neurons (Hansen et al., 2010; Hari & Puce, 2017; Palva & Palva, 2012). Both EEG and MEG offer an excellent temporal resolution with modern devices having a sampling rate of 1000 Hz. In combination with structural MRI, high-density EEG and MEG also allow for a good spatial resolution of neuroanatomical mapping of signal sources. Although both techniques capture activity from the same type of neuronal populations, they vary in sensitivity to different anatomical sources. MEG is mostly sensitive to tangentially oriented sources located in the sulci of the brain but not to radial sources in the cortical gyri, which do not produce detectable magnetic fields outside the head (Baillet, 2017), unless they are very close to the magnetic sensors (Hillebrand & Barnes, 2002). EEG, on the other hand, is sensitive to signals stemming from sulci and gyri but they become distorted by volume conduction, as the different electric conductivities of the brain, cerebrospinal fluid, skull and skin tissues result in a lateral spread of the electrical potential (van den Broek et al., 1998). The magnetic fields recorded by MEG are not affected by tissue conductivities.

Because dynamic oscillatory networks manifest in fast, multidimensional connections of distant, specialized brain areas, it is not surprising that they have been found to change along with varying cognitive task demands as outlined in the next sections. Frequencies relevant to human cognition are grouped into the delta (1 to 3 Hz), theta (4 to 8 Hz), alpha (7 to 12 Hz), beta (13 to 30 Hz), and gamma (30+ Hz) bands, although there is some slight variation in the upper and lower limits of the frequency bands in the field. These frequency band boundaries

have classically been defined by the specific reactivity in amplitude modulations to various tasks that (from delta to gamma bands) include sleep, motivation, attention, movement or visual perception (Klimesch, 2018). Electrophysiology studies have found local, inter-areal and cross-frequency modulations in these frequency bands in WM and cognitive control.

2.3 Oscillations in VWM

In accordance with fMRI results, cortical oscillations in visual, but also frontoparietal control regions are thought to be fundamental for VWM. Task-dependent local amplitude modulations in these areas have been shown in multiple frequency bands in EEG (Blacker et al., 2016; Ratcliffe et al., 2022; Román-López et al., 2019; Sauseng et al., 2009; Scheeringa et al., 2009), MEG (Grimault et al., 2009; Honkanen et al., 2015; Palva & Palva, 2011; Roux et al., 2012; van Ede et al., 2017), and intracranial EEG (Bahramisharif et al., 2018; Howard et al., 2003). Additionally, oscillatory activity within different frequency bands seems to play specialized roles for VWM.

Transient theta increases in EEG or decreases in MEG are often found during VWM across many brain areas of which prefrontal theta oscillations have been associated with cognitive control processes in VWM tasks (Riddle et al., 2020; Sauseng et al., 2010). On the other hand, evoked theta modulations in VWM that are time-locked to the onset of visual information are hypothesized to arise from hippocampal neurons supporting episodic memory (Herweg et al., 2020; Hsieh & Ranganath, 2014; Lega et al., 2012; Nyhus & Curran, 2010; Rudoler et al., 2023). Furthermore, local beta and gamma band oscillations over visual areas are thought to mediate the memory of features such as color and shape in VWM (Bahramisharif et al., 2018; Daume et al., 2017; Honkanen et al., 2015; Proskovec et al., 2018). Of special interest to VWM are posterior alpha-band oscillations, which are primarily associated with attentional deployment in visuospatial attention (Cruz et al., 2025; Gould et al., 2011; Haegens et al., 2011; Jensen & Mazaheri, 2010; Lobier et al., 2018; Peylo et al., 2021; Sokoliuk et al., 2019; Thut et al., 2006) and spatial VWM (Liu et al., 2022; Myers et al., 2015; Palva & Palva, 2012; Poch et al., 2014; Poch et al., 2017; Sauseng et al., 2009; Sauseng et al., 2005; van Ede et al., 2017).

2.4 Alpha oscillations and individual VWM capacities

Furthermore, local increases of alpha and gamma amplitudes in the frontoparietal regions have been found to strongly predict individual VWM capacities (Palva & Palva, 2011). Traditionally, the underlying mechanism is thought to be increased neuronal excitability (Iemi et al., 2017; Lange et al., 2013). This view arises from experimental designs presenting the relevant stimulus in only one visual hemifield (unilateral), resulting in amplitude suppression of the local alpha amplitudes in the hemisphere contralateral to the stimulus. Conversely, increased alpha amplitudes in the ipsilateral hemisphere are believed to reflect inhibition of

task-irrelevant stimuli presented in the other hemifield (Capilla et al., 2014; Gould et al., 2011; Van Dijk et al., 2008). Together, these alpha amplitude modulations are often interpreted in accordance with the inhibitory role of alpha oscillations (Jensen & Mazaheri, 2010; Klimesch et al., 2007), which are thought to regulate neuronal excitability and optimize cortical processing states (Haegens et al., 2011; Iemi et al., 2017; Lange et al., 2013; Romei et al., 2008).

However, recent evidence challenges this perspective, suggesting that distinct alpha sources contribute differently to task performance (Benwell et al., 2022; Benwell et al., 2017; Cruz et al., 2025; Palva & Palva, 2011). Additionally, it is unclear if the lateralized alpha suppression only facilitates hemisphere-specific spatial VWM or whether there exists a mechanism for interhemispheric integration. Some studies propose that the hemifield in which stimuli are presented affects only by which hemisphere they are encoded initially, but that information is then rapidly transferred between hemispheres (Bourne, 2006; Gazzaniga, 2000; Sperry et al., 1969), suggesting a shared VWM storage (Galeano Weber et al., 2020). Other studies have, however, found crossover costs resulting from memory transfers between hemispheres (Brincat et al., 2021; Minami et al., 2019; Strong & Alvarez, 2020) and within-hemifield memory interference (Buschman et al., 2011), which together indicate hemisphere-specific storage.

A possible mechanism for interhemispheric information exchange is large-scale and long-range phase synchronization. In WM, increased phase synchronization has been found between frontal, parietal and visual areas (Fell & Axmacher, 2011; Mamashli et al., 2021; J. M. Palva et al., 2010; Sato et al., 2018; Siegel et al., 2012). These frontoparietal networks operating in the alpha band have been associated with visuospatial attention (D'Andrea et al., 2019; Lobier et al., 2018) and VWM (Ericson et al., 2024). A few studies have investigated the role of large-scale alpha- and beta (13 to 30 Hz) band network synchronization for individual VWM capacities (Ericson et al., 2024; Mamashli et al., 2021; J. M. Palva et al., 2010), but the evidence remains scarce. Especially, it has not been tested whether interindividual differences in the strength of interhemispheric phase synchronization could also predict differences in VWM performance. Furthermore, it has remained unclear how such behavioral differences associated with phase synchronization would differ following uni- versus bilateral stimulus presentation, indicating either a hemisphere-specific or shared VWM storage. If such an integration mechanism existed and was important to VWM, it should be directly linked to the behavioral performance. The goal of Study I was therefore to identify the large-scale oscillatory network mechanisms of uni- and bilateral VWM and to understand whether individual capacity limits would be predicted by differences in these dynamics.

2.5 Oscillations in cognitive control

Task-dependent local and inter-areal oscillatory modulations have also been found in cognitive control studies. In line with the PFC's crucial role in cognitive control (Bissonette et al., 2013; Panikratova et al., 2020; Ravizza & Ciranni, 2002; Robbins et al., 1996; Tsuchida & Fellows, 2013), a large body of EEG research links theta oscillations, particularly in the PFC and midline regions, to global cognitive control (Cavanagh et al., 2009; Cavanagh & Frank, 2014; Cohen, 2011; Cohen et al., 2007; Sauseng et al., 2010). This includes conflict monitoring (Cohen & Cavanagh, 2011; Riddle et al., 2020; Sauseng & Liesefeld, 2020) as well as proactive or anticipatory control dynamics needed for externally cued task switching (Cooper et al., 2015; Cunillera et al., 2012; Sauseng et al., 2006). It is thought that the PFC's numerous connections to other cortical and subcortical areas allow for hierarchical networks in which top-down control is exerted via those connections from the PFC to other regions (Canales-Johnson et al., 2023; Miller & Cohen, 2001).

However, modulations of oscillations in multiple frequency bands have been found over various cortical areas in cognitive control (G. Gratton et al., 2018). Specifically, higher frequencies are more involved in tasks that require abstract and anticipatory control functions such as task switching (Cooper et al., 2016). These oscillation amplitude modulations have also been connected to improved performance in task-switching. Besides increased theta (Cooper et al., 2017; Duprez et al., 2020; Muralidharan et al., 2023), gamma band oscillations (Proskovec et al., 2019) have been linked to reduced behavioral switching costs. In contrast, suppression of alpha (Foxe et al., 2014; Murphy et al., 2016; Verstraeten & Cluydts, 2002) and beta band activity (Cunillera et al., 2012; Gladwin et al., 2006) is associated with improved performance in cued task-switching. Modulations of alpha band oscillations in sensory and parietal regions (Kaiser et al., 2023; Keitel et al., 2019) are believed to enhance top-down attentional selection of task-relevant features and facilitate the advance preparation required for cued task switching (Cunillera et al., 2012; Foxe et al., 2014; Gladwin et al., 2006; Mansfield et al., 2012; Murphy et al., 2016; Proskovec et al., 2019; Verstraeten & Cluydts, 2002).

Research on neuronal mechanisms of task switching has largely focused on externally cued paradigms, leaving the oscillatory basis of internally driven (un-cued) task switching unclear. In cued paradigms, participants know the correct task rule after each cue and simply adjust their behavior (Kiesel et al., 2010). In contrast, the un-cued Wisconsin Card Sorting Test (WCST) requires integrating error monitoring with preparative switching to deduce the correct rule (Barcelo, 2003; Martin, 2006). This adds a dimension of task uncertainty, making the WCST well-suited for studying intrinsic task-switching that is based on feedback ("correct" or "incorrect") rather than on explicit cues. Because the WCST tests an individual's ability to use feedback to adjust the behavior, and ultimately, their cognitive flexibility to change behavioral rules that are context-dependent, this test has been widely used to assess general frontal lobe function in healthy populations and populations suffering from psychiatric conditions (Milner, 1963). However, evidence suggests that brain areas outside

the frontal lobe also contribute to cognitive flexibility as tested with the WCST (Nyhus & Barceló, 2009). Therefore, in Study II, we use the WCST to understand the time-resolved whole-brain neural mechanisms that enable the integration of feedback to switching the internal behavioral rule representation. In addition, we aimed to resolve underlying factors of individual variability in cognitive flexibility by implementing a new behavioral sequential learning model which estimated sensitivity to different kinds of feedback (Bishara et al., 2010).

2.6 Inter-areal and cross-frequency integration of cognitive control functions

FMRI research on large-scale network interactions has identified the ventral cingulo-opercular and dorsal frontoparietal attention networks as key players in tonic alertness and top-down attention (Dosenbach et al., 2008; Dosenbach et al., 2007). These networks operate in the theta band (Cooper et al., 2015; C. Gratton et al., 2018; Sadaghiani & D'Esposito, 2014) and could facilitate bottom-up detection of rule changes and subsequent goal shifts. While fMRI and sensor-level EEG have mapped spatial patterns, source-reconstructed MEG provides more precise neuroanatomical mapping of human electrophysiological networks (Palva & Palva, 2018; Palva & Palva, 2012). Previous MEG studies suggest that long-range alpha band phase synchronization between the PFC and sensory regions supports top-down attentional selection (D'Andrea et al., 2019; Lobier et al., 2018) and enhances performance in VWM tasks (Ericson et al., 2024; J. M. Palva et al., 2010). While there are no studies linking these networks to cognitive flexibility in humans, research in non-human primates has shown that the mediodorsal thalamus and its interactions with the PFC are key to enable cognitive flexibility (Rikhye et al., 2018; Wolff & Halassa, 2024), especially under task uncertainty (Huang et al., 2024; Kosciessa et al., 2021; Kosciessa et al., 2024; Zhang et al., 2025).

Additionally, long-range cross-frequency interactions between slow theta or alpha bands and higher beta and gamma frequencies have been linked to improved attention and WM (Bahramisharif et al., 2018; Brooks et al., 2020; Lisman & Jensen, 2013; Siebenhühner et al., 2016). Especially theta-gamma phase amplitude coupling has been connected to ordering of information in various cognitive functions (Alekseichuk et al., 2016; Axmacher et al., 2010; Brooks et al., 2020; Heusser et al., 2016; Ursino & Pirazzini, 2024). Originally discovered in sequence memory, this mechanism is thought to integrate feature-specific information of multiple memory items each encoded in a single gamma cycle into the ongoing theta wave of hippocampal place cells to enable multi-item WM (Lisman & Buzsáki, 2008; Lisman & Idiart, 1995; O'keefe & Burgess, 2005; Tamura et al., 2017). Theta-gamma coupling has since been found across frontal, parietal, occipital, and posterior cortices in WM (Abubaker et al., 2021), so that the ratio of posterior gamma to frontal theta cycles predicts the individual WM capacity (Roux & Uhlhaas, 2014).

Interestingly, only a few studies have investigated the role of theta-gamma PAC in executive control functions, even though its reduction has been related to impaired performance on various cognitive tasks (Brooks et al., 2020; Brooks et al., 2024; Goodman et al., 2018) and to be a sensitive marker of prefrontal cortical dysfunction (Brooks et al., 2024). In healthy subjects, theta–gamma coupling has therefore only been reported in attention (Cansler et al., 2023; Esghaei et al., 2022; Papaioannou et al., 2022) and a conflict-processing task (Chen et al., 2022). However, evidence for theta-gamma PAC in cognitive flexibility requiring top-down attentional control and task switching is lacking, leaving the role of dynamic oscillatory networks in cognitive rule-switching largely unexplored. In Study II, we therefore aimed to investigate whether internally driven un-cued task switching would depend on concurrent modulations of local oscillations and large-scale, cross-frequency oscillatory networks.

3 Aims

While the importance of local, inter-areal, and cross-frequency modulations of oscillatory networks across the cortex has been demonstrated for a variety of cognitive tasks in humans, several questions have remained unanswered thus far. Specifically, it has been unclear how oscillation amplitude modulations and inter-areal synchronization in the distinct frequency bands contribute to individual differences in task performance. This thesis therefore elaborates on the spectral, temporal, and anatomical dynamics of oscillatory networks that are associated with working memory and cognitive control. Special emphasis is put on the individual differences in cognitive task capacities and how they can be explained by these network dynamics.

Study I: The aim of Study I was to investigate the neuronal oscillatory mechanisms of the BFA in VWM. More precisely, the aim was to reveal whether bilateral VWM displays oscillatory markers of enhanced attentional coordination or also oscillatory markers of increased VWM storage capacity. To this end, we used source-reconstructed high-density EEG recordings of participants performing a delayed match-to-sample VWM task and estimated the correlation of oscillatory neural activity with memory accuracy, precision and reaction times.

Study II: The aim of Study II was to discover the oscillatory mechanisms underlying individual variability in endogenous cognitive flexibility. To achieve this, we analyzed MEG data recorded during the Wisconsin Card Sorting Test measuring un-cued task switching. By using a new computational modelling framework, our objective was to resolve the subject-specific factors of individual trial-by-trial performance variability and to investigate the oscillatory mechanisms of differences in task-switching performance.

4 Methods and materials

4.1 Participants and cognitive experiments

For study I, we recruited 26 healthy volunteers (12 females) with a mean age of 28.58 ± 4.67 years and an age range of 19 to 40 years to take part in the experiment. The cohort of Study II consisted of another 26 healthy adults (11 females) with a mean age of 33.2 ± 10.2 years and an age range of 18-57 years. These sample sizes were selected in accordance with previous studies' effect sizes (Honkanen et al., 2015; J. M. Palva et al., 2010) and based on our large number of trials per participant per condition (N = 300 in Study I and N = 450 in Study II). All participants reported normal or corrected-to-normal visual acuity and color vision and no recent history of neurological or neuropsychological illness and were physiologically eligible to undergo both EEG or MEG and MRI measurements. No subjects were excluded during either analysis. The study was approved by the University of Helsinki's ethical committee and was performed in accordance with the Declaration of Helsinki. Written informed consent was obtained from each participant prior to the experiments.

For the VWM experiment in Study I we used a delayed match-to-sample task (Luck & Vogel, 1997) where stimuli were presented in the left, right, or both hemifields (Fig. 1A). In the task, subjects were instructed to memorize the color and location of the rectangular Sample stimuli (S1, 0.15 s) and to indicate after a delay (1.8 to 2.2 s) whether the Test stimuli (S2, 0.5 s) were the same or different compared to S1. Memory load varied between 2, 4, and 6 squares and was randomized across hemifield conditions (left, right, bilateral). Participants were instructed to make a two-step decision about whether there was a change or not and, in the case of a change, indicate which feature had changed. A white fixation cross was present throughout the whole trial in the center of this stimulus window. Each participant completed 300 trials per load-hemifield condition, yielding in total 2,700 trials, which were recorded over 3 sessions with a task duration of approximately 1.5 hours each.

The task used in Study II was a computer-version (Barcelo, 2003) of the Wisconsin card sorting test (WCST) by Berg (1948), which uses a set of 24 unambiguous cards of the original 64 WCST cards Fig 1B) (Barceló & Knight, 2002; Periánez et al., 2004). Here, the participants needed to sort cards according to the currently active rule out of three possible rules including shape (circle, star, cross, or triangle), color (blue, yellow, red, or green), and number of items (one to four). The rule changed based on a pseudo-random design on every fifth trial, but the participants were not instructed about this rule change interval. The active rule then needed to be deducted by the participant through trial and error based on feedback. In each trial, a sample card (bottom row), a white fixation cross, and the standardized four target cards (top row) were shown (Stimulus, 2.5 s) followed by a delay (1.5 s). The participant then selected one of the target cards (same number, color, or shape or no match) during the stimulus presentation or the delay. A subsequent green or red feedback cross

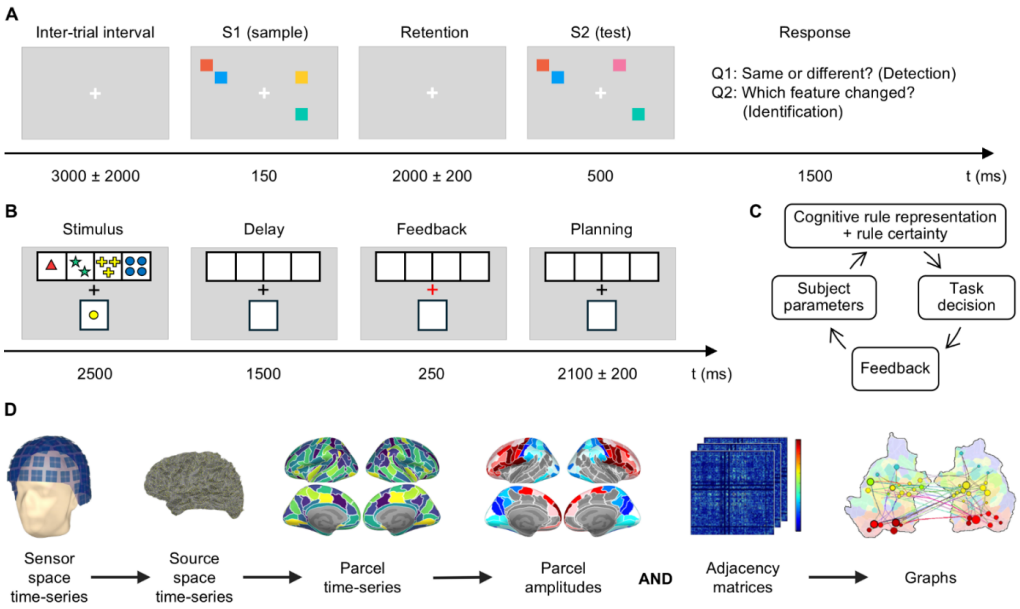


Figure 1. Experimental paradigms. A. Schematic of one trial of the VWM task from Study I. A Sample stimulus (S1) with memory loads 2, 4, or 6 was presented in the left or right hemifields or bilaterally. After a retention period, a Test stimulus (S2) appeared, and the participant indicated whether S2 was the same as S1 or different. In the latter case, after the first response, the participant also indicated the feature in which the change had occurred (color, location, or color and location). **B.** Schematic of one trial of the WCST task used in Study II. In each trial, a sample card (bottom row) and the four target cards (top row) were shown and the participant sorted the sample card to one of the target cards. A green or red feedback cross was shown after the response to indicate a correct or incorrect response, respectively. **C.** Schematic of the behavioral modelling. In the beginning of each trial, the participant had a cognitive rule representation, based on which they made a task decision to match the card to one of the three categories, leading to positive or negative feedback. Depending on the subject's individual tendency to respond to feedback as estimated by the subject parameters, this feedback modified the rule representation and increased the certainty of that rule. **D.** Schematic of the EEG/MEG analysis. Cortical sources were reconstructed from broad-band EEG/MEG time-series data using individual anatomical models. The source space time-series was then collapsed into 200 cortical parcels of the Schaefer/Destrieux atlas and filtered into 38 frequencies using Morlet wavelets, yielding the filtered parcel time-series. From this, we estimated parcels' oscillation amplitudes and phase-synchronization between parcels by constructing adjacency matrices. The network architecture of selected adjacency matrices was visualized as graphs that show the most important parcels (nodes) and their strongest connections to other parcels (edges).

(0.25 s) indicated a correct or incorrect response, respectively, and was followed by the planning stage (1.9 to 2.3 s). A centered black fixation cross and black outlines of the stimulus and target cards were present throughout the whole trial. Each participant completed 450

trials in total, which were divided into 3 blocks of 150 trials, lasting approximately 15 minutes each.

4.2 Behavioral analysis

In Study I, hit rates (HRs) were calculated as the proportion of correct responses from all trials. We analyzed detection HRs and identification HRs separately, with detection HRs being defined as the proportion of correctly identified "same" and "different" trials and identification HRs as the proportion of correctly identified "same" trials and correctly identified feature changes in "different" trials. Detection reaction times (RTs) were estimated as the duration from the onset of S2 to the first button press, whereas identification RTs were calculated as the duration from S2 onset to the second button press. We computed mean HRs and RTs separately for each hemifield condition and load. Trials without response or with RT deviating by more than 2 SD from the mean were removed from the analysis (4.2 % and 5 % of all trials for detection and identification, respectively). Individual VWM capacity was estimated for all hemifield conditions at load 6 with Pashler's formula, wherein the capacity is given by a plateau value, kP, that is obtained for each load that is as large or larger than the individual capacity. The kP values are given by $kP(LM) = LM \times (H - FA)(1 - FA)^{-1}$, where H is the proportion of correctly identified "different" trials and FA is the proportion of "same" trials incorrectly identified as "different"(J. M. Palva et al., 2010; Pashler, 1988; Rouder et al., 2011). Again, this was done for both detection and identification tasks, at load 6 to ensure a large enough set size to accurately calculate capacities.

We tested HRs, RTs, and capacities between conditions for significant differences with separate repeated-measures analyses of variance (ANOVAs) with the main factors load (only HR and RT) and hemifield in the software SPSS (IBM Corp., 2021). Next, we calculated differences in HRs and RTs between loads 4 and 2 as well as between loads 6 and 2 separately for every hemifield condition and tested these for significance with additional separate repeated-measures ANOVAs with the main factor hemifield. Additionally, we applied Bayesian statistics with uniform priors to estimate the likelihood of all models and factors using the software JASP (JASP Team, 2024). We assessed the model of best fit for detection and identification HRs and RTs and their load-related changes as well as for capacity with Bayesian repeated-measures ANOVAs. The best fit model was estimated as the model with the highest BF10 compared to the null model. Additionally, we calculated Bayes factors by including each independent variable to the null model. Lastly, we correlated HRs and RTs of detection and identification tasks across subjects using Spearman's r to check for a speed–accuracy tradeoff.

For the behavioral analysis of Study II, trials without response and trials with a reaction time (RT) deviating by more than 2 SDs from the mean were removed from the analysis (4 % of all trials). RTs were calculated as the duration from stimulus onset to response. Hit rates (HRs) were calculated as the proportion of correct responses from all correctly and incorrectly

answered trials. We referred to trials following negative feedback as shift trials and those following positive feedback as stay trials, and consequently, to RTs in these trial types as shift RTs and stay RTs, respectively. We also categorized incorrect responses during the first two trials of a rule series as early errors and all subsequent errors as late errors, allowing us to estimate rule learning speed (Barceló & Knight, 2002). We then computed HRs for every trial in a rule series separately to confirm that the mean performance during early trials was at chance level and exceeded thereafter. Next, we compared subjects' mean shift and stay RTs with a two-tailed t-test for paired samples and subsequently checked if shift and stay RTs were correlated to the number of late errors across subjects using the Pearson correlation coefficient.

In addition to performance analysis, we applied a novel sequential learning model (Bishara et al., 2010) to disseminate the effects of positive and negative feedback sensitivity and feedback-independent behavioral tendencies on performance and neuronal modulations. We then estimated the subject-wise parameters reward sensitivity, punishment sensitivity, exploration tendency, and rule change anticipation tendency across trials. While reward and punishment tendency assess the subject's responsivity to feedback, we added exploration tendency to assess the effect of rule shifting despite preceding positive feedback and the anticipation tendency as the subjects' ability to predict an upcoming rule change after 5 trials. We then used separate multiple linear regressions to check if these parameters could explain interindividual variance in behavioral performance measures. Lastly, we also estimated the trial-to-trial rule certainty by creating a vector that represents the participant's chosen rule in the previous trial. Each value in this vector represents whether the active rule is shape, number, or color (e.g., [0,0,1] for color). This vector is updated on every trial based on the card choice of the participant.

4.3 Measuring oscillatory networks with EEG, MEG and structural MRI

EEG recordings for Study I were carried out at our EEG lab in the Haartman institute at the University of Helsinki (Haartmaninkatu 3B, 00290 Helsinki), using a 256-channel high-density EEG system (Electrical Geodesics, Inc.). Stimuli were presented with the Psychopy module in Python (Peirce et al., 2019) on a 24-inch monitor (resolution: 1,920 × 1,080 pixels; refresh rate: 60 Hz) positioned roughly 53 cm away from the participant. The head was stabilized in a chin rest to minimize movement. A photodiode was used to achieve ±1 ms precision of stimulus presentation. EEG data were acquired with NetStation (Electrical Geodesics, Inc.) at a sampling rate of 1 kHz and a band-pass filter of 0.1 to 450 Hz. Behavioral responses were collected with one set of two button boxes (VPixx Technologies, Inc.) for the left and right hand.

For Study II, we recorded MEG with 204 planar gradiometers and 102 magnetometers with a Triux (Elekta Neuromag Ltd.) system at 1000 Hz sampling rate and an online band-pass filter of 0.03–330 Hz at the BioMag Laboratory in the Helsinki University Hospital. Stimuli were presented with the Presentation™ software (Neurobehavioral Systems, Inc.) on a projector screen (VPixx Technologies, Inc.; resolution: 1920 × 1080 pixels; refresh rate: 120 Hz) and a photodiode was used to achieve ± 1 ms precision of stimulus presentation. Ocular artifacts were measured with electro-oculogram electrodes. Participants' responses were recorded with a hand-held fiber-optic response device that responded to finger lifts.

Additionally, for both studies, we collected T1-weighted anatomical MRI scans for cortical surface reconstruction models with a magnetization-prepared rapid acquisition gradient echo (MPRAGE) sequence at a resolution of 1 mm voxel size with either a 3T or 1.5T MRI scanner (both Siemens).

4.4 Data preprocessing

EEG and MEG data were processed following the same data analysis pipeline (Fig. 1C) with only minor differences. Because the MEG sensors are not attached to the scalp as in EEG, we used the Maxfilter software (Elekta Neuromag Ltd.) and temporal signal space separation to suppress extra-cranial noise, to adjust for head position changes during the measurements, and to interpolate bad channels (Taulu & Kajola, 2005; Taulu & Simola, 2006). Head position changes over 10 mm were excluded from the raw MEG data. Then, in both studies, raw electrophysiological data was first notch-filtered at 50 Hz and harmonics and band-pass filtered to 1 to 250 Hz. Bad EEG channels were now interpolated using the real positions of electrodes and re-referenced to the average of all channels.

A low-pass-filtered (120 Hz) copy of the data was used to obtain 100 independent components with independent components analysis using minimum norm estimates (MNE) in Python (Gramfort et al., 2014) in Study I and Matlab (The MathWorks, Inc.) in Study II. Components that captured blinks, heartbeats, and obvious facial muscle artifacts were rejected, which were identified with the electro-oculogram in Study II. We then re-referenced the EEG data in Study I to the average of all channels and filtered it into 38 logarithmically spaced Morlet wavelets from 3 to 102 Hz with 7 cycles. The MEG data from Study II was frequency-filtered using 38 approximately logarithmically spaced Morlet wavelets with 5 cycles from 3 to 143 Hz, which were selected so that the ratio of their center frequencies lay within 5 % deviation of the desired 1:m integer ratio for phase amplitude coupling analysis (see section 4.7).

4.5 Source modelling

We applied a source modelling approach to the electrophysiological data in both studies to decrease the effects of signal mixing. The open-access software FreeSurfer (Fischl, 2012) was used for the automatic volumetric segmentation of the MRI data, surface reconstruction, flattening, and cortical parcellation, as well as neuroanatomical labeling into 200 parcels with the Schaefer atlas in Study I (Schaefer et al., 2018) and the Destrieux atlas in Study II (Destrieux et al., 2010). These parcels were then grouped into 17 functional networks in Study I and 7 networks in Study II (Yeo et al., 2014).

For every subject, we created the source space with 5 mm interdipole separation, a 3-layer boundary element method (BEM) model, and the BEM solution using MNE. Noise covariance matrices (NCMs) were used to estimate noise originating from the sensors and were computed using 150 to 250 Hz filtered broadband data from the baseline (−0.5 to −0.2 s before S1) in Study I and 151 to 299 Hz filtered resting-state data (1 min) in Study II. The subject's NCM was then used to compute a forward solution and the inverse operator to transform the filtered complex single-trial EEG/MEG time series to source-vertex time series with dipole orientations fixed to the pial surface normals and a 5 mm inter-dipole separation.

Source-vertices time-series data were then collapsed into the parcels of the neuroanatomical atlas using source-reconstruction-accuracy (fidelity) weighted collapse operators that maximized the parcel fidelities in each subject's source space (Korhonen et al., 2014). For Study I, we collapsed vertices directly into 200 parcels before epoching the data into trial sequences of 2.5 s length and rejecting trials where the mean amplitude deviated by 2 SD from the mean amplitude of all trials of the same recording. For Study II, we first collapsed vertices into 400 smaller parcels using more accurate fidelity weighted operators, after which we morphed them into 200 parcels to increase statistical power. We then epoched data into trial sequences of 2.65 s length and rejected trials with blinks during the feedback.

4.6 Oscillation amplitude and phase synchronization analysis

In both studies, we computed oscillation amplitudes as the envelope of the complex signal across overlapping time windows for all trials, wavelet frequencies, and parcels. Oscillation amplitudes were then averaged across trials for each subject and condition and normalized by dividing it by the mean pre-stimulus baseline.

Interareal phase synchrony was computed with the imaginary part of the phase locking value (iPLV), which in contrast to the phase locking value (PLV), is not sensitive to zero-lag interactions arising from volume conduction, and thus reports fewer artificial interactions (Lachaux et al., 1999; Palva et al., 2018). The iPLV between all parcel–parcel pairs and for each wavelet frequency with a sliding time window. The trial-averaged iPLV values of each condition were baseline-corrected through subtraction to obtain subject-level adjacency matrices that contained the iPLV of all edges (connections) across time and frequencies.

To estimate the robustness of oscillation amplitude modulations and changes in inter-areal phase synchronization across the whole cortex, we calculated the fraction of cortical parcels with a significant effect out of all 200 parcels (P+/P-) and the connection density (K+/K-), that is the fraction of significant parcel-parcel connections out of all connections. Two-sided Wilcoxon-signed rank tests were used to test the amplitudes and phase synchrony for statistical differences between conditions. For assessing correlations of subjects' behavioral performance measures such as HRs and RTs with mean amplitude and phase synchrony patterns we used Spearman's rank correlation. We also calculated Spearman's r to investigate the neuronal load effects in Study I and the trial order effect in Study II. In both studies, we estimated effect sizes by selecting time-frequency (TF) windows of interest showing the most robust (largest P+/P- values for amplitude and K+/K- for phase synchronization) differences between conditions and calculating the average difference between all parcels/edges as r = ZvN (Rosenthal, 1991).

All statistical comparisons were corrected for multiple comparisons by rejecting a percentage of the highest p values in each TF bin corresponding to the used alpha level of significant parcels. Therefore, we rejected the highest 5 % if alpha level was 0.05. Additionally, we adjusted our results to account for multiple comparisons by applying a threshold q. This q threshold was calculated as the percentage of significant tests that are expected to arise by chance given the number of hypothesis tests and alpha level. We only visualized oscillation amplitude modulations and inter-areal synchronization changes that exceeded the q-threshold across frequencies in time-frequency representations (TFRs).

4.7 Phase amplitude coupling analysis

In Study II, we additionally estimated n:m phase amplitude coupling (PAC), for which we compared the phase of all low frequencies (3 to 8 Hz) to the phase of the amplitude envelope of high frequencies (9 to 143 Hz) by computing the PLV between all edge pairs. Because this was a comparison between the concurrent fluctuations in the amplitude of one frequency and the phase of another frequency, no cross-talking effects can be expected, making PLV a suitable measure. This was done for each subject and for the averaged trials of shift and stay conditions separately in the time window 0.6 to 1.6 s after feedback onset.

Because PLV is sensitive to the number of trials, we equalized the number of trials between conditions to the lowest number within each subject before averaging, excluding 3 subjects with $N < 60$ shift trials. We then estimated the statistical significance compared to baseline across the remaining subject population of each pairwise interaction for each of the 1:m ratios using time-shifted surrogate data. Spurious connections were removed by estimating amplitude coupling between low and high frequencies and identifying triangle motifs (Siebenhühner et al., 2020). Shift and stay condition PAC were contrasted using a two-sided Wilcoxon signed-rank test and corrected for multiple comparisons in the same way as

amplitude and phase synchrony. The trial order effect and behavioral correlations were again obtained with Spearman's r.

4.8 Visualization of results

In both studies, we demonstrated the robustness of neuronal effects across the brain by visualizing statistically significant modulations across frequencies in TFRs. These show the significant fraction of cortical parcels (P+/P-) with an effect in amplitude or the connection density (K+/ K-) with an effect in phase synchrony. Additionally, we also estimated effect sizes of modulations in mean oscillation amplitude and mean graph strength (GS, the mean strength of all connections in the graph) in TF regions of interest. Finally, for amplitude modulations, we plotted inflated brain surfaces highlighting the cortical locations with effects and also visualized parcels whose amplitudes were significantly correlated with behavioral measures.

Graph visualization was carried out for frequency bands showing a significant effect in phase synchrony. While using iPLV to estimate interareal synchronization excludes the direct effects of zero-phase lagged signal mixing, spurious interactions still remain (Palva & Palva, 2018). We therefore removed edges between parcels for which the source reconstruction accuracy was low and further excluded edges that exhibited the greatest signal leakage with their neighbors, measured with cross-patch PLV. In both studies, this resulted in exclusion of around 15 % of all possible edges from the analyses. To further mitigate the contribution of spurious interactions caused by the concurrent presence of true interactions and linear mixing, a hyperedge-bundling approach was used in the visualization of interareal network synchronization (Wang et al., 2018).

The final graphs were visualized overlaid on the complete left and right flattened cerebral hemispheres. In Studies I and II, degree was used to identify nodes that were central in the graphs and thus putatively played a key role in network communication. In Study I, we additionally used K-coreness to visualize maximal subgraphs in which every node has at least degree *k* to identify the most tightly connected parts of the network (Ashtiani et al., 2021; Kong et al., 2019; S. Palva et al., 2010). In all graphs, lines indicate the 200 strongest edges of the interaction matrix and are colored according to the connected parcels and networks. Spheres and annotations indicate parcels, with radii proportional to their degree and borders proportional to their eigenvector centrality.

5 Results

5.1 Study I: Differences in oscillatory dynamics between uni- and bilateral VWM

Study I investigated the behavioral and neuronal differences of VWM after stimuli have been presented in one hemifield (unilateral) or across both hemifields (bilateral). To this end, we collected EEG data during a lateralized delayed match-to-sample task, in which subjects needed to memorize 2, 4, or 6 colored rectangles presented in the left, right, or both hemifields. Local amplitude modulations and large-scale phase-synchronized networks were obtained from the source-reconstructed EEG data. The network architecture was mapped using graph theory, whereby the cortical parcels were nodes and the synchronization between parcels the edges. We show that multiple, concurrent amplitude modulations in the alpha and low-beta bands as well as decreased alpha-band synchronization characterize bilateral VWM, so that the memory capacity is preserved at higher loads.

5.1.1 BFA only at high memory loads

We calculated HRs and RTs for change detection and change identification. In every hemifield condition, detection HRs and identification HRs decreased with increasing load. Detection HRs decreased on average from 94 % in the load 2 condition to 86 % and 77 % in loads 4 and 6, respectively, and identification HRs showed a mean decrease from 87 % to 76 % and 65 %. This load effect was moderated by the hemifield, so that identification HRs decreased less across bilateral (by 9 % for load 4 to 2 and by 20 % for load 6 to 2) than unilateral (by 12 % and 24 %, respectively) load increments. This was true for detection HRs only in the comparison of loads 6 to 2 (16 % for bilateral versus 18 % for unilateral conditions).

RTs were shorter in bilateral than in unilateral trials with a significant average difference of 12 ms in detection and 15 ms in identification RTs, and in trials with a lower load than those with a higher load, with an average difference of 40 ms and 20 ms between loads 2 and 6, in detection RTs and identification RTs, respectively. Similarly to HRs, individual capacities calculated at load 6 revealed a hemifield effect for identification, but not detection. Interestingly, while detection capacities ranged between 3.5 ± 0.7 consistent with earlier studies (Cowan et al., 2005; Luck & Vogel, 2013; Park et al., 2007), identification capacities were on average lower with 2.1 ± 0.8 for the bilateral and 1.9 ± 0.9 for the unilateral conditions.

Taken together, we found that the BFA of VWM is more pronounced in change identification than in change detection. Additionally, while RTs were always shorter following bilateral

stimulus presentation, improved identification HRs and capacities were observed at high loads only, highlighting the nuanced nature of the effect when memory demand is low.

5.1.2 Stronger lateralized alpha-beta suppression in bilateral VWM

Next, we studied if the local oscillation amplitudes differ between bilateral and unilateral conditions in source-reconstructed EEG data. In all hemifield conditions, VWM encoding (0 to 0.45 s) was characterized by an early transient theta (3 to 8 Hz) band increase and subsequent alpha (7 to 14 Hz) and beta (17 to 30 Hz) band decreases following the S1 onset. Encoding in the bilateral condition comprised stronger transient theta (3 to 6 Hz) band amplitudes and more suppressed alpha to low-beta (alpha-beta, 8 to 17 Hz) and reduced gamma (30 to 102 Hz) amplitudes than in either unilateral condition (Fig. 2A). The comparisons of bilateral and left- and right-hemifield conditions revealed a typical lateralization pattern so that stimulus presentation in any one hemifield was associated with alpha suppression in the contralateral hemisphere (Fig. 2B). Consequently, bilateral stimuli were followed by equally strong suppression in both hemispheres, so that bilateral VWM was in total characterized by stronger decreases in alpha amplitudes.

During the retention period (0.5 s to 1.9 s), bilateral VWM displayed stronger sustained alpha-beta (10 to 17 Hz) suppression in the striate and extrastriate cortices, as well as in postcentral and somatomotor parcels, dorsal and lateral PFCs, the insula, the inferior parietal lobule (IPL), and the parietal and frontal opercula (Fig. 2C). This effect was mostly driven by differences between bilateral and left-hemifield-stimulation induced oscillation amplitudes.

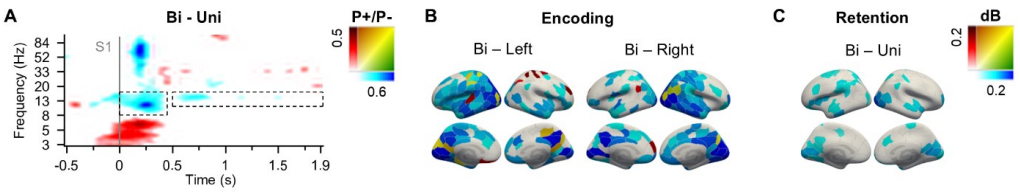


Figure 2. Oscillation amplitude changes by hemifield condition. A. Group-averaged oscillation amplitude differences between bilateral and mean unilateral conditions averaged across load conditions. **B.** Brain anatomies showing the parcels with amplitude differences between bilateral and left, and bilateral and right hemifield conditions during encoding (0 to 0.5 s) in the alpha to low beta (8 to 17 Hz) bands. **C.** Mean amplitudes of the parcels where suppression in the alpha and beta (10 to 17 Hz) bands during retention (0.5 to 1.9 s) was significantly stronger following bilateral than unilateral stimuli.

5.1.3 Late alpha-beta amplitude increases more robustly in bilateral VWM

To investigate differences in the memory load effect by hemifield, we calculated a rank correlation of amplitudes across loads 2, 4, and 6 separately for the left, right, and bilateral hemifield conditions. This revealed an early (0.5 to 1 s) load-related decrease of low-alpha to low-beta (6 to 17 Hz) band amplitudes and a subsequent increase of alpha-beta band amplitudes during the later retention period (1 to 1.9 s) in all hemifield conditions (Fig. 3A). Here, bilateral VWM was characterized by a stronger load effect in the late alpha-beta amplitude increase, whereas unilateral VWM differed more in the early load-related alpha-beta suppression.

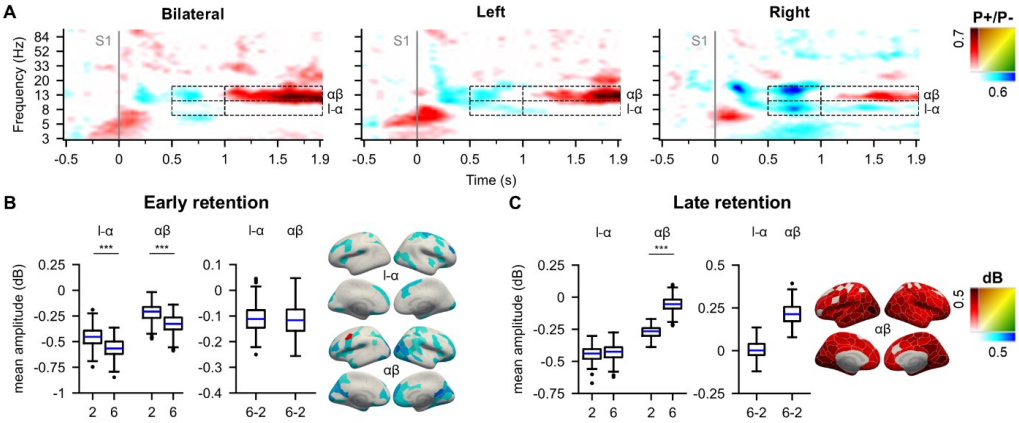


Figure 3. Load effect in oscillation amplitudes. A. Load effect in oscillation amplitudes by hemifield. Color indicates the fraction of brain regions (P) with a statistically significant effect and black dashed boxes indicate the TF windows of interest during the early and late retention period in the low-alpha (l-α, 6 to 10 Hz) and alpha-beta (αβ, 10 to 17 Hz) bands, where mean amplitudes are visualized below and where correlations with HRs were calculated. **B-C.** Boxplots showing the mean amplitudes and the corresponding brain anatomies for load 2 ("2"), load 6 ("6"), and their difference ("6-2"), for the bilateral hemifield condition during early (0.5 to 1 s; B) and late retention (1 to 1.9 s; C). Asterisks indicate significant differences (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). The box of the boxplots indicates the range between the first quartile to the third quartile of the data, with a line at the median, while the whiskers extend to the farthest data point lying within 1.5x the inter-quartile range from the box, and fliers indicate all data points outside the whiskers' range.

By comparing the mean amplitudes of all parcels in the low-alpha (6 to 10 Hz) and alpha-beta frequency ranges during the early retention period of the bilateral VWM condition, we discovered that the early low-alpha suppression was a highly localized effect whereas the concurrent alpha-beta suppression was present in a higher number of parcels (Fig. 3B). We therefore visualized the parcels where the significant effects were observed. In all hemifield

conditions, the parcels with an early low-alpha suppression were largely spatially overlapping and comprised the lateral PFC, precuneus, and striate and extrastriate visual parcels of both hemispheres. The strongest alpha-beta band amplitude suppression was found in the medial and dorsal PFC and visual cortices in all hemifield conditions.

Similarly, we contrasted the mean oscillation amplitudes in the low-alpha and alpha-beta bands during the late retention period (Fig. 3C). Here, we found that only the unilateral conditions showed a significant load-related suppression in the low-alpha band, whereas all hemifield conditions displayed a bilateral increase in alpha-beta band amplitudes. The strongest alpha-beta amplitude increases were found in visual, parietal, and temporal parcels including the striate and extrastriate cortices, precuneus, sensory cortex 2, and insula, as well as the lateral and ventral PFC. Overall, this effect was more robust as it was found in more parcels in bi- than in unilateral VWM.

5.1.4 High-alpha and low-beta increase boosts change identification performance, low-alpha suppression preserves bilateral HRs

Next, we studied if the load-related low-alpha and alpha-beta band amplitude changes were relevant to subjects' task performance. To test this, we correlated each participant's mean amplitudes with their individual HRs and RTs. We also correlated the change in oscillation amplitudes of both frequency bands between low and high memory load conditions with the respective impairments in HRs and RTs.

Better change detection and identification HRs and RTs at memory loads 4 and 6 were predicted by the late-retention alpha-beta band increase. In unilateral conditions, this correlation was the strongest at memory load 4 whereas in the bilateral condition it was stronger at load 6. The alpha-beta amplitude increase predicted identification HRs more robustly than detection HRs in all hemifield conditions. Furthermore, larger amplitude increases in the alpha-beta band from load condition 2 to 6 resulted in preserved unilateral identification HRs but also slower RTs in the right hemifield condition. We localized the effects in the alpha-beta band to frontal, parietal, and visual parcels which were consistent across hemifield conditions.

Only HRs in the bilateral VWM condition profited from larger load-related suppression in the low-alpha band. This correlation was more robust with detection than identification HRs. Left-hemifield condition RTs showed the opposite effect, so that increased low-alpha suppression from load 2 to load 6 was associated with higher increments in RTs. Hence, while the overall HRs at high loads were predicted by higher amplitudes in alpha-beta oscillations, low-alpha suppression predicted better-preserved HRs between memory loads in bilateral, but not unilateral VWM. This correlation of low-alpha band amplitudes and HRs was found in medial PFC and somatomotor parcels.

5.1.5 Interhemispheric frontoparietal alpha synchronization at higher memory load in the bilateral condition

After having mapped out the local amplitude dynamics associated with uni- and bilateral VWM, we then analyzed the differences in interregional synchronization, for which we calculated the phase synchrony between all pair-wise parcels in each hemifield condition. Across all conditions, we found a pattern of a transient theta-band increase and alpha-band decrease in phase synchronization during encoding (0 to 0.5 s) compared to baseline. The subsequent retention period (0.5 to 1.9 s) showed a sustained synchronization in the high-alpha (10 to 15 Hz) band and desynchronization in the beta band. While the encoding-related alpha decrease was stronger for the bilateral condition, the subsequent high-alpha synchronization was weaker overall than in unilateral conditions (Fig. 4A). Phase synchronization effects during encoding are likely to reflect stimulus-locked processes rather than induced synchronization, so that I do not discuss them here further.

To see the size of the hemifield effect during the retention period, we first compared the mean graph strength (i.e., the mean strength of all connections in the graph) in the TF window of interest between the bilateral and mean unilateral conditions (Fig. 4B). This revealed a medium effect size of larger high-alpha synchronization in unilateral VWM. However, investigation of the load-related phase synchrony changes in the same TF window revealed that high-alpha synchronization increased strongly from load 2 to 6 in bilateral VWM (Fig. 4C).

Because the alpha-beta (10 to 17 Hz) amplitude suppression and the reduced synchronization (10 to 15 Hz) overlapped in the spectral and temporal dimensions, we investigated whether these dynamics covaried within individuals and if they arose from the same brain parcels. We therefore computed the correlation between the mean amplitude and mean graph strength in the TF window (10 to 15 Hz, 0.5 to 1 s) for all conditions and for the difference between bilateral and unilateral conditions. This revealed that amplitude and phase synchrony did not generally covary within individuals, but that subjects with larger alpha-beta suppression in the bilateral than unilateral conditions also exhibited less high-alpha synchronization. On the other hand, we found mixed results for the phase-amplitude correlation within parcels, which was only significant in some subjects. This suggests that the high-alpha to low-beta effects in amplitude and inter-areal synchrony reflect a common underlying phenomenon relevant to the task with nonetheless large individual differences.

As a next step, we visualized the high-alpha band network differing between bilateral and unilateral VWM conditions (Fig. 4D) and the network with the largest load-dependent increase in synchronization in bilateral VWM (Fig. 4E). Both networks' cores consisted of interhemispheric frontoparieto-occipital connections with the most central hubs being localized to the prefrontal cortices, early visual and somatomotor (SM) parcels, and the left and right insulas. Both networks formed connections between ventral attention (VA-A and

VA-B), somatomotor (SM-A and SM-B), temporoparietal (TP), and visual (VisA and VisB) functional subsystems.

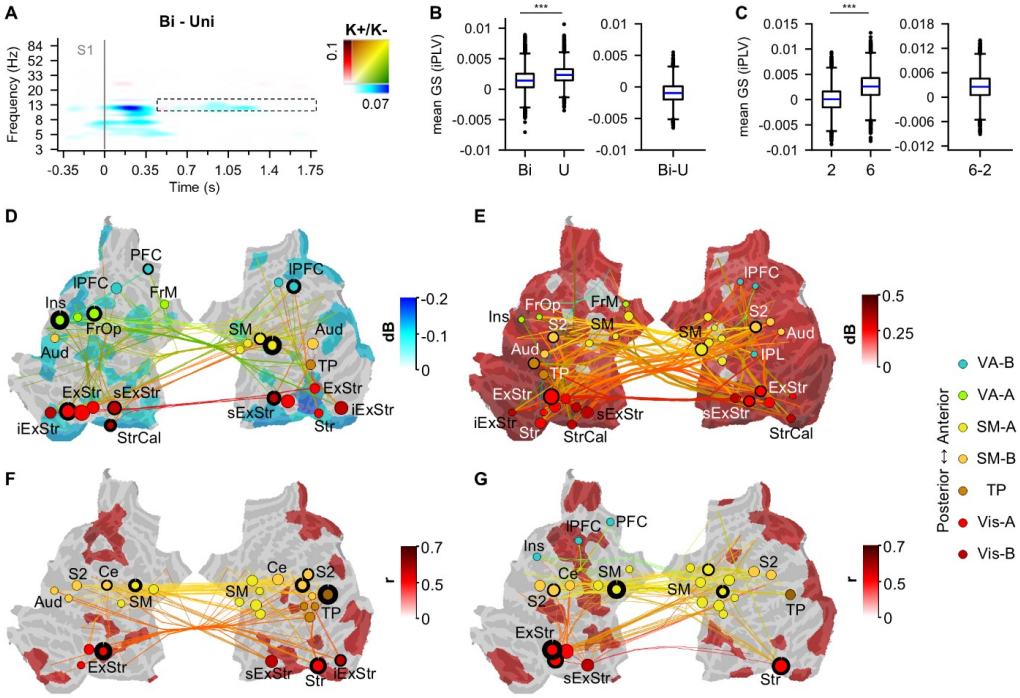


Figure 4. The load-related high-alpha band network. A. The difference in high-alpha phase synchronization between mean hemifield conditions. **B-C.** Boxplots showing the mean GS of all edges and their differences in the TF window of interest for bilateral ("Bi") and unilateral ("U") conditions, and between loads 2 ("2") and 6 ("6") in the bilateral hemifield condition. Asterisks indicate significant differences (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). The box of the boxplots indicates the range between the first quartile to the third quartile of the data, with a line at the median, while the whiskers extend to the farthest data point lying within 1.5x the inter-quartile range from the box, and fliers indicate all data points outside the whiskers' range. **D.** Graph showing the high-alpha networks with the largest *k*-cores differing between bi- and unilateral conditions in the TF window of interest. The background shows parcels with concurrent significant amplitude decreases in the alpha-beta band (10 to 17 Hz). **E.** The synchronization differences of load 6 to 2 in the bilateral condition with concurrent significant amplitude increases in the alpha-beta band the background. **F-G.** Graphs of high-alpha band edges correlating with detection (F) and identification (G) HRs in the bilateral load 6 condition, the coefficients of alpha-beta amplitude correlations with HR in the background.

Furthermore, HRs were correlated with mean graph strength across individuals in each hemifield condition, so that subjects with higher high-alpha synchronization achieved higher

HRs. While the correlation in unilateral VWM was strongest at load 4, in the bilateral condition, this was the case at load 6, where the correlation was also the strongest out of all conditions. The identification HR correlations with high-alpha band synchronization in unilateral (but not bilateral) conditions were slightly more robust, indicating that increased synchronization predicted better precision of VWM.

Finally, we visualized the networks that correlated with detection (Fig. 4F) and identification HRs (Fig. 4G), which revealed tight interhemispheric parieto-occipital connections with main hubs in striate and extrastriate visual cortices, parcels of the somatomotor area, and the temporoparietal junction. The network underlying change identification further included hubs in the PFC. In contrast to HRs, the high-alpha band network had only weak correlations with RTs such that stronger synchronization between memory loads predicted smaller changes in RTs, this being slightly weaker in identification than detection. In summary, we found a load-related increase in high-alpha synchronization in all hemifield conditions predicting higher HRs at high memory load, but this correlation was maximal in the bilateral condition.

5.2 Study II: The oscillatory network dynamics of un-cued task switching

In Study II, we investigated whether internally driven un-cued task switching depends on concurrent modulations of local oscillations and large-scale oscillatory networks as well as cross-frequency PAC. To this end, we recorded MEG data of 26 healthy participants completing a computer-based version of the WCST in which the active sorting rule changed without cue after every 5th trial (Barcelo, 2003). From this data, we identified changes in local oscillation amplitudes, phase-synchronized networks, and PAC from their source-reconstructed cortical activity during the planning period of the task where error monitoring, inhibition of alternative rules and preparative switching take place.

5.2.1 Large variability in task-switching behavior

We first categorized the different error types into early errors made during the first two trials of a new rule series and late errors made within the last three trials. This categorization was based on the probability of guessing the correct rule from feedback at perfect performance, which is 0 % in the first trial, 50 % in the second trial and 100 % thereafter. Accordingly, participants made more early than late errors, demonstrating their rule learning. The number of late errors thus served as a measure of learning speed, in which we found a large interindividual variability. Next, we analyzed HRs as the number of correct responses from all responses as well as RTs as the reaction times between stimulus onset and response. Average HRs increased with every trial within a rule set, showing a steep improvement

within the first three trials from 15 % and 52 % to 78 %, after which HRs remained rather constant at 84 % and 85 %.

We then grouped trials following positive or negative feedback into stay and shift trials, respectively. Comparison of RTs between shift and stay trials differed on average by 102 ms, meaning that participants reacted more slowly after negative feedback. Additionally, both shift and stay RTs were positively correlated with the number of late errors across participants. Finally, we verified that none of the outcome measures were significantly confounded by the age or sex of our participants.

To investigate if these results were driven by higher responsiveness to positive or negative feedback, we estimated the subject-wise parameters reward (positive feedback) sensitivity, punishment (negative feedback) sensitivity, exploration tendency, and rule change anticipation tendency. Multiple linear regressions revealed that interindividual variance in mean HRs and the number of late errors, but not RTs, was well explained by the parameters. Additionally, we correlated reward and punishment sensitivity across subjects which showed that responsiveness to positive and negative feedback covaried within subjects.

5.2.2 Amplitude decreases in alpha and beta, but increases in theta and gamma

To investigate the neuronal dynamics that underlie task switching, we computed oscillation amplitudes from source-reconstructed MEG data. Compared to baseline, shift and stay trials were both characterized by a strong sustained low-theta band (3 to 6 Hz) increase and a concurrent increase and suppression of alpha (7 to 13 Hz) and beta (13 to 32 Hz) band amplitudes throughout the planning period (Fig. 5A). In addition, shift trials were also associated with an increase in the gamma (52 to 96 Hz) band. In contrast to stay trials, shift trials displayed significantly stronger amplitude increases in theta and gamma bands and stronger suppression in alpha and beta bands. To identify oscillation amplitude modulations specifically related to rule learning, we correlated all mean amplitudes with their trial order in a rule set and additionally computed the regression of the amplitudes with the trial-to-trial rule certainty. Decreased theta amplitudes alongside amplitude increases in the alpha and beta bands (0.6-1.8 s after feedback) as the rule set progressed (Fig. 5B) indicated a spectral change from rule shifting towards staying at a rule, which was further associated with increased rule certainty.

Then, we asked in which brain areas the amplitude differences between shift and stay conditions would be the largest in all frequency bands, so we plotted the mean parcel amplitudes within the TF windows of interest. We found the largest amplitude differences in the theta band, which were mainly increased in frontal, temporal and visual parcels. The alpha and beta amplitudes were suppressed over parietal areas with a concurrent amplitude increase in visual and prefrontal parcels, largely overlapping between the two frequency

bands. Finally, the gamma band showed increases in mid-frontal, temporal and visual parcels next to weak suppression in superior parietal parcels (Fig. 5C).

Lastly, we investigated how the condition-averaged amplitudes would relate to differences across individuals in the number of late errors, and shift and stay RTs. All three performance measures were correlated positively with alpha and beta amplitudes but negatively with gamma amplitudes, this being the strongest for the number of late errors. We thus visualized the correlation coefficients of cortical parcels whose amplitudes predicted the number of late errors (Fig. 5D). In the alpha and beta bands, the parcels with the highest correlation coefficients overlapped largely and were mostly found in the PPC, striate, insula and mid-frontal parcels. On the other hand, the strongest negative correlations with gamma amplitudes were located in visual parcels, the intraparietal sulcus, the parietal cortex and prefrontal cortex (PFC).

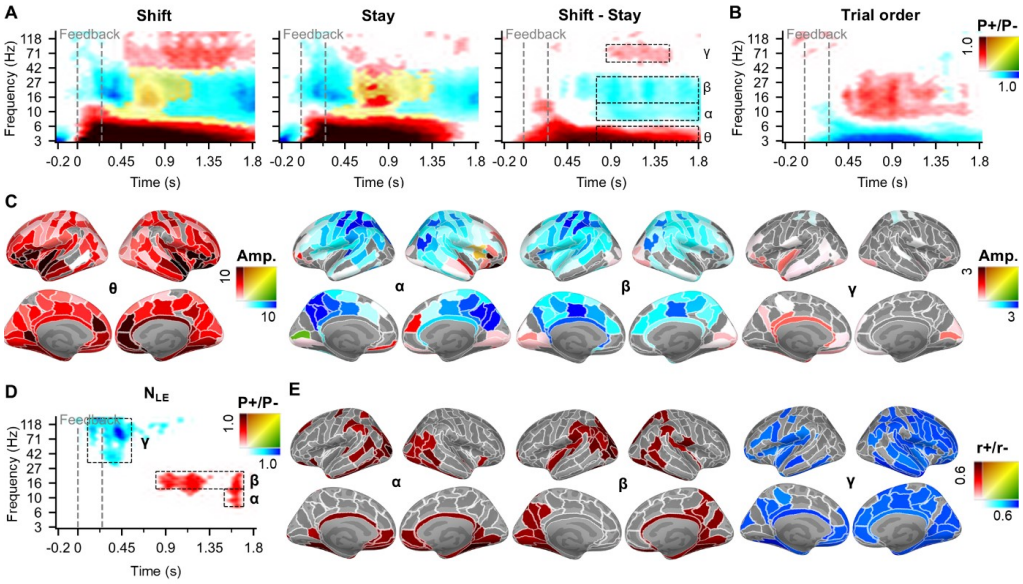


Figure 5. Oscillation amplitude effects and correlations with performance. A. Group-averaged oscillations amplitudes of shift and stay trials compared to baseline, and their contrast. Color indicates the fraction of brain regions (P) with a statistically significant effect in the theta (θ, 3 to 6 Hz), alpha (α, 7 to 13 Hz), beta (β, 13 to 32 Hz), and gamma (γ, 52 to 96 Hz) bands. The dashed black box indicates the TF bins of interest during planning. **B.** Trial series effect showing the fraction of parcels whose amplitude significantly in- or decreased across a rule set. **C.** Inflated brain plots showing the mean amplitude of parcels with significant oscillation amplitude changes between shift and stay trials. **D.** Correlation of parcel amplitudes with number of late trial errors (Spearman's r, $p < 0.05$, FDR corrected, $q = 0.08$). **E.** Brain anatomies showing the parcels with a significant correlation with number of late errors. Color indicates the strength of the correlation coefficient.

5.2.3 Theta synchronization and alpha desynchronization predict late errors

We then estimated inter-areal phase synchronization for assessing the functional connectivity across the cortex in un-cued task-switching. Shift and stay trials displayed strong theta (3 to 8 Hz) band synchronization compared to the baseline that was sustained throughout the planning period (Fig. 6A). Both conditions also showed a subsequent alpha (9 to 13 Hz) desynchronization starting at 0.6 s after feedback. The contrast of shift and stay conditions revealed both effects to be stronger in shift trials. To see whether changes in phase synchronization would follow the trial order of a rule set, we correlated the edge strength of every connection with the trial order, revealing a decrease in theta synchronization throughout the whole retention period (Fig. 6B).

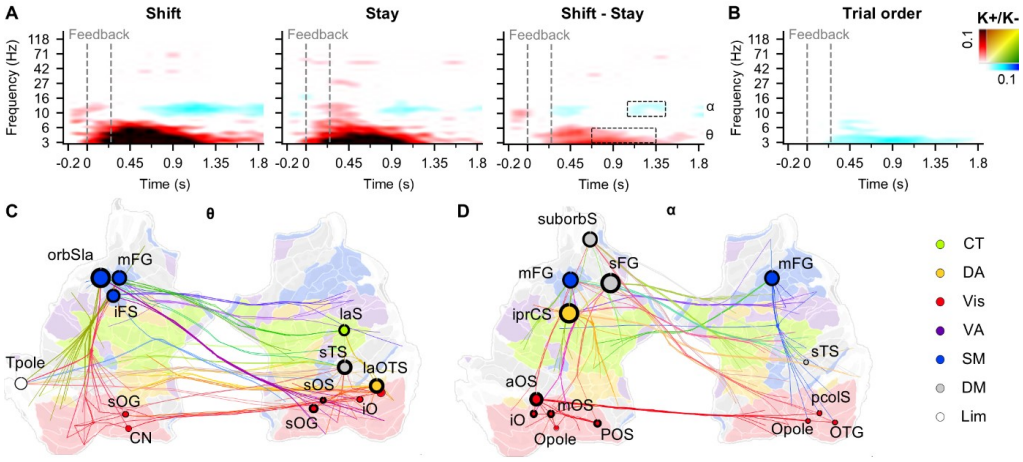


Figure 6. Phase synchrony (iPLV) results for shift and stay conditions and the networks that correlate with performance. A. Inter-areal phase-synchronization during shift and stay trials compared to baseline and the contrast between the two conditions. Color indicates the connection density (K) of significant connections. **B.** Trial series effect showing the K of edges that significantly in- or decreased in phase synchronization across a rule set. **C.** Theta-band (θ, 3 to 6 Hz) matching graph showing the vertices with the highest source degree and the 150 edges with the strongest phase coupling in shift compared to stay trials during the TF window of interest (0.7 to 1.3 s). **D.** Graphs of the early theta (0 to 0.6 s after feedback) and late alpha-band (α, 9 to 13 Hz, 0.6 to 1.8 s) networks that correlated with the number of late errors across participants during the retention period. Depicted are the nodes with the largest degrees and strongest edges correlating with the number of late errors.

The architecture of the theta band network that was stronger during rule shifting consisted mostly of fronto-parietal edges, connecting the left prefrontal nodes to right parietal and bilateral visual parcels (Fig. 6C). We also found the orbitofrontal cortex, medial and lateral

PFC to connect to especially many other parcels, making them central hubs of this network. As a result, the graph consisted of edges between all 7 functional networks, comprising the control (CT), dorsal attention (DA), visual (Vis), ventral attention (VA), somatomotor (SM), default mode (DM) and limbic (Lim) networks.

Next, we investigated whether mean phase synchronization of edges predicted the individual behavioral performance. We found that fewer late errors were predicted by early (0 to 0.6 s after feedback onset) theta synchronization and subsequent (0.6 to 1.8 s) alpha band desynchronization. We hence visualized the behaviorally relevant theta and alpha networks (Fig. 6D), of which the theta network connected left prefrontal parcels with bilateral parietal and visual parcels. Central hubs with a large number of edges were the left lateral and medial PFC, bilateral inferior and left superior parietal lobules. On the other hand, the alpha network comprised edges between bilateral prefrontal nodes, the right superior temporal sulcus and bilateral visual parcels, and had central hubs in the left primary motor cortex and bilateral dorsolateral PFC.

5.2.4 Theta phase coupling to all amplitudes improves task-switching performance

Finally, we investigated whether integration of cognitive processes happening in different cortical parcels and frequencies would take place in the form of cross-frequency interactions, specifically PAC between low and high frequencies. Both shift and stay conditions were characterized by strong PAC between low to high-theta (3 to 8 Hz) phase and alpha to gamma amplitudes (9 to 143 Hz). Additionally, theta-gamma PAC was stronger in shift than stay trials and decreased over the course of a rule series.

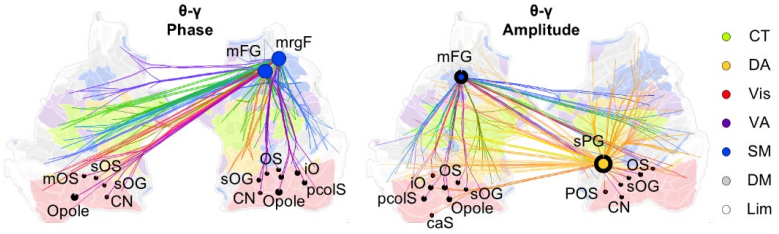


Figure 7. Phase amplitude coupling results for the contrast of shift and stay conditions. Graphs showing the significant theta-gamma PAC networks by largest degree of phase to amplitude coupling (left) and amplitude to phase coupling (right).

Post-hoc correlative analysis revealed that individuals with stronger coupling of high-theta phase to amplitudes of all HFs predicted fewer late errors, and shorter shift and stay RTs. When plotting the strongest significant connections of the theta-gamma PAC network, we

found that the phase of the right medial PFC was most coupled to gamma amplitudes across the brain and especially to bilateral visual nodes (Fig. 7, left). Gamma amplitudes of the left medial PFC and right superior parietal lobule were the most strongly coupled to the theta phase of frontal, parietal and visual nodes (Fig. 7, right).

6 Discussion

Cognitive functions are crucial for humans to use the rich information they are constantly surrounded by. Previous research has associated cognitive functions with various changes in rhythmic neuronal oscillations that provide a mechanism for regulation and temporal coordination of information processing across local and large-scale neuronal populations. Yet, the question of how individual and moment-to-moment variability in spatio-temporal patterns of neural oscillations would predict performance variability in cognitive tasks has remained largely unresolved. In this thesis, I studied the local and inter-areal network dynamics leading to individual differences in task behavior, using EEG and MEG of healthy adult volunteers performing a VWM task and another cohort performing the WCST.

In Study I, we investigated the behavioral and neuronal differences between unilateral and bilateral VWM to discover whether local neuronal oscillations and their large-scale network interactions could predict the BFA of VWM. Moreover, our aim was to understand whether bilateral VWM displays oscillatory markers of enhanced attentional coordination or increased VWM storage capacity. To this end, we analyzed oscillation amplitude modulations and inter-areal phase synchronization from high-density EEG recordings of subjects (n = 26, 14 males) performing a VWM task with uni- and bilateral visual stimuli. We found that bilateral VWM capacity was preserved at high memory demands together with shorter bilateral RTs, and that multiple dissociable, but concurrent amplitude modulations in the alpha- and low-beta bands characterized bilateral versus unilateral VWM. Additionally, we found a concurrent load-dependent interareal synchronization in the high-alpha band that connected prefrontal and posterior brain areas across the left and right hemispheres. The strength of these changes in oscillations correlated with better performance across the study cohort, demonstrating their relevance for the preserved VWM capacity in bilateral conditions. Taken together, Study I revealed three distinctive amplitude patterns in the low-alpha to low-beta bands which were separated in frequency, anatomy, and time, next to dynamic modulations of high-alpha band phase synchronization. These findings support the conclusion of multiple, concurrent neurophysiological phenomena underlying individual differences in bilateral versus unilateral attention and VWM capacity, including both markers of enhanced attention as well as an only slightly increased, shared storage capacity.

In Study II, we asked whether oscillatory mechanisms could explain individual variability in un-cued task switching. Specifically, we aimed to resolve the subject-specific factors that underlie trial-by-trial performance variability and to investigate the oscillatory mechanisms of differences in task-switching performance between individuals. To this end, we analyzed MEG data (n = 26, 15 males) recorded during the WCST, where we mapped changes in local oscillation amplitudes, large-scale phase synchronization and cross-frequency coupling resulting from un-cued task-switching and general rule learning across the task. Crucially, we implemented a novel sequential learning model to identify the impact of feedback sensitivity

on oscillation dynamics and task performance. Better performance was predicted by gamma band amplitude increases together with parietal alpha and beta band suppression following feedback, together with sustained alpha desynchronization that correlated with higher learning speed. Higher sensitivity to positive feedback explained modulations in the alpha- and beta-band amplitudes as well as theta and alpha phase synchronization, whereas sensitivity to negative feedback was mainly associated with larger gamma amplitudes. Lastly, we found increased theta-gamma phase amplitude coupling during switch trials to be associated with better performance. Our results from Study II demonstrated that un-cued task switching is characterized by local amplitude changes in the prefrontal and parietal cortex in all frequency bands, fronto-parietal alpha desynchronization and inter-areal theta band synchronization and that the strength of these neural effects depend on the individual's responsivity to different types of feedback. We further revealed the role of theta-gamma phase amplitude coupling in cognitive flexibility. In conclusion, our results show that the great inter-individual variability in cognitive flexibility in the WCST depends on multiple concurrent modulations of oscillation amplitudes and their phase interactions, which are predicted by differences in individual feedback sensitivity.

My thesis offers new insights about how the tuning of local neuronal processing and modulation of the long-range information transfer between distal cortical regions explains variability in VWM and cognitive flexibility. My findings extend the current understanding of the functional role of the different frequency bands in human cognition, especially that of the alpha-band. I further demonstrate that cognitive functions cannot be explained by local amplitude changes of isolated brain areas alone. Instead, I show that the brain operates as a complex system dependent on inter-areal phase-synchronized networks next to multiple concurrent in- and decreases in oscillation amplitudes as well as their cross-frequency interactions. Together, these findings improve our understanding of the complex and dynamic changes in brain activity that characterize human cognition.

6.1 Enhanced precision and processing speed in bilateral VWM

Both visuospatial attention and VWM capacities are higher for stimuli that are displayed bilaterally rather than unilaterally, resulting in the BFA. However, while the capacity is up to doubled in bilateral attention (Alvarez & Cavanagh, 2004b), the BFA of VWM has been found to be nuanced in healthy participants (Delvenne, 2005; Galeano Weber et al., 2020; Umemoto et al., 2010; Zhang et al., 2018), possibly due to early interhemispheric integration of encoded information (Bourne, 2006; Galeano Weber et al., 2020; Gazzaniga, 2000; Sperry et al., 1969). However, it has remained unclear whether VWM storage is hemisphere-specific or globally shared, the latter of which would result in similar capacity limits in unilateral and bilateral VWM, and which neuronal mechanism might underlie this interhemispheric integration.

In Study I, we revealed an interaction effect of stimulus hemifield and memory load on VWM performance, so that enhanced precision (change identification HRs) in the bilateral condition was only found at high but not low memory demands. Additionally, detection and identification RTs were significantly shorter in the bilateral than left- or right-hemifield condition. Lastly, we found a BFA in maximum memory capacity for the change identification condition.

Our results therefore indicate that especially the precision of bilateral VWM suffers less from load increases than that of unilateral VWM. This is in line with earlier studies finding a BFA only at high memory loads (Banich & Belger, 1990; Belger & Banich, 1992, 1998; Delvenne & Holt, 2012). This indicates a shared VWM storage between the left and right hemispheres leading to similar HRs at low memory loads. Importantly, we also found evidence for a BFA of RTs in VWM that was independent of memory load, showing that at least some aspects of VWM profit from enhanced local processing after bilateral stimulus presentation. This highlights that different angles of the BFA are captured by VWM precision and processing speed, together forming a complementary analysis.

6.2 Multiple concurrent processes in the alpha and low-beta band during VWM

Bilateral VWM differed from unilateral VWM in Study I in a complex way, involving multiple spatially, temporally, and spectrally overlapping mechanisms in the alpha to low-beta bands. Firstly, we found bilateral VWM to be associated with larger alpha to low-beta (6 to 17 Hz) band amplitude suppression during encoding. This was mostly due to suppression over the visual areas of both hemispheres, as compared to only the contralateral hemisphere in the unilateral VWM. Secondly, during the early retention period, sustained alpha-beta (10 to 17 Hz) band suppression was stronger in bilateral than left-hemifield VWM. Importantly, it was concurrent early sustained low-alpha (6 to 10 Hz) band suppression in medial PFC and somatomotor parcels that predicted preserved HRs in bilateral but not unilateral VWM.

Thirdly, we found a load-related increase of prefrontal and posterior high-alpha and low-beta (10 to 17 Hz) band amplitudes during the late retention period that plateaued at higher memory loads and robustly predicted higher HRs and shorter RTs in the bilateral condition. In Study I, we demonstrated that all of these amplitude modulations together, namely the sustained suppression of both low-alpha and alpha-beta oscillations and an altered load-related late alpha-beta amplitude increase, may explain differences in performance between bilateral and unilateral VWM as memory load increases.

These results support modern accounts of heterogeneity of alpha sources across frequencies and space (Benwell et al., 2022; Benwell et al., 2017; Cruz et al., 2025; Lobier et al., 2018; Palva & Palva, 2011; Trajkovic et al., 2024), and indicate that these might play dissociable roles in perception (Benwell et al., 2022; Benwell et al., 2017; Di Gregorio et al., 2022;

Samaha et al., 2017; Samaha et al., 2022) and working memory (Palva & Palva, 2011; Poch et al., 2017; Rodriguez-Larios et al., 2022). Here, we also found the low-beta band to overlap functionally with the high-alpha band. The results of Study I also demonstrate that the distinct amplitude modulations in the alpha and beta bands track individual differences in VWM performance well. As such, our results do not only underscore the functional role of the oscillatory dynamics for VWM but also offer an understanding of the physiological mechanism leading to individual capacity limitations and the variety therein.

6.3 Alpha suppression during VWM encoding and retention

In Study I, we found low-alpha to low-beta amplitude suppression during unilateral encoding that followed a typical lateralization pattern of being larger in contralateral than ipsilateral visual parcels. During bilateral encoding, this suppression was stronger due to it engaging both hemispheres. As contralateral alpha oscillations are suppressed relative to attended visual space (Bonnefond & Jensen, 2025; Haegens et al., 2011; Jensen & Mazaheri, 2010; Thut et al., 2006), it appears from our results that this space is larger for bilateral than unilateral stimuli and overlaps less between visual representations (Cohen et al., 2014; Franconeri et al., 2010; Franconeri et al., 2008; Liu et al., 2009; Scalf & Beck, 2010; Scalf et al., 2013; Störmer et al., 2014; Torralbo & Beck, 2008). Previous studies have connected the encoding-related low-alpha suppression with individual attention capacities (Lobier et al., 2018; Rouhinen et al., 2020), which are larger for bilaterally than unilaterally presented stimuli (Alvarez & Cavanagh, 2004b; Delvenne & Holt, 2012). Our results therefore suggest that stronger low-alpha suppression resulting in higher neuronal excitability during encoding explains larger attention capacities in bilateral VWM, indicating that the BFA may result partly from enhanced encoding of visual information.

In Study I, we also found that sustained low-alpha band suppression during the retention period was correlated with smaller HR drops in bilateral VWM, whereas sustained high-alpha and low-beta band suppression was unrelated to performance. The stronger behavioral relevance of low-alpha suppression for bilateral VWM stimuli are in agreement with findings that trial-to-trial fluctuations of neuronal excitability could be modulated according to the task demands via low-alpha oscillations (Balestrieri & Busch, 2022) of the contralateral visual cortex (Haegens et al., 2011; Iemi et al., 2017; Lange et al., 2013), even beyond the encoding period. On the other hand, we found that the low-alpha amplitude was correlated more robustly with detection HRs than identification HRs. It appears therefore that low-alpha suppression is associated with nonspecific regulations of neuronal excitability. This is further supported by a previous study where alpha suppression was not colocalized with feature-specific gamma amplitudes (Honkanen et al., 2015).

6.4 Late alpha-beta amplitudes predict VWM capacity

Individual differences in VWM performance in Study I were best explained by increased alpha-beta amplitudes in the second half of the retention period. Higher alpha-beta amplitudes were predictive of higher processing speed (RTs), detection accuracy (detection HRs), and memory precision (identification HRs) of the VWM stimuli. Additionally, higher memory precision in bilateral than in unilateral VWM was also correlated with enhanced alpha-beta amplitudes. Importantly, alpha-beta amplitudes were the highest of all load conditions at load 4 in unilateral VWM and thus reached a plateau, while this was true only at load 6 in bilateral VWM.

Increases of alpha-beta amplitudes during late retention are often thought to enhance the inhibition of irrelevant stimuli in attention (Capilla et al., 2014; Peylo et al., 2021) and protect memories from interference (Bonnefond & Jensen, 2012; Miller et al., 2018; but see also van Ede et al., 2017), thus enhancing performance (Tuladhar et al., 2007; Wianda & Ross, 2019). Others have debated this perspective by providing evidence for late alpha-beta amplitudes unrelated to the presence of distractors (Foster & Awh, 2019; Noonan et al., 2016; Poch et al., 2018; Van Moorselaar & Slagter, 2020). In Study I, we found the alpha-beta amplitude increase to be behaviorally relevant, such that it specifically predicted the memory precision and processing speed, unlike the low-alpha or alpha-beta suppression. This speaks for a more complex role of increased alpha-beta amplitudes in also maintaining the memory representations as previously associated with beta and gamma band amplitudes (Honkanen et al., 2015). Further support for this interpretation is lent by the performance being most strongly correlated with increased alpha-beta amplitudes in bilateral striatal, somatomotor, and prefrontal parcels, which have previously been connected to VWM maintenance (Bonnefond & Jensen, 2012; Miller et al., 2018; Palva & Palva, 2011; Tuladhar et al., 2007; van Ede et al., 2017; Wianda & Ross, 2019). On top of that, we did not find lateralization of the alpha-beta amplitude modulation, but instead it presented in left-right-balanced topologies. Our results therefore provide evidence for a feature storage that is shared between hemispheres and depends on increased alpha-beta amplitudes in the later retention period.

6.5 Interhemispheric alpha-beta phase synchronization in VWM

Earlier studies have demonstrated inter-areal phase synchronization between distant brain areas to enable dynamic functional connections relevant to cognition (Fries, 2005; Fries, 2015; Gross et al., 2004; Palva & Palva, 2012). In addition to local amplitude modulations, we therefore also investigated the role of phase synchrony for unilateral and bilateral VWM in Study I. Here, alpha and low-beta (10 to 15 Hz) band phase synchronization among interhemispheric connections of the visual cortices, PPC and PFC characterized VWM retention. Our findings are in accordance with previous studies showing increased phase synchronization between frontal, parietal and visual areas in WM (Fell & Axmacher, 2011;

Mamashli et al., 2021; J. M. Palva et al., 2010; Sato et al., 2018; Siegel et al., 2012). In Study I we also show this synchronization to increase with load but reach a maximum at lower loads in unilateral than bilateral VWM conditions, resulting in an overall stronger alpha-beta band phase synchronization in unilateral VWM.

In addition, we found connections that predicted behavioral performance between frontoparietal and visual parcels. This suggests that synchronization supports communication pathways connecting parietal and visual sensory information storage (Christophel et al., 2017; Pasternak & Greenlee, 2005; Todd & Marois, 2004) with prefrontal cognitive control centers (Koechlin et al., 2003; Menon & D'Esposito, 2022). Lastly, alpha-beta synchronization showed a positive correlation with individual HRs and faster RTs in our study, demonstrating that increased synchronization was functionally beneficial. Notably, memory precision was more dependent on prefrontal connections than detection accuracy. Alpha-beta phase synchrony might therefore specifically enable top–down-driven retention of internal memory representations stored in posterior regions (Curtis & D'Esposito, 2003; Lara & Wallis, 2015).

Previous studies have shown that inter-areal alpha-beta band phase synchronization accurately tracks individual VWM capacity limits (Ericson et al., 2024; J. M. Palva et al., 2010) and multi-object attention capacity (Rouhinen et al., 2020) by increasing with memory load up to the individual capacity but leveling off thereafter (J. M. Palva et al., 2010). While our findings are in line with this, they extend this notion to explain the preserved memory precision in bilateral VWM. Furthermore, we found this alpha-beta network to be interhemispheric and not lateralized, providing evidence for shared processing even of unilaterally encoded visual stimuli. Our results thus underline the relevance of dynamic synchronization among bilateral visual cortices and PPC to support successful VWM performance both for unilateral and bilateral memory.

6.6 Task-switching in the WCST

Cognitive flexibility requires swift behavioral adaptation to changing environmental demands and is a crucial ability for healthy cognitive functioning. Individuals vary widely in their adaptation speed and accuracy, but it has remained unclear which precise physiological mechanisms enable successful task-switching and how they relate to individual differences therein. In Study II, we therefore first investigated how un-cued task-switching affected performance in the WCST and further pinpointed behavioral differences between individuals.

Firstly, we found shorter RTs in stay than shift trials which is consistent with previous studies showing that switching behavior between tasks results in switching costs (Monsell, 2003). Secondly, subjects showed large variability in the number of late errors, that is errors made in the last 3 trials of a rule set, and in their reaction times in trials following negative feedback (shift RTs) and trials following positive feedback (stay RTs). These three behavioral measures evidenced differences between individuals in task-switching efficiency in our

results. Furthermore, these measures correlated with each other so that individuals with more late errors also responded more slowly in shift and stay trials, demonstrating that they underlie a common mechanism.

By fitting a novel sequential learning model (Bishara et al., 2010) to the task performance, we revealed that the task-switching efficiency (number of late errors) but not the processing speed (shift and stay RTs) were explained by reward and punishment sensitivity, as well as exploration and anticipation tendency. This demonstrates that both forms of feedback were relevant to task performance in addition to feedback-independent behavioral flexibility. Furthermore, responsiveness to positive and negative feedback covaried within subjects, further evidencing the importance of both parameters for task-switching efficiency.

6.7 Amplitude modulations across all frequency bands during task-switching

Next, we identified the task-related amplitude modulations during the planning period of the WCST. Traditionally, cognitive flexibility has been associated with prefrontal (Cohen & Cavanagh, 2011; Cooper et al., 2015; Cunillera et al., 2012; Sauseng et al., 2006; Sauseng & Liesefeld, 2020) and right centroparietal theta band oscillations (Cooper et al., 2017). Also, local modulations of alpha (Kaiser et al., 2023; Keitel et al., 2019), beta (Cunillera et al., 2012; Gladwin et al., 2006) and gamma (Proskovec et al., 2019) band oscillation amplitudes over sensory and parietal areas have been found in cued task-switching. However, it remained unclear how changes in the different frequency bands, particularly in the alpha and theta bands, contribute to cognitive control (van Driel et al., 2012) and un-cued task switching.

In Study II, we found un-cued task-switching to elicit amplitude increases in the theta (3 to 6 Hz) and gamma (52 to 96 Hz) band oscillations, alongside alpha (8 to 13 Hz) and beta (13 to 32 Hz) band suppression over the PPC. Interestingly, less late errors and faster processing speed were correlated with alpha and beta suppression as well as increased gamma, but not theta amplitudes across individuals.

Theta amplitudes commonly associated with cognitive control were therefore strongly increased during shift trials in our data but did not influence behavior directly. One potential reason for this might be that theta oscillations play a more global but indirect role in task-switching, where they promote integration of information across neural assemblies and enable goal-directed control processes (Cooper et al., 2015; Sauseng et al., 2010). Indeed, theta amplitudes predicted rule learning and increased rule certainty across a trial series, on top of larger theta amplitudes being explained by a higher tendency to anticipate rule changes. This is in line with earlier studies associating prefrontal theta oscillations with task uncertainty (Kosciessa et al., 2021; Kosciessa et al., 2024). Our results thus indicate that increased theta amplitudes are not a facilitating mechanism for behavioral switching per se, but rather

characterize the subject's understanding of the task, so that upcoming rule changes can be better anticipated and new rules learnt quickly.

Instead, we also found gamma amplitudes over visual, parietal, and prefrontal cortices to enhance task-switching efficiency. This was driven by higher levels of punishment sensitivity and exploration tendency, indicating that subjects responding more strongly to negative feedback displayed larger gamma amplitudes, leading to fewer late errors and shorter RTs. So far, there has been only sparse evidence linking gamma amplitudes to cognitive control performance in humans, where increased gamma amplitudes have been associated with enhanced behavioral switching (Proskovec et al., 2019) and faster reorienting of attention (Spooner et al., 2020), as opposed to diminished gamma amplitudes and impaired cognitive control abilities (Cho et al., 2006; Minzenberg et al., 2010). While it is generally assumed that gamma amplitudes reflect processing of sensory information in cognitive tasks (Fitzgibbon et al., 2004; Honkanen et al., 2015; Jensen et al., 2007), we provide novel evidence for their role in un-cued task switching and show that their variance across subjects is directly linked to performance differences in the WCST.

In addition to gamma, we also found the alpha and beta band suppression over the PPC to be crucially involved in un-cued task switching, as the decrease in their mean amplitudes was predictive of the number of late errors and RTs across individuals, driven by differences in reward sensitivity. Posterior alpha suppression has been found in connection with cued task-switching in previous studies (Capizzi et al., 2020; Foxe et al., 2014; Murphy et al., 2016; Verstraeten & Cluydts, 2002). Along with the existing literature, we thus postulate that decreased alpha amplitudes might reflect increased allocation of attention to the switch-relevant sensory domain (Cooper et al., 2016; Proskovec et al., 2019; Rapela et al., 2012; Sauseng et al., 2006; Wu et al., 2015) putatively tuning neuronal excitability in visual and sensorimotor regions (Balestrieri & Busch, 2022; Bonnefond & Jensen, 2025; Haegens et al., 2011; Iemi et al., 2017; Jensen & Mazaheri, 2010; Klimesch, 2012; Klimesch et al., 2007; Lange et al., 2013).

Additionally, beta suppression has been shown in connection with switch cues, particularly over posterior-occipital regions and the left premotor cortex, which has been interpreted within a motor control framework (Cooper et al., 2016; Cooper et al., 2017; Cunillera et al., 2012; Gladwin et al., 2006). Beta oscillations might therefore facilitate remapping of the task motor response in preparation for using an alternative rule in the following trial. Supporting evidence for this interpretation also comes from studies showing the role of suppression in beta amplitudes for inhibitory control in task switching (Cunillera et al., 2012; Gladwin et al., 2006) and in VWM (Lundqvist et al., 2024; Wessel & Anderson, 2024). Therefore, alpha and beta band suppression, while overlapping in location and time, might improve cognitive flexibility in different manners (Capizzi et al., 2020; Cooper et al., 2016; G. Gratton et al., 2018).

6.8 Alpha phase desynchronization predicts learning speed

In Study II, we also carried out a whole-brain analysis of phase synchronization networks during the WCST. Both shift and stay trials showed a pattern of sustained theta phase synchronization and alpha desynchronization, which were stronger in the shift condition. However, stronger prefrontal theta-band network synchronization was not directly linked to performance differences and was instead increased in subjects with lower levels of reward sensitivity and anticipation tendency, but greater exploration tendency. Our results therefore provide new evidence that large-scale networks of prefrontal theta-band network synchronization might be a crucial neural inter-areal mechanism for rule exploration and internally guided flexible task-switching, but not for feedback-driven rule learning.

On the other hand, we also found prefrontal alpha desynchronization to be stronger in task switching, which correlated with the number of late errors across subjects so that individuals with more alpha desynchronization made fewer errors and were also more sensitive to positive feedback. This is surprising as larger alpha synchronization is associated with higher top-down attention in attention tasks (Doesburg et al., 2009; Lobier et al., 2018; Mima et al., 2001) and VWM (J. M. Palva et al., 2010; Sauseng et al., 2005; von Stein & Sarnthein, 2000; Zanto et al., 2011) and is typically positively correlated with better task performance (Ericson et al., 2024), as in Study I. One possible explanation for our result is that disengagement of the alpha network served as a reset of the internal top-down goal (i.e., the current sorting rule). This is supported by some earlier studies in which alpha desynchronization during visual tasks was related to the tuning of attention in presence of competing sensory stimuli (Gross et al., 2004; Mylonas et al., 2016). In our study, alpha desynchronization may therefore reflect disengagement from the previously chosen wrong rule.

6.9 Theta phase synchrony and amplitude coupling coordinate rule selection

While we found that theta network synchronization did not lead to direct improvements of task-switching performance, theta phase coupling to all amplitudes played a crucial role in higher switching accuracy and speed. Particularly, the theta phase of the right dorsolateral PFC was significantly coupled to left PFC and bilateral parietal and visual gamma amplitudes. Furthermore, we found stronger theta-gamma PAC to predict fewer late errors, and shorter RTs, along with PAC in the other frequency bands. While there is emerging evidence pointing out the significance of nested oscillations and specifically theta-gamma coupling for cognitive functioning in attention and working memory (Abubaker et al., 2021; Berger et al., 2019; Brooks et al., 2020; de Lara et al., 2018; Hermiller et al., 2020; Lisman & Jensen, 2013; Spooner et al., 2020) and global cognitive control (Alekseichuk et al., 2016; Bramson et al., 2020; Moser et al., 2024; Riddle et al., 2021; Turi et al., 2020), we prove here for the first time its role in un-cued task-switching. It has been proposed that theta-gamma PAC could

allow for rapid communication between brain areas to implement pro- and reactive cognitive control (Pagnotta et al., 2024; Verguts, 2017; Voytek et al., 2015). Consequently, theta-gamma coupling appears to coordinate the top-down selection of the correct rule set in the WCST. This interpretation is further supported by our finding that theta-gamma PAC decreased over the course of a rule series. Our study therefore extends previous notions of the role of prefrontal theta amplitudes as a cognitive control mechanism and provides detailed insights into the significance of theta phase synchronization and its dynamic interactions across anatomy and frequencies.

6.10 The role of the alpha-band across VWM and cognitive flexibility

Together, our results from Studies I and II provide new evidence for the role of frequency-specific modulations in cognitive tasks. Specifically, both studies revealed multiple concurrent modulations in the alpha-band to be predictive of task performance in VWM and cognitive flexibility, allowing for an integrated understanding of the role of alpha-band oscillations in visual cognition. Traditionally, alpha-band suppression has been associated with increased attention (Haegens et al., 2011; Jensen & Mazaheri, 2010; Thut et al., 2006), which is a core executive function intrinsically required for VWM and cognitive control tasks. Alpha oscillations have been proposed to constitute a control mechanism for neuronal excitability, tuning the cortex to an optimal neuronal state for processing (Haegens et al., 2011; Iemi et al., 2017; Lange et al., 2013; Romei et al., 2008), so that alpha amplitude increases reflect inhibitory processes (Capilla et al., 2014; Gould et al., 2011; Van Dijk et al., 2008), and conversely, their suppression facilitate neuronal excitability (Iemi et al., 2017; Lange et al., 2013; Lobier et al., 2018).

In Study II, we found alpha (8 to 13 Hz) band suppression over the PPC to predict individual differences in un-cued task-switching performance. Because interindividual variability in parietal alpha-band suppression was explained by a diminished sensitivity to positive feedback, these decreased alpha amplitudes appear to be related to increased allocation of attention to the sensory domain relevant to the switch task (Cooper et al., 2016; Proskovec et al., 2019; Rapela et al., 2012; Sauseng et al., 2006; Wu et al., 2015) and putatively modulating neuronal excitability (Balestrieri & Busch, 2022; Haegens et al., 2011; Iemi et al., 2017; Lange et al., 2013). While the findings on Study II are in accordance with previous notions of alpha-band purely reflecting attention, where the parietal alpha-band suppression could have facilitated enhanced perception and VWM encoding of the card features in the upcoming trial, it cannot explain why multiple concurrent modulations in the alpha band explained larger VWM capacities in Study I. Here, we found larger alpha to low-beta (6 to 17 Hz) band amplitude suppression over visual areas during encoding, followed by sustained alpha-beta (10 to 17 Hz) band suppression and a load-related increase of prefrontal and posterior high-alpha and low-beta (10 to 17 Hz) band amplitudes. These amplitude

modulations together, namely the sustained suppression of both low-alpha and alpha-beta oscillations and an altered load-related late alpha-beta amplitude increase, explained differences in VWM capacity between bilateral and unilateral VWM.

Therefore, our results support the view that multiple dissociable alpha sources across frequencies and space are involved in visual cognition (Benwell et al., 2019; Cruz et al., 2025; Lobier et al., 2018; Palva & Palva, 2011; Trajkovic et al., 2024), independently supporting attention (Benwell et al., 2022; Benwell et al., 2017; Di Gregorio et al., 2022; Samaha et al., 2017; Samaha et al., 2022) and VWM (Palva & Palva, 2011; Poch et al., 2017; Rodriguez-Larios et al., 2022). The combined findings from Study I and II also demonstrate a functional overlap of the high-alpha and low-beta bands in visual cognition, suggesting that the low-beta band can further support functions traditionally associated only with alpha activity.

Additionally, we also found phase synchronization between frontal and parietal brain areas to be crucially involved in both VWM and cognitive flexibility. While larger VWM capacity was predicted by stronger synchronization in the alpha band, the opposite was true for better performance in the WCST. Similarly to alpha-band amplitude modulations, these findings therefore suggest a double role for the frontoparietal alpha network, so that it on the one hand supports top-down attention (D'Andrea et al., 2019; Lobier et al., 2018), whose reset in task switching was critically associated with fewer late errors in Study II. On the other hand, increased synchronization in this network also explained individual performance variability in VWM performance in Study I in line with previous research (Ericson et al., 2024; J. M. Palva et al., 2010). In conclusion, both local and large-scale oscillatory activity in the alpha band seem to underlie distinct roles in attention and VWM, which together enhance performance also in cognitive flexibility.

6.11 Limitations and outlook

In this thesis, I used EEG and MEG to record the local and large-scale network activity of neuronal oscillations while participants were completing tasks to measure their cognitive functions, specifically VWM and cognitive flexibility. The excellent temporal resolution of EEG and MEG makes them well-suited for investigating brain oscillations underlying cognitive functions, as they directly measure neuronal activity and thus avoid the delays associated with the hemodynamic response in fMRI. Both modalities allow for the investigation of spectral properties of neural activity, providing insight into concurrent modulations of local oscillation amplitudes and inter-areal phase synchronization between neuronal populations. However, EEG and MEG face limitations rooted in their physical principles, most notably, the inverse problem of signal source estimation, which requires mathematical assumptions that can limit spatial accuracy (Hari & Puce, 2017). Additionally, both modalities have reduced sensitivity to deep brain structures, which is due to magnetic field decay with distance in MEG, and volume conduction in EEG, where the varying conductivity of head tissues lead to a lateral spread (van den Broek et al., 1998). Moreover, MEG is largely insensitive to radial

sources because of magnetic field orientation, while EEG can detect sources of all orientations, albeit with lower spatial precision (Baillet, 2017).

Here, to address the limitations of EEG in spatial resolution and source localization, we constructed individual source models using the MNE framework, which allows for anatomically constrained inverse solutions (Gramfort et al., 2014; Hari & Puce, 2017). In addition, we used 256-channel high-density EEG with improved spatial resolution in comparison to traditional EEG systems and combined it with subject-specific conductivity models derived from structural MRIs to improve the accuracy of the forward model and reduce spatial smearing caused by volume conduction. Additionally, advanced preprocessing techniques, including artifact rejection and independent component analysis, were applied to enhance signal quality and minimize contamination from non-neural sources (Barbati et al., 2004; Urigüen & Garcia-Zapirain, 2015). Looking ahead, there are emerging techniques making use of computational approaches, such as deep learning-based source reconstruction (Awan et al., 2019; Hecker et al., 2021; Sun et al., 2023) and (real-time) multimodal data fusion of EEG or MEG with fMRI (Cichy & Oliva, 2020), which may further improve the spatial accuracy of non-invasive brain electrophysiology in the future.

Beyond methodological considerations, future research should also include further exploration of the cognitive constructs investigated in this thesis to deepen our understanding of the neuronal mechanisms underlying VWM and cognitive flexibility. In Study I, we set out to understand the neural correlates of the BFA of VWM. Our results revealed modifications in oscillation amplitudes and inter-areal phase synchronization, specifically in the alpha and beta band, to predict differences in VWM capacity between the unilateral and bilateral conditions. While it has been widely acknowledged that the right brain hemisphere has an advantage at spatial processing over the left hemisphere, the exact mechanisms underlying this have remained subject to suspicion. Here, we presented oscillatory dynamics associated with processing of unilateral stimuli, which takes place largely in the contralateral hemispheres. While we presented compelling evidence for phase-synchronized networks operating between anterior and posterior brain areas as well as between hemispheres for bilateral VWM, future research could integrate EEG/MEG phase-synchrony analysis with diffusion-weighted imaging and VWM tasks to determine whether these oscillatory network dynamics are supported by underlying white matter architecture. In particular, the role of the corpus callosum in mediating interhemispheric communication warrants further investigation, as it has been linked to synchronized neural activity and cognitive performance across hemispheres (Caffarra et al., 2024; van der Knaap & van der Ham, 2011). While behavioral performance in a visuospatial attention task has been associated with more directional and linear white-matter connectivity (Tuch et al., 2005), the link to functional connectivity has remained poorly understood. Exploring whether specific callosal subregions facilitate the BFA in VWM could therefore provide insights into the anatomical basis of interhemispheric integration in healthy individuals and the resulting functional network possibly underlying a shared VWM storage.

In Study II, we demonstrated that individual variability in un-cued task switching is driven by differences in learning speed and sensitivity to feedback, which are underpinned by distinct local and large-scale oscillatory network mechanisms. Higher switching accuracy was predicted by local gamma band amplitude increases and parietal alpha and beta band suppression as well as sustained frontoparietal alpha band network desynchronization. Importantly, the strength of these neural mechanisms was modulated by individuals' responsiveness to positive and negative feedback, highlighting a dynamic interaction between feedback sensitivity, learning speed and oscillatory modulations. However, as our study cohort consisted of healthy young adults, future research should investigate whether these brain-behavior relationships are preserved or altered across the adult lifespan, particularly given that cognitive flexibility tends to decline with age (Guarino et al., 2020) associated with changes in brain activity (Kupis et al., 2021; Peltz et al., 2011). Special emphasis could be placed on how age-related changes in local and inter-areal oscillatory dynamics during task switching are mediated by reward and punishment sensitivity.

7 Conclusions

In this doctoral thesis, I investigated the dynamic changes in neuronal oscillations during VWM and un-cued task-switching associated with interindividual performance differences. Previous research has associated cognitive functions with various changes in rhythmic neuronal oscillations that provide a mechanism for regulation and temporal coordination of information processing across local and large-scale neuronal populations. However, there is a limited understanding of how individual and moment-to-moment variability in spatio-temporal patterns of neural oscillations would predict performance variability in cognitive tasks. Here, I examined the oscillatory mechanisms underlying the variability in VWM capacity and cognitive flexibility to show how these dynamics relate to behavioral differences between individuals, using EEG and MEG.

In this thesis, I revealed the dynamic changes in neuronal oscillations during VWM and un-cued task-switching. In Study I, we found the BFA to be associated with multiple concurrent, but anatomically and spectrally separate, modulations in the alpha band to predict higher maximum capacities in bilateral than unilateral VWM. Study I therefore demonstrated that the electrophysiological basis of the BFA in VWM is both in the changes in attentional deployment and enhanced interareal integration. In Study II, we revealed alpha, beta, and gamma band amplitudes together with alpha desynchronization following feedback to predict better performance in un-cued task-switching. These brain-behavior relationships were mediated by sensitivity to positive and negative feedback. In addition, we found increased theta-gamma phase amplitude coupling during switch trials to be associated with better performance. Study II demonstrated that un-cued task switching is characterized by a multitude of concurrent modulations in amplitude and phase across frequency bands, the size of which is explained by the individuals' reactivity to feedback.

Both studies presented in this thesis offer compelling evidence for the critical role of neuronal oscillations in visual cognition, specifically in explaining individual differences in VWM and task-switching performance. These findings extend the current knowledge of the functional contributions of distinct frequency bands, particularly the alpha band. Contrary to the traditional view that alpha oscillations primarily subserve attentional processes, my results demonstrated that multiple mechanisms operating in the alpha band independently support attention and WM. This dual role highlights that task performance is best predicted not by isolated local amplitude changes, but by a combination of multiple concurrent amplitude modulations and dynamic changes in inter-areal phase-synchronized networks.

Importantly, we also discovered that in contrast to previous notions, the theta band did not predict the interindividual variability in cognitive flexibility but was instead indirectly involved in anticipatory processes including task learning. On the other hand, our results reveal that alpha band suppression related to attention supported task switching through advance

attentional preparation of the next trial. Additionally, we demonstrate that individual variability in un-cued task switching is due to differential learning speed and sensitivity to feedback, the neural basis of which relies on distinct local and large-scale oscillatory network mechanisms. Collectively, these findings deepen our understanding of the complex, distributed, and frequency-specific dynamics of neuronal oscillations that underlie key cognitive functions, emphasizing the spectrally, temporally, and anatomically unique contributions of oscillatory activity to VWM and cognitive control.

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