NEURAL OSCILLATIONS FOR COGNITIVE COORDINATION & INTEGRATION

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Abstract

Attention influences perception, perception builds the basis of memory and memory shapes future action. Human everyday behavior is based on a complex cascade of interactive cognitive processes. Just like a perfectly functioning clockwork requiring the exact timing of each of its gears to enable flawless interaction between the individual system components, this cognitive cascade calls for the precise coordination of the underlying neural processes and their integration. Neural oscillations reflect ongoing fluctuations of neural network excitability, creating more or less favorable time windows for successful information processing. In this thesis, it will be argued that this characteristic makes neural oscillations an ideal candidate for coordinating the timing of individual cognitive processes and their interaction.

For this purpose, three projects will be presented, which investigated the suggested role of neural oscillations for cognitive coordination and integration. The first two projects evaluated the causal relevance and temporal dynamics of attention-driven alpha power lateralization. The third project probed theta:gamma phase-phase coupling and evoked gamma activity as emerging signatures of memory matching in visual perception. Together, the results of these three projects suggest that dynamic alpha power modulations support attentional tuning to task-relevant points in space and time and that theta:gamma phase-phase coupling and evoked gamma activity provide time windows for the interaction between visual perception and mental templates stored in working and long-term memory, respectively.

List of Abbreviations

EEG	Electroencephalography
ERP	Event-related potential
LTM	Long-term memory
MUM	Match-and-utilization model
WM	Working memory

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1. Introduction

1.1. A Cascade of Interactive Cognitive Processes

As you read this thesis, you pay attention to its content while ignoring distracting email notifications, you remember the individual words to combine them into coherent sentences and you access your knowledge about the introduced concepts to evaluate the validity of the expressed statements. This cascade of cognitive processes, while having long been considered a unidirectional series of distinct cognitive events, is increasingly viewed as highly dynamic and interactive (Styles, 2005). The need for such complex cognition arises from the constantly changing and multidimensional world surrounding us, permanently providing way more information than severely limited human processing systems could handle. This limitation of cognitive resources implies that only a small subset of information from the rich sensory environment can be processes at a time and that this information needs to be carefully selected from the overwhelming amount of information constantly competing for access to limited human processing systems (*biased competition model;* Desimone & Duncan, 1995). *Top-down selective attention*, defined as the ability to focus on information that is relevant to the current behavioral goals (such as a spatial location, time point, object or feature) while ignoring task-irrelevant information (Carrasco, 2011; Posner, 1980), is the solution to such limitation problems and therefore a central component in many cognitive processes.

1.1.1. Working Memory & Attention

Working memory (WM) describes the ability to actively maintain and manipulate a limited amount of information (in the range of a few chunks) for a limited amount of time (in the range of a few seconds) to guide behavior when this information is no longer accessible in the external world (Baddeley, 2003; Baddeley et al., 2009; Cowan, 2001, 2008; Luck &

Vogel, 1997; Miller, 1956). Selective attention provides the opportunity to reduce the negative consequences of WM limitations by focusing encoding, maintenance and retrieval on task-relevant information (Awh et al., 2006; Chun & Turk-Browne, 2007; Souza & Oberauer, 2016). In line with this reasoning, attended information (both in the sensory and mental space) has been found to be remembered better than unattended information (Botta et al., 2010; Griffin & Nobre, 2003; Schmidt et al., 2002) and improved WM performance has been associated with successful attentional filtering, preventing limited storage units to be occupied by task-irrelevant information (Vogel et al., 2005; Zanto & Gazzaley, 2009). Conversely, secondary attention tasks have been observed to disrupt WM maintenance (Feng et al., 2012; Liang et al., 2019), highlighting the dependence of WM processes on attentional resources and the efficient allocation of such.

In addition to this close behavioral association, attention and WM have both been found to top-down modulate stimulus-related processes (i.e., facilitate processing of relevant information and/or suppress processing of irrelevant information) in largely overlapping sensory areas, supervised by a common fronto-parietal control network (Corbetta et al., 1990; Hillyard et al., 1998; Lepsien & Nobre, 2007; Nobre et al., 2004; Rutman et al., 2010; Schoenfeld et al., 2007; Zanto, Rubens et al., 2011). Attention and WM have therefore been suggested to represent two highly related concepts associated with information selection in the external and internal world respectively (Chun, 2011; Chun et al., 2011), with fronto-parietal top-down control as common neural principle (Awh & Jonides, 2001; Corbetta & Shulman, 2002; Gazzaley, 2011; Gazzaley & Nobre, 2012; Postle, 2006).

1.1.2. Memory, Attention & Perception

Not only can memory benefit from attention, but also vice versa. Top-down predictions of future events based on prior experience (such as the knowledge about a friend typically wearing a specific shirt) can help to allocate limited attentional resources more efficiently. Such top-down predictions have been suggested to be implemented as mental templates, which are stored in memory where they can be compared against incoming bottom-up information (known as *memory matching* or *template-to-input matching*) and be updated accordingly (*predictive coding;* Friston, 2005).

In line with this hypothesis, attention has been found to be guided by the contents of memory (Soto et al., 2008; Woodman & Chun, 2006), leading to shorter search times when target-defining features are known in advance and hence pre-activated (Hodsoll & Humphreys, 2005) or when real-world scenes provide semantic and/or episodic information about likely target locations (Võ & Wolfe, 2015). Such memory-based attention guidance can also be implicit, such as in the case of contextual cueing where target detection is typically faster for repeated stimulus configurations (Chun, 2000). Conversely, loading WM with task-irrelevant information has been found to impair attention (Feng et al., 2012; Woodman & Luck, 2004), with a decreasing protection against distractor interference for increasing memory loads (de Fockert et al., 2001). Attention, perception and memory thus seem to be far more dynamic and interactive than originally proposed (Styles, 2005).

1.1.3. Working Memory & Long-Term Memory

Similar to the emergent evidence for a large conceptual overlap and functional interaction between attention, memory and perception, there is an increasing amount of literature suggesting that WM and *long-term memory* (LTM) might be less compartmentalized than traditional models suggest (D'Esposito & Postle, 2015; Schurgin, 2018). Based on the definition of LTM as passive storage system that (in contrast to WM) is theoretically unlimited in capacity and duration (Baddeley et al., 2009; Cowan, 2008; Fell & Axmacher, 2011), short- and long-term memory retention have originally been considered two separate processes (Atkinson & Shiffrin, 1968).

The prominent *multi-component model* of WM (Baddeley, 1986, 1991, 1992; Baddeley & Hitch, 1974), for example, assumes the existence of two specialized systems that are dedicated to temporary (rather than permanent) information storage, namely the *visuospatial sketchpad* for visual/spatial material located in right parieto-occipital cortices and the *phonological loop* for verbal material located in left temporal-parietal cortices. These two slave systems are thought to be coordinated by an attentional control system, referred to as the *central executive* based in frontal brain areas. While these WM systems have traditionally been considered as largely separate from LTM, in a later version of the model a fourth component was added in the form of a multidimensional memory system called the *episodic buffer*, which is proposed as an interface for the interaction between the various components of WM, as well as for their interaction with LTM (Baddeley, 2000, 2003, 2010, 2012).

Recent state-based models of WM go even one step further and suggest that WM does not only interact with LTM, but rather reflects an attention-based reactivation of LTM contents, rendering the transfer of relevant memory representations into dedicated WM buffers unnecessary (D'Esposito & Postle, 2015). The *embedded process model* of WM (Cowan, 1988, 1999, 2001, 2008) as one of its most famous representatives, for example, interprets WM as capacity-unlimited but decay- and interference-susceptible reactivation of relevant LTM contents (i.e., *activated LTM*), of which only a small portion can be actively maintained and sufficiently protected through attention (i.e., *focus of attention*). WM and LTM are therefore supposed to reflect two different states of the same memory system, rather than two separate stores *per se*.

In line with the proposed link between WM and LTM, contents with an existing representation in either of these two memory systems have been associated with improved performance when being probed in the other domain thereafter (Cotton & Ricker, 2021; Jackson & Raymond, 2008); and the fidelity of a few items simultaneously maintained in WM has been closely linked to the fidelity of hundreds of items stored in LTM (Brady et al., 2013; Xie et al., 2020). Moreover, brain activation patterns recorded during a categorical LTM task have proven to be successful classifiers for the same stimulus categories used in a WM task (Lewis-Peacock & Postle, 2008). And spatial locations either maintained in WM or retrieved from LTM have been associated with similar, sensory-like activation patterns in retinotopic, parieto-occipital cortices (Vo et al., 2022), highlighting the close relationship between the behavioral effects and neural representations of WM and LTM.

Thus, the above sections suggest that, just like the gears in a clockwork, perception, attention, and memory constitute key components of the cognitive cascade, of which successful coordination and interaction is fundamental to everyday behavior. This ‘cognitive clockwork’ requires the precise temporal tuning of individual mental processes with respect to the dynamically changing requirements of the external world and the other contributing internal events. In the next section, it will be suggested that *neural oscillations* might be the ideal neural candidate for the temporal coordination of individual cognitive processes and their interaction.

1.2. Neural Oscillations for Cognitive Coordination & Integration

The basis for the herein suggested role of neural oscillations in the coordination and integration of higher-order cognition, is their physiological origin and consequent potential to affect neural communication via diverse parameters and their interaction, which will be further described in the following passages.

1.2.1. Origin & Characteristics of Neural Oscillations

In a resting neuron, the intracellular space is more negatively charged than the surrounding extracellular space, giving rise to a transmembrane potential (Buzsáki et al., 2012). When a neuron receives excitatory postsynaptic input from an upstream neural population, this leads to an influx of positive charges at the synapse, creating a local extracellular sink. The resulting depolarization of the transmembrane potential drives positive charges away from the synapse and out of the cell, resulting in a local extracellular source, creating an electric dipole. If this event takes place in a large population of neurons at the same time, the resulting dipoles sum up and give rise to a measurable extracellular field potential. The sinusoidal fluctuation of this extracellular field as primary result of rhythmic postsynaptic inputs synchronized across large groups of neurons therefore provides a close link to neural network activity and is called a neural oscillation (Buzsáki, 2006).

Neural oscillations can be recorded non-invasively in humans with excellent temporal resolution (in the millisecond range) and reasonable spatial resolution (in the centimeter range) by placing electrical sensors on the scalp, a method known as electroencephalography (EEG). Each of the hereby recorded oscillations can be characterized by three key features. The *frequency* of a neural oscillation (i.e., the number of cycles per second) depends on the size and proximity of the underlying cell population, with small, local networks (associated with short conduction delays) operating via high-frequent (spatially quickly degrading) oscillations and large, global networks (associated with long conduction delays) operating via low-frequent (spatially slowly degrading) oscillations (Buzsáki, 2006; Buzsáki & Draguhn, 2004; von Stein & Sarnthein, 2000). The *amplitude* or *power* of a neural oscillation (i.e., its magnitude) depends on the number, architecture and synchronicity of neuronal inputs, with an increasing signal strength for a growing number of parallel and synchronously active neurons, and can thus be considered a signature of overall network activity or readiness to respond (Buzsáki et al., 2012). The *phase* (i.e., the position within the oscillatory cycle) reflects the momentary excitability of the underlying neuronal population (i.e., its sensitivity to synaptic input and its likelihood for synaptic output) and is thus indicative of more or less favorable time intervals for successful information transmission (Buzsáki & Draguhn, 2004).

In line with these considerations, the amplitude of neural oscillations has been linked to activation patterns in brain imaging (Laufs, 2008; Laufs et al., 2003; Zumer et al., 2014) and, together with the momentary phase, has been found to affect the strength with which the brain responds to magnetic stimulation (Berger et al., 2014; Sauseng, Klimesch, Gerloff & Hummel, 2009). Similarly, oscillatory amplitude and phase have been shown to affect if and how quickly an external stimulus is processed by the brain (Busch et al., 2009; Ergenoglu et al., 2004; Lakatos et al., 2008); and neuronal spiking has been shown to be limited to certain phases of the surrounding network oscillation, accordingly (*duty cycle;* Haegens, Nácher et al., 2011). Together, the amplitude and phase of a neural oscillation can thus strongly influence signal transmission in the brain and have hence been suggested to provide valuable information about a range of different cognitive processes (Sauseng & Klimesch, 2008).

In addition to their individual contribution to the tuning of cognition, oscillatory amplitude and phase might further exert interactive effects on signal transmission. In contrast to the traditional assumption that amplitude modulations equally affect the oscillatory peaks and troughs, power changes in some oscillations have been found to affect one phase more strongly than the other (Mazaheri & Jensen, 2010). Such asymmetric amplitude modulations might change the ratio between excitatory and inhibitory phases and thus the relative duration of the duty cycle and the time window for successful information transmission (Jensen & Mazaheri, 2010). Oscillatory power changes might therefore indirectly influence the timing of cognitive processes by modulating relative phase contributions (and hence the probability of a stimulus to be successfully and quickly processed by the brain).

1.2.2. Interactions of Neural Oscillations

The previous section highlighted the importance of oscillatory amplitude and phase for local information processing. However, as illustrated in the previous chapter, cognitive processes (especially those of high complexity) are typically associated with large-scale neural activity across anatomically distinct networks, calling for spatial integration. Synchronization of distributed neural activity has been suggested as key mechanism for the dynamic formation of functional cell assemblies (Singer, 1999), the communication therein (Fries, 2005, 2015) and, accordingly, large-scale integration (Varela et al., 2001). More specifically, based on the close relationship between oscillatory phase and neural excitability (Buzsáki & Draguhn, 2004), phase synchronization has been suggested to support the successful communication between anatomically distinct cell assemblies by providing time windows for cortical integration through temporal alignment between the output of the sending population and the excitable phase of the receiving population (*communication through coherence;* Fries, 2005, 2015). According to this account, neural oscillations would thus not only affect local cognitive events through their amplitude and phase, but also their interaction in distributed networks through inter-areal phase synchronization; a proposal that has received empirical support from various cognitive domains (Sauseng & Klimesch, 2008; Siegel et al., 2012).

However, as outlined in the previous chapter, cognitive functions are not only supported by distributed neural networks, but they are also highly interactive. If individual cognitive processes are supported by specialized neural networks of different complexity (e.g., local perception vs. global attention) and if the network dimensionality is related to the frequency with which these networks communicate (Buzsáki, 2006; Buzsáki & Draguhn, 2004; von Stein & Sarnthein, 2000), then it becomes clear that spatial integration through within-frequency synchronization is not sufficient for such interactions. Instead, successful information exchange between different cognitive operations and their underlying neural networks (oscillating at different frequencies) calls for spectral integration through cross-frequency synchronization (Canolty & Knight, 2010; Palva & Palva, 2018).

The two most prominent mechanisms for cross-spectral integration are *phase-amplitude coupling* and *phase-phase coupling* (Canolty & Knight, 2010; Palva & Palva, 2018). Phase-amplitude coupling describes the amplitude modulation of a fast oscillation by the phase of a slow oscillation (Palva et al., 2005; Vanhatalo et al., 2004). It has been suggested that such phase-amplitude coupling might cooperate with low-frequency phase entrainment to align spike-based computation coordinated by high-frequent oscillations with external sensory events or internal cognitive processes (Canolty & Knight, 2010). However, since phase-amplitude coupling is independent of the phase of the faster oscillation, it does not relate to spike-time correlations as central prerequisite for neuronal communication (Palva & Palva, 2018). Phase-phase coupling, in contrast, refers to a stable phase relationship between a slow and a fast oscillation (Palva et al., 2005; Tass et al., 1998), allowing for millisecond-range synchronization of neural activity (Palva & Palva, 2018). In line with these theoretical considerations, cross-frequency synchronization has been suggested as key mechanism for several cognitive processes and their interaction (Canolty & Knight, 2010; Fell & Axmacher, 2011; Palva et al., 2005; Sauseng & Klimesch, 2008), with phase-amplitude and phase-phase coupling supporting different cognitive functions (Siebenhühner et al., 2016).

Taken together, oscillatory amplitude and phase, as well as their synchronization across brain areas and frequency bands constitute two possible mechanisms for the coordination of individual cognitive processes and their interaction; the former by tuning local information processing and the latter by providing time windows for cortical integration. Empirical evidence for the role of neural oscillations in coordinating individual cognitive processes and their interaction will be presented in the following chapter.

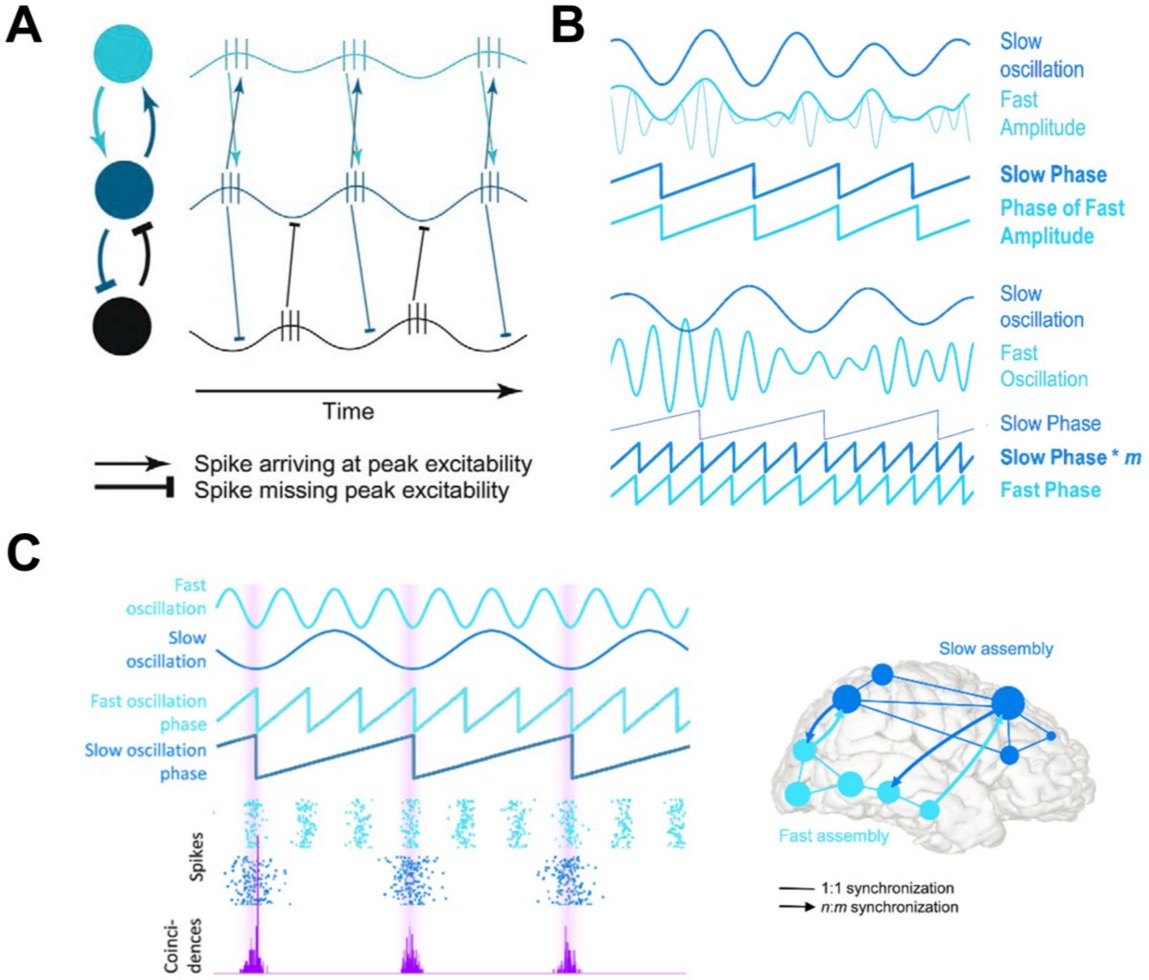

Figure 1. Principles of neural communication through coherence and cross-frequency synchronization. Successful information transmission requires the output of the sending population to reach the receiving population at states of high excitability (A). Phase-amplitude coupling and phase-phase coupling (B) describe a stable relationship between the phase of a slow oscillation and the amplitude (upper panel) or phase (lower panel) of a fast oscillation, respectively. Phase-phase coupling (but not phase-amplitude coupling) is associated with synchronized neural activity between the involved cell assemblies (C). (A) modified from Trends in Cognitive Sciences, Vol. 9(10), Fries, ‘A mechanism of cognitive dynamics: Neuronal communication through neuronal coherence’, 474-480, Copyright (2005)

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1.3. Oscillatory Signatures of Attention, Perception & Memory

In line with the different cognitive processes operating via specialized neural networks (e.g., local perception vs. global attention) and the suggested inverse relationship between network size and oscillatory frequency (Buzsáki, 2006; Buzsáki & Draguhn, 2004; von Stein & Sarnthein, 2000), different cognitive operations have been assigned to different oscillatory frequency bands (Başar et al., 2001; Sauseng & Klimesch, 2008; Ward, 2003). This chapter summarizes the current state of research about the oscillatory signatures of attention, perception and memory (and their interaction in memory matching) as central components in the cognitive cascade underlying everyday behavior.

1.3.1. Alpha Oscillations & Attention

Alpha oscillations, rhythmical brain activity around 8-12 Hz, are a dominant feature of the human EEG (Berger, 1929) and, while traditionally having been assigned a passive idling function (Adrian & Matthews, 1934; Pfurtscheller et al., 1996), are now widely accepted as active mechanism for cortical (dis-)inhibition and oscillatory correlate of (top-down) attention (Foxe & Snyder, 2011; Jensen & Mazaheri, 2010; Klimesch et al., 2007; Palva & Palva, 2007). In line with this interpretation and the inverse relationship between alpha oscillations and cortical excitability (Haegens, Nácher et al., 2011; Romei, Brodbeck et al., 2008; Romei, Rihs et al., 2008; Sauseng, Klimesch, Gerloff & Hummel, 2009), low pre-stimulus alpha power over posterior brain areas has been predictive for successful visual detection and contrast discrimination (Ergenoglu et al., 2004; Hanslmayr et al., 2005, 2007; van Dijk et al., 2008). Alpha oscillations have also been associated with the active allocation of attentional resources in memory and perception (Cooper et al., 2003; Gevins et al., 1997; Klimesch et al., 1996), including the top-down prioritization of relevant task elements and/or the selective suppression of task-irrelevant ones (Foxe et al., 1998; Haegens et al., 2010; Jokisch & Jensen, 2007; Sauseng, Klimesch, Heise et al., 2009).

One of the most prominent electrophysiological signatures, detectable even through visual inspection of the raw EEG signal, are alpha power modulations following covert visuospatial attention shifts (i.e., changes of mental focus without movement of the gaze; Posner, 1980). Attention-driven alpha amplitude changes typically include posterior *alpha power desynchronization* (referring to a signal decrease due to a reduction of synchronized neuronal activity) contralateral to the locus of attention (Barne et al., 2020; Popov et al., 2019; Sauseng, Klimesch, Stadler et al., 2005; Yamagishi et al., 2005) and sometimes *alpha power synchronization* ipsilateral to it (Kelly et al., 2006; Rihs et al., 2007; Worden et al., 2000). The strength of such attention-driven alpha power lateralization has been shown to impact task performance, with a facilitation for previously prioritized information and an impairment for previously suppressed information (Händel et al., 2011; Kelly et al., 2009; Thut, 2006). Accordingly, alpha power stimulation in one hemisphere has been shown to impair perception in the stimulation-contralateral hemifield and to bias top-down attention away from it (Romei et al., 2010; Schuhmann et al., 2019; Taylor & Thut, 2012), suggesting that posterior alpha amplitude modulations are causally involved in spatial, top-down attention.

Despite this evidence, the causal relevance of alpha oscillations for visuospatial attention and its potential functional mechanism are still a matter of ongoing debate. While some authors support the idea of alpha-mediated *gain control* (i.e., top-down changes of local excitability in early visual brain areas; Brefczynski & DeYoe, 1999; Popov et al., 2019), other authors favor the hypothesis of a *gating function* of alpha (i.e., control of information flow from low- to high-level visual areas; (Gundlach et al., 2020; Jensen & Mazaheri, 2010; Zhigalov & Jensen, 2020; Zumer et al., 2014) and even other authors question the causal effect of alpha oscillations for spatial, top-down attention altogether (Antonov et al., 2020). A critical evaluation of the causal relevance and potential functional mechanism of alpha oscillations for visuospatial attention shifts was the first aim of this thesis (summarized in Chapter 2).

In addition to the tuning of alpha oscillations through spatial attention, there is also some evidence for a modulation of posterior alpha power through temporal attention. Posterior alpha power de-synchronization (together with a slow negative potential) has, for example, been observed around the onset of an expected target (Praamstra et al., 2006), improving subsequent stimulus discrimination and event-related potentials (ERPs; Rohenkohl & Nobre, 2011). Conversely, reductions of anticipatory alpha power desynchronization and slow negative potentials have been linked to temporal expectation deficits in older adults (Zanto, Pan et al., 2011). Whether alpha power modulations can be dynamically tuned to task-relevant moments in time to meet the requirements of our constantly changing environment, and if (or how) they interact with spatial attention, however, has not been investigated so far. Answering these questions was the second aim of this thesis.

1.3.2. Gamma Oscillations & Object Representation

Gamma oscillations, rhythmical brain activity around 30-80 Hz, are (in contrast to alpha oscillations) generally considered an electrophysiological marker of cortical engagement (Jensen & Mazaheri, 2010). More specifically, gamma waves have been suggested to enable the millisecond-range synchronization required for coherent perception (Engel & Singer, 2001; Fries, 2009; Singer & Gray, 1995) and have experimentally been closely associated with the analysis of individual sensory features and their integration into meaningful objects, accordingly (Herrmann et al., 2010; Kaiser & Lutzenberger, 2005; Martinovic & Busch, 2011; Rodriguez et al., 1999; Tallon-Baudry & Bertrand, 1999). Previous studies have, for example, reported a modulation of gamma band activity over sensory brain areas by the size, focality, contrast and spatial frequency of visual stimuli (Busch et al., 2004; Fründ et al., 2007; Schadow et al., 2007). Increased gamma power has further been observed for stimuli perceived as a coherent percept (Tallon-Baudry et al., 1996, 1997; Zion-Golumbic & Bentin, 2007); and increased gamma coherence has been found between distant neural networks involved in the representation of the same object (Rose et al., 2006), an effect that has been related to developmental improvements in Gestalt perception (Uhlhaas et al., 2009). Moreover, the latency of gamma activity has been found to mirror the behavioral delay associated with the need to perceptually rotate misoriented stimuli for object recognition (Martinovic et al., 2007). Increased pre-stimulus gamma coherence has further been observed in trials with successful perception of a short-duration stimulus (Hanslmayr et al., 2007); and high gamma power has been found to be characteristic for individuals with conscious awareness about the existence of a global stimulus structure (Ohla et al., 2007), supporting a functional role of gamma oscillations for low- and high-level perception.

Gamma oscillations have, however, not only been linked to bottom-up perception, but also to top-down processes including memory (Fell et al., 2003; Fell & Axmacher, 2011; Herrmann et al., 2010; Jensen et al., 2007; Kaiser & Lutzenberger, 2005; Roux & Uhlhaas, 2014). Enhanced gamma power and coherence have been reported during encoding, maintenance and retrieval across different WM tasks and modalities (Haegens et al., 2010; Jokisch & Jensen, 2007; Kaiser et al., 2008; Palva et al., 2010; Tallon-Baudry et al., 1998). Such WM-related gamma responses have been localized to feature-specific visual cortices (Honkanen et al., 2015), suggesting a direct link between gamma oscillations and the maintenance of WM contents. This interpretation has received additional support from findings of WM load-dependent gamma activity (Howard et al., 2003), which was further indicative of individual WM capacity (Palva et al., 2011). In line with the proposal that high-speed gamma oscillations are ideally suited to promote spike timing-dependent plasticity (Fell & Axmacher, 2011), enhanced gamma activity has also been reported during successful LTM encoding (remembered > forgotten) and retrieval (old > new; Gruber et al., 2004; Osipova et al., 2006; Sederberg et al., 2003), with stronger memory-dependent gamma effects for high- compared to low-performers (Busch et al., 2008). Similarly, gamma power has been found to increase with stimulus familiarity (Anaki et al., 2007; Zion-Golumbic & Bentin, 2007), highlighting the role of gamma oscillations for the short- and long-term storage of memory representations. Together, these results imply a general role of gamma oscillations for object representation in both, online perception and offline memory (Tallon-Baudry & Bertrand, 1999).

1.3.3. Theta Oscillations & Working Memory

Theta oscillations, rhythmical brain activity around 4-8 Hz, over frontal brain areas and their interaction with parietal cortices have been closely associated with memory processes and the top-down executive control of WM more specifically (Fell & Axmacher, 2011; Hsieh & Ranganath, 2014; Klimesch, 1999; Roux & Uhlhaas, 2014; Sauseng et al., 2010). In line with this interpretation, increased frontal theta power and fronto-parietal theta coherence have been observed across a variety of WM-dependent tasks and processes, from encoding over maintenance to retrieval (Mizuhara & Yamaguchi, 2007; Raghavachari et al., 2001; Sarnthein et al., 1998; Sauseng et al., 2004; Sauseng, Klimesch, Schabus & Doppelmayr, 2005; Sauseng, Hoppe et al., 2007; von Stein & Sarnthein, 2000). Theta power has hereby been found to parametrically increase not only with WM load, but with task demands more generally, highlighting the executive role of theta oscillations in WM processes (Deiber et al., 2007; Gevins et al., 1997; Jensen & Tesche, 2002; Onton et al., 2005; Scheeringa et al., 2009). Moreover, high theta activity during encoding and recall has been associated with successful memory retrieval (Klimesch et al., 1996, 1997; Osipova et al., 2006; Sederberg et al., 2003) and parietal theta stimulation has been found to increase WM capacity, accordingly (Jaušovec & Jaušovec, 2014). Similarly, in-phase fronto-parietal theta stimulation has been associated with speeded memory performance compared to control and out-of-phase stimulation (Polanía et al., 2012).

Theta oscillations have further been suggested to temporarily coordinate and bind individual memory items (stored in different cycles of a nested, high-frequent gamma oscillation) into one ordered multi-item memory, providing a direct link between theta oscillations and WM capacity (Canolty & Knight, 2010; Jensen & Colgin, 2007; Jensen & Lisman, 2005; Lisman & Buzsáki, 2008; Lisman & Idiart, 1995; Lisman & Jensen, 2013; Roux & Uhlhaas, 2014; Sauseng et al., 2010, 2019). Increased theta:gamma cross-frequency coupling has indeed been observed during memory retention in a variety of studies (Canolty et al., 2006; Griesmayr et al., 2010; Mormann et al., 2005; Schack et al., 2002), with its precision and load-dependent increases being indicative of individual WM performance and capacity, respectively (Axmacher et al., 2010; Chaieb et al., 2015; Sauseng, Klimesch, Heise et al., 2009). Moreover, the ratio between the length of theta and gamma oscillations has been found to significantly correlate with the capacity of short-term memory storage (Kamiński et al., 2011); and experimentally decreasing the frequency of theta oscillations (i.e., increasing the theta:gamma cycle-length-ratio) has been associated with increased memory capacity, accordingly (Vosskuhl et al., 2015). Conversely, experimentally increasing the frequency of theta oscillations has been related to a decrease of WM capacity, which was limited to stimuli presented in the stimulation-contralateral hemifield, highlighting the causal role and spatial specificity of theta oscillations and their interaction with gamma activity during WM processes (Wolinski et al., 2018).

1.3.4. Theta/Gamma Oscillations & Memory Matching

Based on the presented evidence for the role of theta oscillations in executive control processes of WM on the one hand and gamma oscillations in perception and memory storage on the other, two models have been suggested for the interaction between memory-based, top-down mental templates and bottom-up sensation during memory matching. The authors of the *match-and-utilization model* (MUM; Herrmann, Munk & Engel, 2004; Herrmann et al., 2010) suggest that gamma oscillations have been associated with both perception and memory, because even the simplest perceptual task relies on memory information and vice versa (e.g., feature binding being affected by object knowledge) and because it is exactly this interaction between perception and memory (rather than either of these two processes *per se*) that is reflected by gamma activity.

More specifically, they suggest that the comparison between memory-based mental templates and bottom-up sensation is reflected by evoked (i.e., phase-locked) gamma activity in early sensory cortices around 100 ms post-stimulus. The strength of this evoked gamma response is supposed to depend on the contingency between template and percept, with stimuli matching an already existent memory representation eliciting stronger responses due to increased synaptic connections between the corresponding neural networks. This evoked gamma response is supposed to be followed by induced (i.e., non phase-locked) gamma activity around 300 ms post-stimulus, reflecting the utilization of the matching outcome (e.g., for response selection or model updating). In line with the MUM, increased evoked gamma activity over early sensory areas around 100 ms post-stimulus has been observed for stimuli matching an existing LTM representation (Freunberger et al., 2007; Fründ et al., 2008; Herrmann, Lenz et al., 2004; Herrmann et al., 2010; Mørup et al., 2006).

Despite the empirical support for the MUM, it has been argued that when the stimulus material does not yet exist in semantic LTM (and might thus be unable to benefit from pre-strengthened synaptic connections, in contrast to the majority of stimuli used by previous MUM-supporting studies), but instead has to be actively maintained in visual WM, gamma oscillation alone might not be sufficient for the successful interaction between memory and perception (Holz et al., 2010; Sauseng et al., 2015). Based on the close relationship between gamma oscillations in perception and theta oscillations in WM, matching between these two cognitive processes has been hypothesized to involve an oscillatory signature allowing for spectral integration, namely *theta:gamma phase-phase coupling* (Sauseng et al., 2008, 2010).

In line with this reasoning, theta:gamma phase-phase coupling has been identified as central component in a cascade of oscillatory events during memory matching in a visuospatial attention paradigm (Sauseng et al., 2008). In this task, participants were asked to classify a bar stimulus (presented on the cued or uncued side of the screen) as either short or tall based on example stimuli, which had been learned at the beginning of the experiment and actively maintained as mental templates thereafter (Sauseng et al., 2008). The authors observed increased fronto-parietal theta coherence in preparation of an upcoming probe, which was followed by a reset of parietal theta oscillations shortly (around 100 ms) after its onset. This theta phase reset enabled transient coupling between the phase of local theta and gamma oscillations in parieto-occipital cortices thereafter (around 150 ms post-stimulus). For stimuli presented in the cued hemifield, this theta:gamma phase-phase coupling effect was significantly enhanced in the contralateral compared to the ipsilateral hemisphere (i.e., where bottom-up sensation met a corresponding top-down mental template). Based on these findings, a three-stage model of memory matching with templates stored in WM has been proposed (Sauseng et al., 2008, 2010). In this model, anticipatory fronto-parietal theta coherence (Step 1) is thought to reflect the reactivation of a mental template through frontal cortices, which is replayed back to early visual brain areas. Here, it can be compared against the bottom-up sensory information provided by local gamma oscillations through a phase reset of local theta oscillations (Step 2) and transient theta:gamma phase-phase coupling thereafter (Step 3).

In agreement with the proposed theta-gamma model for memory matching with mental templates stored in WM, increased theta:gamma phase-phase coupling has been observed over right-parietal brain areas around 150-200 ms post-stimulus for matching compared to mismatching probes in a delayed match-to-sample task (Holz et al., 2010). Stimulus-evoked gamma activity, in contrast, was present but did not differentiate between template-matching and template-mismatching probes, supporting the suggested specificity of theta:gamma phase-phase coupling for memory matching with templates actively maintained in visual WM. Additional support for theta:gamma phase-phase coupling in WM-based matching processes comes from a recent study investigating theta:gamma cross-frequency coupling during visual search (Biel et al., 2021). The authors report increased contralateral theta:gamma phase-phase coupling in right-occipital cortex around 150 ms post-stimulus when participants searched for a single template stored in WM compared to when participants searched for one out of three templates simultaneously stored in WM, highlighting the importance of concrete stimulus expectations for theta:gamma phase-phase coupling during memory matching in visual perception.

Contrary to previous studies providing solid evidence for both memory matching models using established mental templates (i.e., those pre-existing in LTM or those newly generated at the beginning of the experiment), real-world mental templates need to be gradually formed through repeated exposure. Investigating memory matching during the formation of new mental templates and their transition from low to high fidelity and from WM to LTM, would therefore be an important step to better understand naturalistic interactions between bottom-up sensation and top-down prediction. Moreover, such a study might help to further elaborate on the suggested sensitivity of theta:gamma phase-phase coupling and evoked gamma activity for memory matching with templates stored in WM and LTM, respectively. Advancing the research field on template-to-input matching in visual perception in that direction was the third and last aim of this thesis. All the dissertation's aims are summarized in the following chapter.

2. Thesis Aims

The overarching goal of this thesis was to probe the herein suggested role of neural oscillations for the temporal coordination of individual cognitive processes and their interaction. To this end, three projects were performed. The goal of the first project was to critically evaluate the evidence for and against a causal role of alpha oscillations in visuospatial attention and to discuss potential underlying mechanisms. This provided the basis for the second project, which examined the proposed function of neural oscillations for temporal coordination of cognition by testing the dynamics of alpha power modulations and their interaction with spatial attention in a WM task, requiring simultaneous tuning of attention in space and time. The third and last project probed the hypothesized role of neural oscillations in cognitive interactions by providing time windows for cortical integration. To address this aim, theta:gamma phase-phase coupling and evoked gamma activity were investigated as potentially complementary signatures of memory matching during the formation of new mental templates.

3. Project 1: Alpha Oscillations in Visuospatial Attention

This chapter includes the opinion article ‘Cause or consequence? Alpha oscillations in visuospatial attention’ (Peylo et al., 2021), which critically evaluates the evidence for and against a causal role of alpha oscillations in visuospatial attention and discusses potential underlying mechanisms. The article was published in *Trends in Neurosciences*.

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Contributions:

Charline Peylo, Yannik Hilla, Paul Sauseng

The author of this thesis is the shared first author of this manuscript together with YH. All authors contributed to the review, discussion and synthesis of literature and together wrote and revised the manuscript.

Cause or consequence?
Alpha oscillations in visuospatial attention

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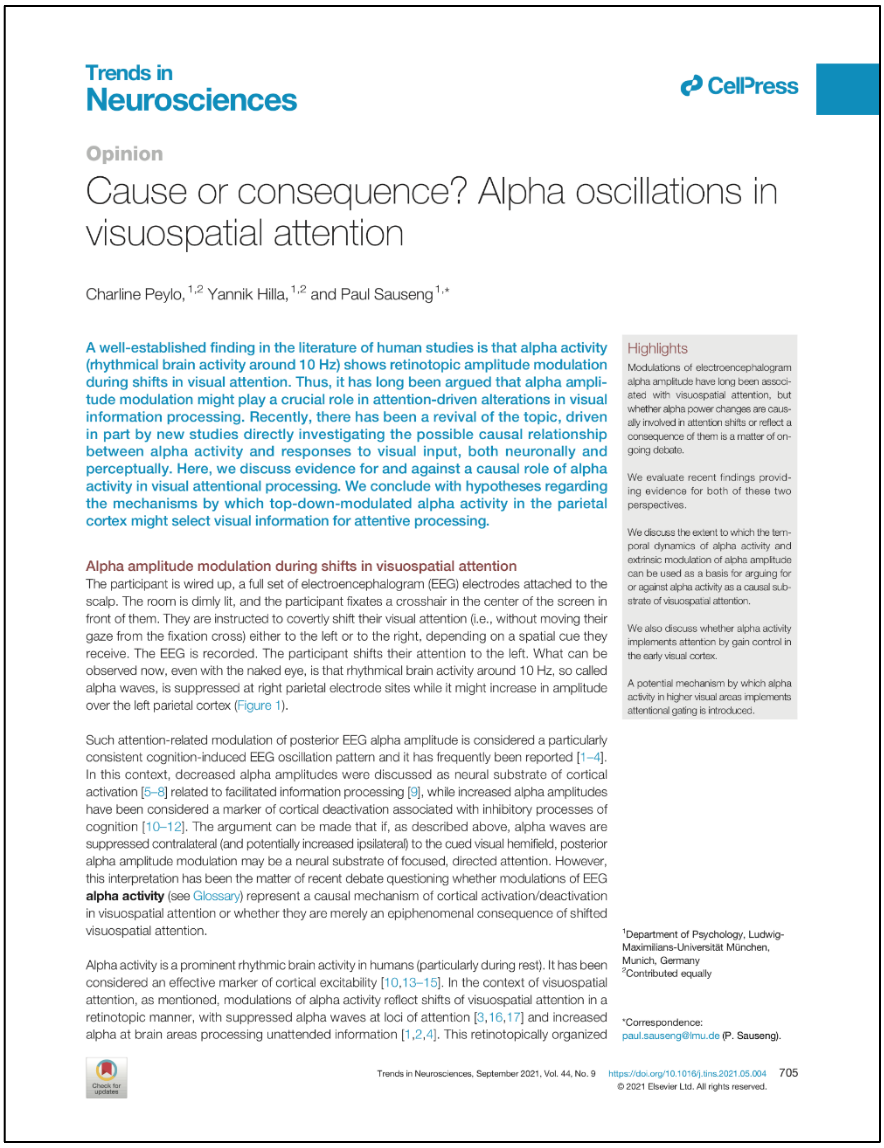

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Opinion

Cause or consequence? Alpha oscillations in visuospatial attention

Charline Peylo,[1,2] Yannik Hilla,[1,2] and Paul Sauseng[1,*]

A well-established finding in the literature of human studies is that alpha activity (rhythmical brain activity around 10 Hz) shows retinotopic amplitude modulation during shifts in visual attention. Thus, it has long been argued that alpha amplitude modulation might play a crucial role in attention-driven alterations in visual information processing. Recently, there has been a revival of the topic, driven in part by new studies directly investigating the possible causal relationship between alpha activity and responses to visual input, both neuronally and perceptually. Here, we discuss evidence for and against a causal role of alpha activity in visual attentional processing. We conclude with hypotheses regarding the mechanisms by which top-down-modulated alpha activity in the parietal cortex might select visual information for attentive processing.

Highlights

Modulations of electroencephalogram alpha amplitude have long been associated with visuospatial attention, but whether alpha power changes are causally involved in attention shifts or reflect a consequence of them is a matter of ongoing debate.

We evaluate recent findings providing evidence for both of these two perspectives.

We discuss the extent to which the temporal dynamics of alpha activity and extrinsic modulation of alpha amplitude can be used as a basis for arguing for or against alpha activity as a causal substrate of visuospatial attention.

We also discuss whether alpha activity implements attention by gain control in the early visual cortex.

A potential mechanism by which alpha activity in higher visual areas implements attentional gating is introduced.

Alpha amplitude modulation during shifts in visuospatial attention

The participant is wired up, a full set of electroencephalogram (EEG) electrodes attached to the scalp. The room is dimly lit, and the participant fixates a crosshair in the center of the screen in front of them. They are instructed to covertly shift their visual attention (i.e., without moving their gaze from the fixation cross) either to the left or to the right, depending on a spatial cue they receive. The EEG is recorded. The participant shifts their attention to the left. What can be observed now, even with the naked eye, is that rhythmical brain activity around 10 Hz, so called alpha waves, is suppressed at right parietal electrode sites while it might increase in amplitude over the left parietal cortex (Figure 1).

Such attention-related modulation of posterior EEG alpha amplitude is considered a particularly consistent cognition-induced EEG oscillation pattern and it has frequently been reported [1–4]. In this context, decreased alpha amplitudes were discussed as neural substrate of cortical activation [5–8] related to facilitated information processing [9], while increased alpha amplitudes have been considered a marker of cortical deactivation associated with inhibitory processes of cognition [10–12]. The argument can be made that if, as described above, alpha waves are suppressed contralateral (and potentially increased ipsilateral) to the cued visual hemifield, posterior alpha amplitude modulation may be a neural substrate of focused, directed attention. However, this interpretation has been the matter of recent debate questioning whether modulations of EEG **alpha activity** (see Glossary) represent a causal mechanism of cortical activation/deactivation in visuospatial attention or whether they are merely an epiphenomenal consequence of shifted visuospatial attention.

Alpha activity is a prominent rhythmic brain activity in humans (particularly during rest). It has been considered an effective marker of cortical excitability [10,13–15]. In the context of visuospatial attention, as mentioned, modulations of alpha activity reflect shifts of visuospatial attention in a retinotopic manner, with suppressed alpha waves at loci of attention [3,16,17] and increased alpha at brain areas processing unattended information [1,2,4]. This retinotopically organized

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Abstract

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Key words

Amplitude Modulation; Electroencephalogram; Entrainment; NIBS; Phase Coherence

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- We discuss the extent to which temporal dynamics of alpha activity and extrinsic modulation of alpha amplitude can be used as a basis for arguing for or against alpha activity as causal substrate of visuospatial attention
- We also discuss whether alpha activity implements attention by gain control in early visual cortex
- A potential mechanism by which alpha activity in higher visual areas implements attentional gating is introduced

Glossary

- **Alpha activity:** Neural oscillatory activity in a frequency range around 10 Hz in humans. It has been claimed that the amplitude of alpha activity is associated with cortical excitability.
- **Duty cycle:** The excitatory part of a neural oscillation's cycle. Usually the duty cycle is characterized by increased neuronal firing.
- **Entrainment:** Alignment of intrinsic oscillatory brain activity using stimulation approaches, usually rhythmic ones, such as sensory, electrical, magnetic or ultrasonic stimulation. This might lead to increased amplitude at respective and/or related frequency ranges or it could result in alignment of the neural oscillation's instantaneous phase.
- **Gain control:** Adjustment of neural activity to put greater or lesser weight on the processing of a specific incoming stimulus. Gain control has been discussed, for instance, to reflect a physiological correlate of a spotlight of attention in early visual cortex [61].
- **Gating:** A neural mechanism of modulating the flow of low-level information to higher visual cortical areas.
- **Noninvasive brain stimulation (NIBS):** Noninvasive techniques to modulate brain activity. Examples of NIBS techniques are TMS and tES. TMS alters neuronal activity by means of electromagnetic pulses generated by a coil that is held against the participant's scalp. tES stimulates neuronal tissue by means of electric currents applied via electrodes attached to the scalp. To gear into ongoing oscillatory brain activity, a series of electromagnetic pulses (rTMS) or rhythmical fluctuations of electrical current (tACS) can be delivered.

- **Phase coherence:** A measure of the presence and strength of a systematic relationship between the phase of two distinct neural oscillations (e.g., at different brain sites, with different frequencies). Phase coherence is high if the phase relationship is consistent over time (usually across trials) and low if the phase relationship varies randomly.
- **Posner Task:** Experimental paradigm to investigate the shifting of visuospatial attention. Participants are asked to keep their gaze at a fixation cross in the middle of a screen. Then, the left or the right visual hemifield is cued. Participants are asked to covertly shift their visual attention into the cued hemifield (i.e., without moving their eyes). This is followed by the presentation of a visual target stimulus either in the attended visual hemifield (valid trial) or in a smaller proportion of trials in the unattended hemifield (invalid trial).
- **Steady-state visually evoked potentials (SSVEPs):** An ERP (i.e., a neural response observable after averaging neural activity over a large number of trials) elicited by a series of rhythmically displayed visual stimuli, which is characterized by an increase in amplitude and a rhythmic amplitude modulation persisting throughout the stimulation. It is modulated by attentional processing, as indicated by an increase in amplitude in response to attended stimuli relative to unattended stimuli.

Alpha amplitude modulation during shifts in visuospatial attention

The participant is wired up, a full set of electroencephalogram (EEG) electrodes attached to the scalp. The room is dimly lit, and the participant fixates a crosshair in the center of the screen in front of them. They are instructed to covertly shift their visual attention (i.e., without moving their gaze from the fixation cross) either to the left or to the right, depending on a spatial cue they receive. EEG is recorded. The participant shifts their attention to the left. What can be observed now, even with the naked eye, is that rhythmical brain activity around 10 Hz, so called alpha waves, is suppressed at right parietal electrode sites while they might increase in amplitude over left parietal cortex (Figure 1).

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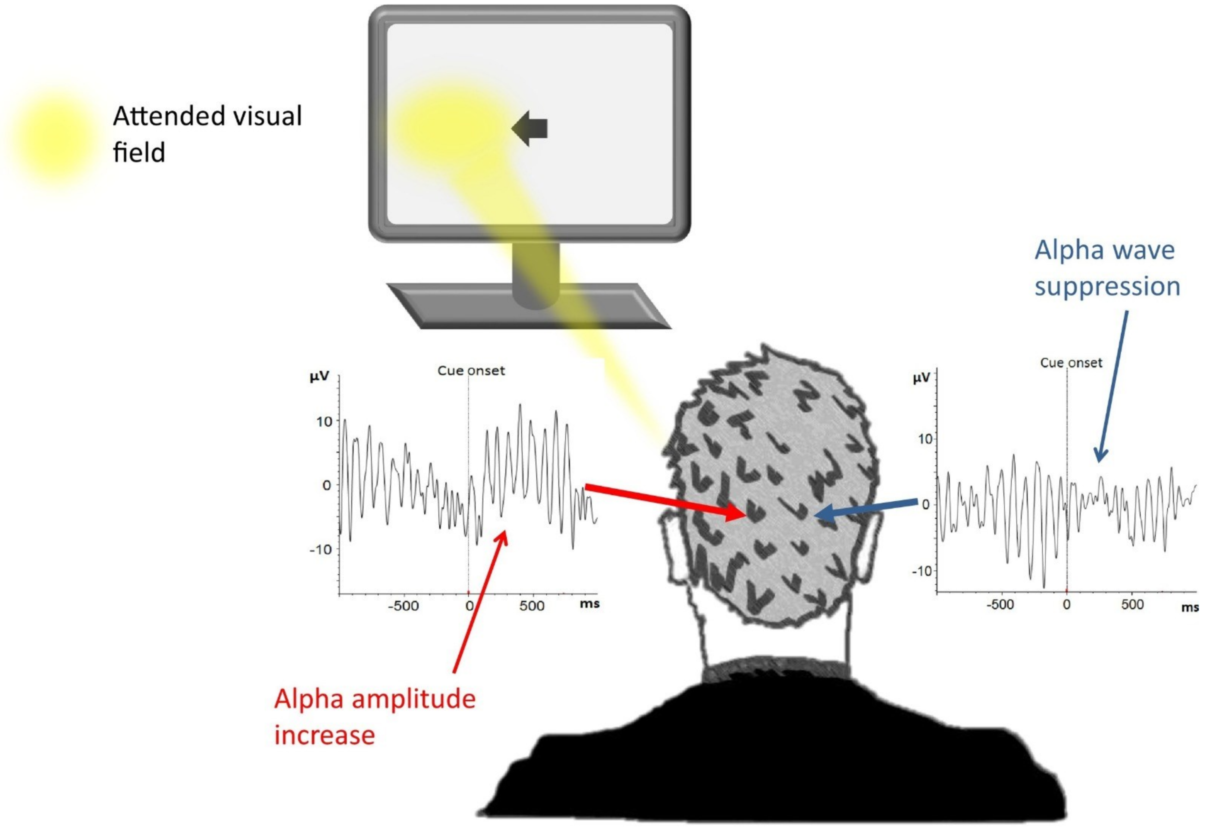

Figure 1. Retinotopic modulation of posterior alpha amplitude during covert shifts of visual attention. A participant is instructed to fixate the middle of a screen. When a cue appears (arrow pointing to the left), visual attention has to be shifted into the respective visual hemifield (i.e., the left hemifield) without any gaze movement. This shifting of visuospatial attention is usually associated with the suppression of alpha waves at parietal electroencephalogram (EEG) recording sites contralateral to the attended hemifield (in this example, the right hemisphere) and it is often paralleled by an alpha amplitude increase ipsilateral to the cued hemifield (here, the left).

Temporal dynamics of visuospatial attention and alpha activity: Arguments against a causal role?

If alpha amplitude modulation is causally involved in attention-related gain control of incoming signals, a clear prediction ensues: alpha amplitude should be the first measurement capturing any attentional effects [i.e., there should be attention-related alpha amplitude changes prior to any effects on event-related potentials (ERPs) or response times]. In line with this prediction, compared with early target-evoked ERPs [25,26], alpha activity seems to exhibit effects much earlier [2–4]; namely, already in response to an attentional cue. However, as correctly pointed out in the context of a recent study [24], this does not necessarily lend evidence to the idea that alpha activity represents the initial neural response of visuospatial attention shifts. To examine the issue further, the forementioned study measured **steady-state visually evoked potentials** (**SSVEPs**) as a proxy for neural activity from the early visual cortex modulated by visual attention [24]. Additionally, EEG alpha activity and behavioral attention parameters were acquired. The authors observed an attention-related increase of SSVEP amplitudes shortly prior to lateralized suppression of alpha waves. Modulation of alpha activation was clearly lagging behavioral estimates of when attention was shifted to the periphery. Therefore, it was concluded that alpha amplitude modulation cannot be the causal substrate of visuospatial attention but rather must be the consequence of shifted attention.

However, in a similar study [23] lateralized alpha modulation preceded attentional alterations of SSVEPs in earlier visual areas. Nevertheless, alpha activity did not have any direct impact on SSVEPs in the visual cortex. Thus, if alpha activity played a direct role in visuospatial attentional shifting, most likely it would not do so by altering sensory gain control in visual areas (as discussed later in greater detail). This is supported by recent findings, which also suggest independence between posterior alpha activity and SSVEPs [22].

Consequently, one could conclude that modulation of alpha activity is not causally involved in shifts of visual attention – but not so fast! First, whereas SSVEPs have a notable signal-to-noise-ratio due to averaging over trials, alpha activity can be far noisier. All signals that do not constitute the evoked response should, in theory, be eliminated from the SSVEP due to averaging. Alpha amplitude is usually rectified before averaging over trials, and therefore random noise overlapping in frequency space with alpha activity will be picked up by the signal. Thus, a high level of noise could make it impossible to relate alpha amplitude with SSVEPs. Second, to obtain estimates of alpha amplitude it is necessary to filter raw EEG data in one way or another. All filters will lead to smearing in the temporal and spectral domains. The exact temporal evolution of true alpha activity, therefore, is difficult to determine. Third, shifting visual attention does not solely modulate alpha amplitude. A concurrent increase in theta activity (rhythmical activity at frequencies slightly lower than the alpha frequency band) has been reported (e.g., [3,27]). Due to spectral smearing when filtering EEG data, this transient increase in theta activity could 'leak' into the alpha band and make the latter look as if its amplitude were decreasing far later than it is the case for the actual, underlying alpha activity.

Most importantly, however, as pointed out in the discussion later, modulation of alpha activity could be causally involved in the implementation of visual attention even if it lags behind other effects in early visual cortex (e.g., SSVEPs); namely, if higher visual areas used alpha activity for filtering or **gating** of upstream visual information.

We would argue then that, based on the findings discussed earlier, it would be premature to dismiss a causal relation between alpha amplitude modulation and shifts of visual attention. To recapitulate: (i) the exact temporal evolution of alpha amplitude modulation is difficult to determine; (ii) genuine alpha activity can be distorted by spectral smearing due to filtering data; and (iii) alpha activity could be used as an attentional implementation mechanism further up the cortical hierarchy.

Closed-loop neural self-regulation of alpha activity and visuospatial attention: Evidence in favor of a causal role?

Closed-loop neural self-regulation (also known as neurofeedback training) is a procedure in which a continuous brain activity marker (e.g., alpha amplitude) is displayed to the participant in real time. Based on operant conditioning, the aim is to make the participant's brain 'learn' which brain activation level or pattern to produce [28,29]. This approach can be used to test whether posterior alpha amplitude modulation plays a causal role during visuospatial attention shifts. Specifically, if participants are trained to display lateralized posterior alpha activity modulation, similar to the modulation observed during shifts of visuospatial attention, their attentional processing should be altered accordingly. In a recent study employing this approach [30], participants were trained to either selectively increase left parietal magnetoencephalographic (MEG) alpha activity or right parietal alpha amplitude. In response to neurofeedback training, evoked responses were attenuated in the hemisphere where alpha had been increased and visuospatial attention performance was increased ipsilateral to the hemisphere with increased alpha amplitudes.

Neurofeedback training itself had been administered without any lateralized visual task and without a task that required shifting of visuospatial attention [30]. It seems reasonable to conclude that the study provides solid evidence for a causal role of lateralized alpha amplitude modulation in visuospatial attention control.

However, again, counter arguments could be raised. It has been argued that even when using a centrally presented, non-visuospatial-attention-like feedback task during the neurofeedback training, participants might adopt a strategy in which they covertly shift their visual attention to either the left or the right visual hemifield to provoke increased alpha activity ipsilateral (as well as decreased alpha amplitudes contralateral) to the attended hemifield [31]. In that case, during the training session participants might learn to indirectly modulate alpha activity by covertly shifting their visuospatial attention to one side (i.e., attentional biasing of one visual hemifield), which would then lead to decreased alpha activity and increased evoked responses in contralateral posterior brain areas, as well as better attentional performance within this hemifield during the subsequent attention task. In this scenario, it cannot be completely ruled out that alpha amplitude might only be the result of shifted visuospatial attention, rather than the basis thereof.

Alpha-related non-invasive brain stimulation (NIBS) and visuospatial attention: Evidence (most likely) in favor of a causal role

One of the most common approaches for testing causality in cognitive neuroscience is **NIBS** [32,33]. By applying either transcranial magnetic (TMS) or transcranial electrical stimulation (tES) in a rhythmical fashion, intrinsic brain oscillations can be entrained or perturbed [34–38]. Empirical studies following this approach provide some evidence that posterior alpha activity is causally involved in the control of visuospatial attention.

In one study, repetitive TMS at 5, 10, or 20 Hz was applied over the parieto-occipital cortex, immediately followed by a visual, near-threshold target shown in the visual field ipsilateral or contralateral to the stimulation [39]. Among the protocols, only 10 Hz stimulation (i.e., stimulation in the alpha frequency range) led to increased detection rates for targets presented ipsilateral to the stimulation site, whereas targets contralateral to TMS were less likely to be detected. So, **entrainment** of alpha activity by external rhythmical stimulation can have the same effect on visual perception as found during voluntary shifting of visuospatial attention. By increasing alpha activity in one hemisphere, visual perception is biased towards more efficient information processing in the ipsilateral visual field. There is recent evidence showing a similar effect even during a visuospatial attention task [40]. It was demonstrated that transcranial alternating-current stimulation (tACS) at participants' individual alpha frequency over the left parieto-occipital cortex altered task performance in a spatial cueing paradigm. Entraining (i.e., increasing) alpha activity contralateral to targets led to increased response times in invalidly cued trials. Importantly, this effect was observed only in endogenous shifts of attention and not in exogenous attention trials, supporting the idea that modulation of alpha activity leads to top-down-controlled changes in visual information processing.

Another noninvasive approach to test causality involves reversible, 'virtual' lesions to specific cortical locations. Applying virtual lesions at cortical regions known to be causally involved in the control of visuospatial attention was shown to impact attention-related alpha activity and task performance. In a study using a **Posner task**, repetitive TMS at 20 Hz (which causes a transient, virtual lesion) applied over the intraparietal sulcus or the frontal eye field (FEF) just following the presentation of a spatial cue led to a collapse of lateralized alpha activity and reduced task performance [41]. Moreover, TMS-induced change of lateralized attention-related alpha activity predicted response times during the Posner task.

Another study found similar results when applying slow repetitive TMS (rTMS) (causing reduced cortical excitability outlasting the stimulation) over the right FEF [42]. The stimulation led to increased response times in valid trials in a Posner task as well as obliteration of attention-related lateralized alpha activity in the cue-target-interval.

It seems reasonable to conclude, then, that posterior alpha activity is a substrate of visuospatial attention: entrainment of alpha activity leads to alterations of attentional task performance that correspond to the location of the activity being manipulated and ‘knocking out’ of lateralized alpha activity using virtual lesions leads to reduced attentional processing. While these lines of research provide evidence for a causal role of alpha modulation in visuospatial attention, the specific ways in which alpha activity might affect cortical processing remain equivocal. An idea of relevance in this context, as discussed later, is that alpha activity might not implement gain control as a neural substrate of cortical excitability in early visual areas but rather acts as a gating mechanism that controls the flow of low-level information to higher visual areas.

Alpha activity in early visual areas, parietal cortex, and frontoparietal networks: What is the specific function of alpha activity in visuospatial attention?

As pointed out earlier, it has been suggested that alpha activity represents a mechanism of controlling cortical excitability [10,12,14,43]. This, of course, should also hold for early visual areas. Related to this, it was shown that spontaneous fluctuations in alpha oscillatory activity recorded at occipitoparietal electrode sites predicted the perception of TMS-induced phosphenes [5]. Higher spontaneous pre-stimulation alpha activity representing cortical deactivation led to a reduced probability of perception of phosphenes. In other studies, it was found that the level of occipital alpha activity determined perceptual performance in visual discrimination tasks, with higher alpha amplitude being associated with poorer perception [44–46].

In addition to alpha amplitude, the instantaneous phase and inter-regional coherence of alpha oscillations are important features in the context of attentional phenomena. In particular, short-term fluctuations in perception and attention seem to correlate with phase-based measures of alpha activity. This observation is consistent with the notion that the current phase of an ongoing EEG oscillation reflects a momentary state of the neuronal population's excitability and is thus indicative of more or less favorable time intervals for successful information processing [47–49]. In a study providing an elegant example of these relationships [50], the processing of near-threshold visual targets was dependent not only on alpha amplitude but also on the alpha phase being in a preferable peak state at target onset, suggesting two supplementary mechanisms based on steady versus pulsed release from alpha-driven inhibition, respectively (see also [10,12,51-53]).

A related point of consideration is the substrates of top-down attentional control. The processes discussed above, of instantaneous alpha-phase-dependent fluctuations in visual perceptual processing, are unlikely to be directly modulated by voluntary top-down control, although they could still be critically involved in implementation of visuospatial attention [49]. By contrast, a good candidate for top-down attentional control is interregional **phase coherence** [18–20] as a proxy for synchrony and successful communication between neuronal populations [54]. During the cue-target interval in a Posner task, increased frontoparietal alpha phase coherence was observed contralateral to the visual hemifield that attention was shifted towards [3]. Moreover, high frontoparietal alpha coherence was associated with a decreased probability of missing the second of two rapidly presented targets, a phenomenon known as attentional blink, suggesting an alpha coherence-dependent tuning of an attentional filter [55]. These findings point towards a vital role of frontoparietal interaction in controlling visuospatial attention and possibly controlling the excitation level of posterior brain areas (indicated by modulated alpha amplitude). Direct evidence for this interpretation comes from a study in which, during an attentional shifting task, the FEF was transiently, virtually lesioned using TMS [42]. As mentioned earlier, this intervention led to reduced modulation of posterior alpha activity. At the same time, the prefrontal drive onto posterior parietal sites at alpha frequency was reduced. Further, this top-down prefrontal-to-parietal coupling reduction predicted interindividual differences in behavioral TMS response in the attention task.

So, does that mean that a frontoparietal attention network [56] synchronized at alpha frequency [18–20,42] controls perceptual gain in the early visual cortex by means of alpha amplitude modulation? Most likely not. As pointed out earlier, SSVEPs in the early visual cortex as a proxy of visual gain control are not correlated with alpha amplitude modulation [22,23]. Also, the FEF does not seem to directly control the excitation level of early visual cortex, as demonstrated by concurrent TMS and electrophysiological recordings [57]. In a recent MEG study [21], no evidence for alpha oscillations implementing gain control in early visual areas was found. Instead it was suggested that attentional modulation of alpha activity in parieto-occipital cortex reflected a gating mechanism; that is, alpha activity would be involved in selecting upstream information from early visual areas to be consciously processed. In other words, unlike the classical view, in which alpha power modulations are proposed as an attention mechanism affecting the likelihood of successful information processing in early visual cortex, alpha power may in fact be involved in a selection process higher up the hierarchy.

This could well explain why, for instance, in the study discussed earlier [24] attention effects of alpha activity were found to set in slightly later than initially expected. Gain control in early visual areas might be implemented largely independent of attention-related alpha amplitude modulations in the higher visual cortex (and be reflected by early effects obtained by SSVEPs). Upstream visual information would then be submitted to attentional gating by alpha activity in higher visual cortex.

How could this suggested gating mechanism reflected by alpha activity work? As discussed earlier, perceptual processes in the early visual cortex seem tightly tied to the instantaneous alpha phase [50,51,53]. The oscillation might represent a rhythmic fluctuation between excitation and inhibition [6,39], with the inhibitory phase being prolonged by the amplitude increase [12,13] (Figure 2); in other words, if the amplitude increases, the **duty cycle** (i.e., the part of the alpha cycle that is associated with increased neuronal firing [14]) becomes shortened; alpha amplitude suppression, by contrast, would lead to a longer duty cycle. If, therefore, rhythmically sampled pre-attentive perceptual information is fed forward to a parietal cortex that exhibits alpha suppression, the likelihood of this information being further processed in parietal areas is high. If this rhythmically sampled perceptual information, however, meets the parietal cortex at high alpha amplitude (and consequently a short duty cycle), the chances are high that this visual information arrives at a time interval of high inhibition. This perceptual information would, therefore, be blocked out from further processing (Figure 2).

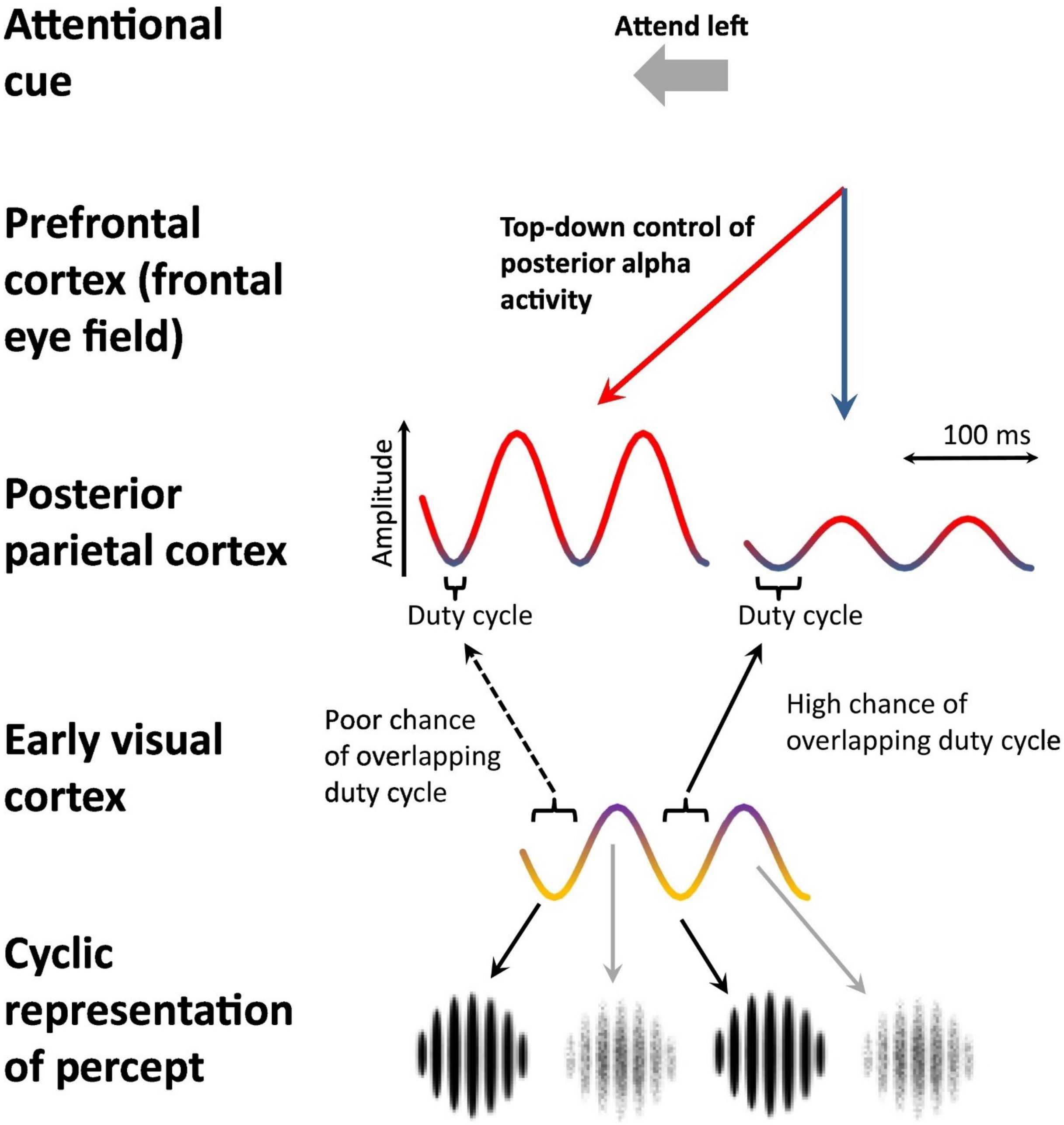

Figure 2. Proposed mechanism by which alpha activity in higher visual areas implements attentional gating. In response to a cue, the prefrontal cortex initiates the modulation of alpha activity in the posterior parietal cortex. The amplitude of the alpha activity will determine the length of the respective duty cycle, with a high amplitude leading to a relatively short duty cycle. At the same time, sensory input is rhythmically sampled at alpha frequency in the early visual cortex. The probability of this upstream information being further processed in the higher visual cortex is increased when the parietal alpha amplitude is low and, therefore, the duty cycle is

long. With the very short duty cycle when alpha activity is high, it is likely that in this scenario the rhythmically sampled sensory input will meet the longer inhibitory phase of alpha and consequently will not be further processed.

Concluding remarks

While alpha activity may represent only one among several mechanisms in attentional processing, it seems reasonable to conclude that it plays a causal role in shifts of visuospatial attention. However, it might not directly implement gain control in the early visual cortex but instead reflect a mechanism higher up the visual hierarchy, possibly attentional gating. There is also good evidence to suggest that alpha activity in higher visual areas is strongly influenced by the prefrontal cortex and frontoparietal attention networks. An analogy to the situation can be drawn from the world of toy cars. For steering a radio-controlled toy car, there is need for a remote control, a receiver, a servomotor, and a wheel suspension system. Collectively, these elements ultimately point the wheels in a certain direction. Obviously, one would not make the case that any of these parts, the wheels' pointing to the right (for instance), has a causal role in the car taking a right turn. Likewise, posterior alpha activity seems causally involved in visuospatial attention (and most likely not on a level of the early visual cortex), but only as one part in a multiple-element control mechanism. Future research needs to address, however, the temporal dynamics and context specificity of the attentional gating mechanism implemented by alpha activity (see Outstanding Questions). Prior work has shown, for instance, that preparatory alpha activity seems to be exclusively associated with target cuing and not with distracter cuing [58–60]. These findings are not fully compatible with the idea of alpha activity reflecting a general gating mechanism of attention, giving rise to the assumption that there might even be further, parallel gating mechanisms involved in attention – potentially reflected by oscillatory brain activity beyond alpha frequency.

Outstanding Questions

- What are the mechanisms by which remote brain areas (e.g. prefrontal cortex) impact on posterior alpha amplitude modulation?
- Which plays a greater role in visuospatial attention processes – alpha amplitude modulation or the instantaneous phase of alpha activity?
- What role does the interaction between alpha activity and oscillatory brain processes in other frequency ranges play in control of visual attention?
- Are there further, parallel attentional gating mechanisms beyond alpha frequency, for instance ones that are reflected by activity in other frequency bands?

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Declaration of Interests

The authors declare no competing interests.

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4. Project 2: Alpha Oscillations in Spatiotemporal Attention

After having established a causal link between alpha oscillations and visuospatial attention, the second project investigated the temporal dynamics of alpha power modulations and their interaction with visuospatial attention in a WM task, requiring simultaneous shifts of attention in space and time. The corresponding manuscript 'Dynamical Alpha Power Modulations and Slow Negative Potentials Track the Allocation of Attention in Space and Time' (Peylo et al., submitted) is presented in this chapter.

Contributions:

Charline Peylo, Carola Romberg-Taylor, Larissa Behnke, Paul Sauseng

The author of this thesis is the first author of this manuscript. CP, CRT and PS conceptualized the experiment, which was programmed and carried out by CP with assistance from LB. Preprocessing of the resulting EEG data (assisted by LB), analysis and visualization was performed by CP. The results were interpreted and the manuscript written by CP under supervision from PS, who acquired funding for the present study. CRT and LB reviewed and approved the manuscript.

Dynamical Alpha Power Modulations and Slow Negative Potentials Track the Allocation of Attention in Space and Time

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Abstract

Alpha power modulations and slow negative potentials have previously been associated with anticipatory processes in spatial and temporal top-down attention. In the present study, we investigated alpha power modulations and slow negative waves in the electroencephalogram during simultaneous shifts of attention in space and time while participants performed a dynamic target detection task. Participants attended the cued side of a bilateral stimulus rotation and mentally counted how often the cued of two remembered sample orientations was displayed. Afterwards, participants performed a delayed match-to-sample task, in which they were asked to indicate if the orientation of a probe stimulus matched the orientation of the previously presented sample stimulus. We hypothesized that during the rotation participants would naturally and dynamically guide attention to task-relevant points in time (i.e., onset of the cued sample orientation) and space (i.e., the cued hemifield); and that such spatiotemporal attention shifts would be reflected by dynamic alpha power decreases and slow negative potentials over posterior electrodes contralateral to the locus of attention. In line with our hypothesis, we observed a reduction of posterior alpha power and an increasing negativity around the cued sample orientation on the cued side of the screen over contralateral electrodes, which was associated with impaired memory performance thereafter (especially for probes of the uncued orientation). We interpret this finding as a preferential allocation of attention to task-relevant points in space and time at the expense of reduced attentional resources and impaired behavioural performance for information outside the current focus of attention.

Keywords

Brain Oscillations; EEG; Spatial attention; Temporal attention

Introduction

In a world with an ever-increasing amount of information permanently competing for access to severely limited human processing systems, top-down predictions of future events can help allocating attentional resources more efficiently. Covert shifts of attention (i.e., changes of mental focus in the absence of ocular movement) towards the location of expected, task-relevant events have been found to bias performance and neural processing in favour of stimuli occurring at the locus of attention at the cost of stimuli occurring elsewhere (Di Russo et al. 2003; Foster et al. 2017; Luck et al. 2000; Posner 1980; Samaha et al. 2016; Sauseng et al. 2005; Woldorff et al. 2002). In addition to such visuospatial attention-driven benefits, an increasing amount of literature suggests that humans can extract temporal regularities from the environment to dynamically guide attention to relevant moments in time, boosting behavioural performance and neural processing thereafter (Correa et al. 2006; Griffin et al. 2001; Lange and Röder 2006; Nobre 2001; Nobre et al. 2007).

Alpha oscillations, rhythmical brain activity around 10 Hz, are one of the most prominent electrophysiological signatures of visuospatial attention. Covertly shifting the attentional focus to one part of the visual field in preparation of an upcoming, task-relevant event is typically associated with sustained alpha power desynchronization in posterior, retinotopically corresponding cortices contralateral to the locus of attention (Barne et al. 2020; Popov et al. 2019; Sauseng et al. 2005; Yamagishi et al. 2005); and occasional alpha power synchronisation ipsilateral to it (Kelly et al. 2006; Rihs et al. 2007; Worden et al. 2000). Such alpha power lateralization is thought to be controlled by a fronto-parietal attention network biasing neuronal processing in favour of the attended hemifield (Capotosto et al. 2009; Popov et al. 2017; Sauseng et al. 2005, 2011). In this context, a decrease of alpha power is thought to reflect cortical activation associated with increased neuronal excitability and facilitated information processing, whereas an increase of alpha power is interpreted as cortical deactivation associated with decreased neuronal excitability and inhibited information processing (Foxe and Snyder 2011; Jensen and Mazaheri 2010; Klimesch et al. 2007; Romei at al. 2008a, b; Sauseng et al. 2009).

In line with this interpretation, posterior alpha power has successfully been used to reconstruct the locus and time course of spatial attention (Foster et al. 2017; Samaha et al. 2016); and low pre-stimulus alpha activity and strong, attention-related alpha power asymmetry have been associated with improved visual performance and increased event-related potentials (ERPs; Ergenoglu et al. 2004; Hanslmayr et al. 2005, 2007; Thut et al. 2006; van Dijk et al. 2008). Moreover, non-invasive alpha power entrainment in one hemisphere has been found to improve visual perception for the ipsilateral hemifield and to impair performance contralaterally (Kasten et al. 2020; Romei et al. 2010; Schuhmann et al. 2019; Taylor and Thut 2012), providing evidence for a causal role of posterior alpha power in spatial, top-down attention (Peylo et al. 2021).

In addition to the strong support for sustained alpha power (de-)synchronization playing an important role in visuospatial attention shifts, some studies suggest that posterior alpha power can also be transiently modulated through the attentional prioritization of relevant moments in time. Temporal expectations about the onset of an upcoming stimulus derived from the rhythmicity of a preceding stimulus sequence have been found to elicit increased posterior alpha power desynchronization around the anticipated target onset (Praamstra et al. 2006), which was associated with speeded stimulus discrimination and increased ERP amplitudes thereafter (Rohenkohl and Nobre 2011). In line with this observation, aging-related impairments in the ability to allocate attentional resources to relevant moments in time have been associated with a reduction of anticipatory alpha power desynchronization (Zanto et al. 2011), suggesting that alpha power modulations might not only support spatial but also temporal top-down attention.

The objective of the present study was to combine these two lines of research and to probe the dynamics of their interaction, approximating the constantly changing, spatiotemporal nature of our environment. To this aim, we used electroencephalography (EEG) to investigate alpha power modulations during simultaneous shifts of top-down attention in space and time, while participants performed a dynamic target detection task, free from potentially confounding stimulus-driven alpha power modulation due to evoked neuronal activity (Kelly et al. 2006; Thut et al. 2006). In this task, participants attended the cued side of a bilateral stimulus rotation and mentally counted how often the cued of two remembered sample orientations was displayed, while ignoring the uncued orientation and the uncued side. Based on the behavioural evidence for a potentiation of visuospatial attention benefits through temporal expectations (Doherty et al. 2005; Rohenkohl et al. 2014), we hypothesized that participants would naturally (i.e., without explicit instructions or cueing) and dynamically guide attention to task-relevant moments in time (i.e., onset of the cued sample orientation) at task-relevant locations in space (i.e., in the cued hemifield); and that such spatiotemporal attention shifts would be reflected by dynamic alpha power desynchronization over posterior electrodes contralateral to the locus of attention.

A second electrophysiological signature of temporal expectancies, which has previously been found to accompany anticipatory alpha power desynchronization in young adults and to mirror a reduction of such in normal aging (Praamstra et al. 2006; Sauseng et al. 2005; Worden et al. 2000; Zanto et al. 2011), is a slow negative deflection over task-relevant cortices. Such negative potentials have consistently been found to increase towards and then peak around task-relevant moments in time before returning back to baseline (Correa et al. 2006; Griffin et al. 2001; Kononowicz and Penney 2016; Miniussi et al. 1999). Their functional role, however, remains a topic of ongoing debate. Whereas some studies suggest that slow negative potentials in anticipation of task-relevant events primarily reflect preparatory processes on the level of response decision and execution (Griffin et al. 2001; Miniussi et al. 1999), other studies suggest that anticipatory benefits might already start on the perceptual level (Correa et al. 2006). However, stimulus-response contingencies in the majority of previous studies have made it difficult to dissociate perceptual and motor-related preparatory processes. Only recently, using simultaneous manipulations of stimulus-response compatibilities and visuospatial attention researchers were able to demonstrate a response-independent increase of anticipatory negative potentials over posterior electrodes contralateral to the locus of attention, which was associated with improved performance thereafter (Di Russo et al. 2021), supporting a functional role of slow negative potentials for the attention-driven tuning of perception towards task-relevant moments in time.

In the present study, we took advantage of our dynamic target detection task, which was largely independent of decision- and motor-related processes (because it neither required overt responses, nor did it enable response decisions until the end of the rotation), to probe the perceptual account and dynamic nature of anticipatory negative potentials. We hypothesized that, if negative slow waves indeed reflect preparatory processes already on the perceptual level, we should observe a dynamically increasing negativity towards the anticipated, task-relevant moments in time (i.e., onset of the cued sample orientation) at task-relevant locations in space (i.e., in the cued hemifield) over electrodes contralateral to the locus of attention, similar to the predictions for anticipatory alpha power reductions.

Materials and Methods

Participants

Thirty-two volunteers recruited at the Ludwig Maximilians University, Germany, participated in the experiment in exchange of financial compensation or lab tokens after having given written informed consent.

Three participants did not fulfil the minimum performance criterion in either of the two tasks described below (counting performance <50% and/or matching performance <60%) and were excluded from all following analyses. The final sample consisted of 29 participants (20 female, 9 male; 27 right-handed, 2 left-handed according to the Edinburgh Handedness Inventory; Oldfield 1971) and had a mean age of 23.62 years (SD = 4.17). All participants reported normal or corrected-to-normal vision and no history of neurological or psychiatric disorders. The study was approved by the local ethics committee and was conducted in accordance with the Declaration of Helsinki.

Experimental Design

In the present experiment, we recorded EEG (see *EEG Recording and Preprocessing*) while participants performed two parallel tasks. In the first part of each trial, participants performed a dynamic target detection task (*counting task*), in which they were asked to mentally count how often the orientation of a continuously rotating stimulus matched the orientation of a previously presented, to-be-remembered sample stimulus. In the second part of each trial, participants performed an event-related, *delayed match-to-sample task*, in which they were asked to indicate if the orientation of a probe stimulus matched the orientation of the previously presented sample stimulus or not (see Fig. 1).

Stimuli in both tasks were controlled using Presentation 20.1 (Neurobehavioral Systems®) and were displayed on a central 17-inch Acer V176 monitor (1280 x 1024 resolution, 60 Hz refresh rate) placed in a dimly lit room. At the beginning of the experiment, participants were seated in a comfortable chair with a standard keyboard placed on their lap and were asked to place their right index, middle and ring finger on the keys “1”, “2” and “3” of the keyboard’s number pad (counting response) and their left middle and index finger on the keys “S” (same) and “D” (different; matching response), respectively.

Each trial started with the presentation of two differently oriented but otherwise identical multi-coloured ring stimuli (1000 ms each, ca. 6.1° x 6.1° visual angle, with detailed colour and texture information for sufficient visual orientation discrimination), which were displayed one after another on opposite sides of a grey screen (50% left-right vs. 50% right-left). Participants were instructed to remember both sample stimuli and their orientation as precisely as possible while maintaining fixation at the central white cross hairs (ca. 0.8° x 0.8° visual angle), which were visible throughout the experiment to help participants stabilize their gaze during the lateralized stimulus presentation. After a delay of 500 ms, a retro-cue was presented in the shape of a central, yellow arrow (300 ms, ca. 1.9° x 0.6° visual angle), pointing to either side of the screen (50% left vs. 50% right) to indicate which of the previously presented orientations and which side of the screen were to be attended (and which to be ignored) during the following counting task.

Immediately after cue offset, both ring stimuli re-appeared in a new pseudo-random orientation. Starting from this position, both rings began to rotate in the same direction (randomly clockwise or anti-clockwise, but never in the same direction for more than two successive trials to minimize potential motion after-effects) and with constant but different speeds (randomly with 90°/sec and 150°/sec or 120°/sec and 180°/sec). During the rotation (lasting between 5333 ms and 6933 ms), participants were instructed to covertly attend the previously cued side and to count as precisely as possible how often (one, two or three times) the cued orientation was adopted, while ignoring the uncued orientation and the uncued hemifield. At the end of the rotation, participants were asked to provide their answer by pressing the corresponding number on the keyboard, which terminated the counting task and the first part of the trial.

Following the response and a short break of 100 ms, the delayed match-to-sample task in the second part of the trial was initiated. In this task, a single ring stimulus (1000 ms) was displayed on either side of the screen (50% left vs. 50% right) with its orientation either matching or mismatching (50% match vs. 50% mismatch; mismatch by +/- 10°/20°/30°/40°/50°/60° with equal probability) the orientation of the probed sample stimulus previously presented on the same side of the screen (50% cued vs. 50% uncued, requiring participants to remember both sample stimuli throughout the trial). Participants were asked to judge as accurately as possible if the probe's orientation matched the orientation of the sample stimulus or not by pressing the corresponding button on the keyboard, which terminated the trial (500 ms inter-trial interval with 10% jitter). In total, the paradigm consisted of three training blocks à 10 trials with feedback (partial or total repetition upon request) and four test blocks à 48 trials without feedback (one of four equiprobable randomization versions) and took approximately 60 minutes adding up to a total experiment duration of about two hours including EEG preparation and breaks.

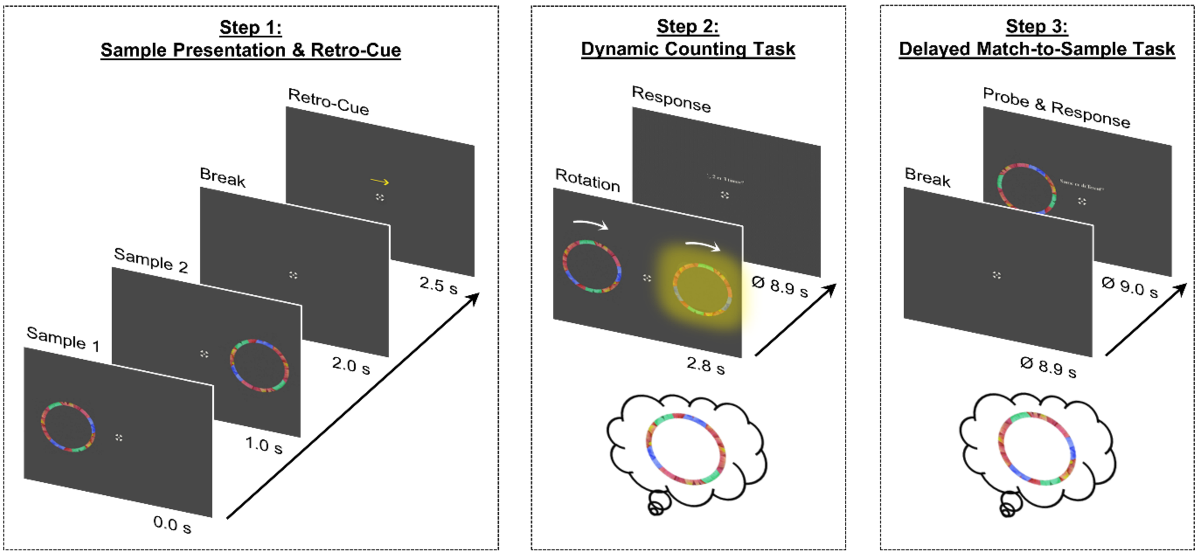

Fig. 1 Example trial of the dynamic target detection task (counting task) and the event-related, delayed match-to-sample task. Each trial started with the presentation of two differently oriented, to-be-remembered sample stimuli followed by a retro-cue (arrow pointing to the left or to the right), indicating which of the previously presented sample orientations

and which side of the screen were to be attended (yellow gleam indicates which hemifield the participant would attend; note, the gleam was not shown in the experiment) during the following stimulus rotation. Participants were asked to count how often the cued stimulus orientation was shown on the cued side of the screen, while ignoring the uncued orientation and the uncued side. Participants registered their response to the counting task by button press. Afterwards, participants were presented with a probe stimulus and were asked to indicate if its orientation matched the orientation of the sample stimulus previously presented on the same side of the screen or not, independent of whether this sample had been cued or uncued

EEG Recording and Preprocessing

Throughout the experiment, EEG was recorded from 62 scalp locations using passive Ag/AgCl electrodes mounted in an elastic cap (Easycap, Brain Products®), which was positioned in accordance with the extended 10-10 system. An electrode on the tip of the nose was used as reference and electrode position FPz served as ground. To correct for ocular artefacts later on, vertical and horizontal eye movements were recorded with two additional electrodes placed above the left eye and next to its outer canthus, respectively. Electrode signals between 0.016 and 250 Hz were digitized using a BrainAmp DC amplifier (1000 Hz sampling rate, 0.1 μV resolution, Brain Products®) and recorded using BrainVision Recorder 2.0.5 (Brain Products®). Electrode impedances were held below 10 kΩ throughout the recording.

EEG data was later offline preprocessed using BrainVision Analyzer 2.1.2 (Brain Products®). First, raw EEG data was filtered using a high- and low-pass filter (zero phase shift Butterworth filters with a slope of 48 dB/oct) with a cutoff at 0.1 and 100 Hz, respectively, and electrical line noise was removed using a 50 Hz Notch filter (with a slope of 96 dB/oct and a bandwidth of 5 Hz). Afterwards, noisy and slow-drift channels were visually identified and replaced using topographic interpolation by fourth-order spherical splines in affected blocks. EEG channels were then re-referenced using a common average reference, and large artefacts were visually identified and excluded from further processing. In the following semi-automatic (ocular correction) Independent Component Analysis (ICA), artefacts caused by eye movements and other systematic sources of interference, as well as channel-specific noise were removed. Lastly, small artefacts remaining after the ICA were visually identified and excluded from all following EEG analyses.

Behavioural Analyses

Performance in the dynamic counting task and the delayed match-to-sample task was quantified using response accuracy and speed (despite both tasks being non-speeded to rule out potential condition differences caused by different speed-accuracy trade-offs). Trials were considered correct if participants provided a single, valid response and the corresponding reaction times were logarithmised and summarised by computing the median for each participant separately. Performance (accuracy/speed) in the delayed match-to-sample task was computed for each probe identity (cued/uncued) and orientation (0°/10°-20°/30°-40°/50°-60°) separately; data was then analysed using two-way repeated measures ANOVAs with Greenhouse-Geisser correction applied where necessary. The following post-hoc tests (0° vs. 10°-20°/30°-40°/50°-60°, 10°-20° vs. 30°-40° vs. 50°-60°) were carried out using Bonferroni-corrected, paired *t* tests. Accuracy in the counting task and the delayed match-to-sample task was correlated using a one-tailed Spearman rank correlation.

All computations and statistical analyses were carried out in the Spyder 4.1.5 environment (Spyder Developer Team 2020) for Python 3.7.3 (Van Rossum and Drake 2009) using custom-written scripts and various open-source packages (EasyGUI 0.98.1, EasyGui Developer Team 2017;

matplotlib 3.3.2, Hunter 2007; more-itertools 8.5.0, More-itertools Developer Team 2020; NumPy 1.19.2, Harris et al. 2020; pandas 1.1.3, McKinney 2010; pingouin 0.2.7, Vallat 2018; prettytable 0.7.2, Prettytable Developer Team 2013; SciPy 1.5.4, Virtanen et al. 2020; seaborn, Waskom 2021; termcolor 1.1.0, Termcolor Developer Team 2011).

EEG Analyses

All EEG analyses were carried out using custom-written Python scripts and the MNE-Python 0.21.0 package (Gramfort et al. 2013). First, preprocessed EEG data from the 62 scalp locations during the stimulus rotation of the dynamic counting task was segmented into epochs from -1000 to +1000 ms around all stimulus orientations of interest (cued/uncued orientation on the cued/uncued, left/right side of the screen). Afterwards, epochs with artefacts, incorrect counting responses and/or saccades in the time window of interest (from -500 to +500 ms around orientation onset) were removed. Differences between the resulting number of available epochs per condition were eliminated using pseudo-random epoch sub-sampling (minimizing timing differences between conditions). On average, 101.00 (*SD* = 24.40) segments remained in each condition for the following analyses.

For alpha power analyses, the resulting epochs of each condition were transformed into time-frequency representations using 5-cycle Complex Morlet Wavelet analyses. To test if the predicted power effects were specific to the hypothesized alpha frequency range (8-12 Hz), time-frequency decompositions were performed for an extended frequency range from 5 to 15 Hz. The resulting power values were averaged across epochs and cropped to the time window of interest (from -500 to +500 ms around orientation onset), cutting off any data potentially affected by edge artefacts (Cohen 2014). Afterwards, power values were baseline-corrected using a z-transformation across the full time window (from -500 to +500 ms around orientation onset) to reveal orientation-dependent power fluctuations over time (similar to Klimesch et al. 1998). Power modulations were statistically tested for each condition separately (cued/uncued orientation on the cued/uncued, left/right side of the screen) using one-tailed, spatio-spectral-temporal cluster-based permutation testing (based on the cluster sum of channel-frequency-time-wise t-values from -500 to +500 ms around the stimulus orientation of interest with 1024 permutations and an initial p-value of $p = .001$ to account for increased cluster extents in 3D space; Maris and Oostenveld 2007).

For ERP analyses, epochs of each condition were averaged into eight separate ERP traces (cued/uncued orientation on the cued/uncued, left/right side of the screen), which were later baseline-corrected (using the first 200 ms as baseline) and smoothed (using a 0.1-30 Hz band-pass FIR filter with Hamming window). Afterwards, ERPs were combined into *Left-Right* difference waves and statistically compared at each channel and time point using a mass-univariate, repeated-measures ANOVA with factors *Orientation* (cued/uncued) and *Side* (cued/uncued). Multiple comparison correction was performed using spatio-temporal cluster-based permutation testing (based on the cluster sum of channel-time-wise F-values from -1000 to +1000 ms around the stimulus orientation of interest with 1024 permutations and an initial p-value of $p = .01$ to account for moderate cluster extents in 2D space; Maris and Oostenveld 2007).

To test the functional relevance of any observed power and/or ERP effects (see *Alpha Power* and *Event-Related Potentials*), we computed each participant's individual cluster mean (i.e., mean power and mean ERP *Orientation-by-Side* interaction for the respective electrodes and time(-frequency) points) and correlated those with performance in the dynamic counting task and the delayed match-to-sample task. Depending on the presence of outliers, we computed either Pearson's correlation coefficient (i.e., for the relationship between EEG parameters and (un-)cued-probe accuracy in the delayed match-to-sample task) or Spearman's rank correlation (i.e., for the relationship between EEG parameters and overall accuracy in the counting task and the delayed match-to-sample task), which were tested against zero using one-tailed *t*-tests (with the assumption that alpha power desynchronization and ERP negativity around the onset of the cued orientation on the cued side of the screen would be beneficial to performance).

Results

Behaviour

In the counting task, accuracy was moderate to high (*M* = 81.25%, *SE* = 2.10%), as were reaction times (*M* = 6.63 ≈ 757.48 ms, *SE* = 0.06; see Fig. 2). In the delayed match-to-sample task, accuracy was somewhat lower compared to the counting task (*M* = 71.37%, *SE* = 1.18%) and was significantly higher for probes of the cued orientation (*M* = 70.55%, *SE* = 1.26%) compared to probes of the uncued orientation (*M* = 65.05%, *SE* = 2.02%; *F*(1, 28) = 8.97, *p* = .006, η_p^2 = .243). Additionally to probe identity, matching accuracy was significantly affected by probe orientation (*F*(3, 84) = 88.93, *p* < .001, η_p^2 = .761): Accuracy was significantly higher for matching probes (0°: *M* = 78.52%, *SE* = 2.14%) compared to mismatching probes (10°-20°/30°-40°/50°-60°: *M* = 64.22%, *SE* = 2.02%; *t*(28) = 4.18, *p* = .001, η^2 = .290) and for large mismatch degrees (50°-60°: *M* = 86.75%, *SE* = 1.84%) compared to moderate (30°-40°: *M* = 67.57%, *SE* = 2.90%; *Large*-Moderate: t(28) = 8.96, *p* < .001, η^2 = .361) and small mismatch degrees (10°-20°: *M* = 38.36%, *SE* = 2.60%; *Moderate-Small*: *t*(28) = 10.67, *p* < .001, η^2 = .494). This increase in accuracy with increasing mismatch degree was by trend more pronounced for probes of the cued orientation (10°-20°: *M* = 36.85%, *SE* = 2.35%, 30°-40°: *M* = 71.98%, *SE* = 3.07%, 50°-60°: *M* = 92.03%, *SE* = 1.52%) compared to probes of the uncued orientation (10°-20°: *M* = 39.87%, *SE* = 4.21%, 30°-40°: *M* = 63.15%, *SE* = 3.50%, 50°-60°: *M* = 81.47%, *SE* = 2.97%; *F*(3, 84) = 3.05, *p* = .060, η_p^2 = .098). Performance in the delayed match-to-sample task was positively correlated with performance in the dynamic counting task ($r(27) = .55$, $p < .001$).

Similarly, reaction times in the delayed match-to-sample task were longer compared to the counting task ($M = 7.32 \approx 1510.20$ ms, $SE = 0.05$) and were significantly affected by probe orientation ($F(3, 84) = 25.55$, $p < .001$, $\eta_p^2 = .477$): Reaction times were significantly shorter for matching probes (0°: $M = 7.29 \approx 1465.57$ ms, $SE = 0.06$) compared to mismatching probes (10°-20°/30°-40°/50°-60°: $M = 7.46 \approx 1737.15$ ms, $SE = 0.06$; $t(28) = -4.99$, $p < .001$, $\eta^2 = .067$) and for large mismatch degrees (50°-60°: $M = 7.34 \approx 1540.71$ ms, $SE = 0.05$) compared to moderate (30°-40°: $M = 7.44 \approx 1702.75$ ms, $SE = 0.07$; *Large*-Moderate: $t(28) = -2.93$, $p = .027$, $\eta^2 = .021$) and small mismatch degrees (10°-20°: $M = 7.60 \approx 1998.20$ ms, $SE = 0.07$; *Moderate-Small*: $t(28) = -4.21$, $p < .001$, $\eta^2 = .042$). This decrease in reaction time with increasing mismatch degree was independent of probe identity ($F(3, 84) = 1.59$, $p = .207$, $\eta_p^2 = .054$), as were overall reaction times (*Cued*: $M = 7.39 \approx 1619.71$ ms, $SE = 0.06$ vs. *Uncued*: $M = 7.44 \approx 1702.75$ ms, $SE = 0.06$; $F(1, 28) = 1.88$, $p = .182$, $\eta_p^2 = .063$).

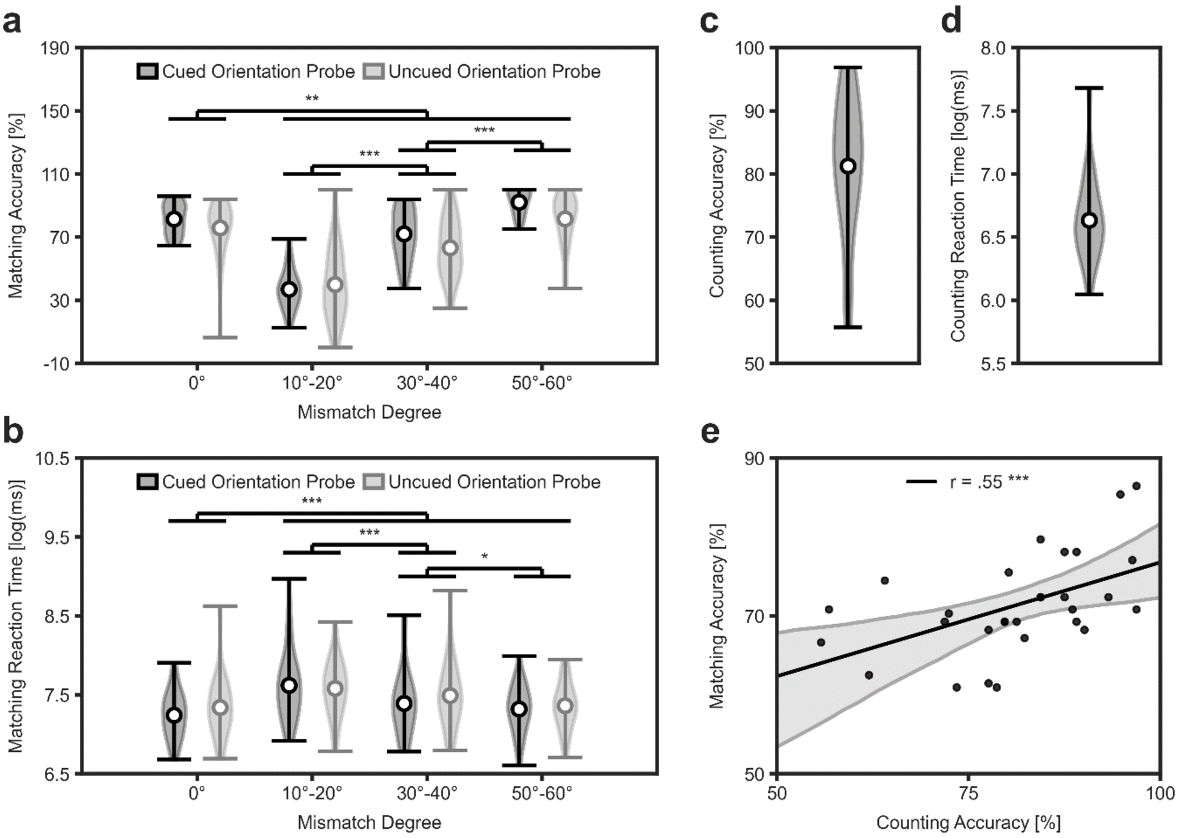

Fig. 2 Performance in the dynamic counting task and the delayed match-to-sample task **a** Accuracy in the delayed match-to-sample task was improved for probes of the cued compared to the uncued sample orientation and for matching compared to mismatching probes (with an increasing advantage for decreasing mismatch degrees) **b** Reaction times in the delayed match-to-sample task showed the same benefit for matching compared to mismatching probes and for larger compared to smaller mismatch degrees **c, d** Performance (accuracy/speed) in the dynamic counting task was slightly better than in the delayed match-to-sample task **e** The correlation between the accuracy in both tasks shows that participants who performed well in the dynamic counting task also performed relatively better in the following delayed match-to-sample task. Note: Dots represent means across the sampling distribution illustrated by violin plots and shaded areas denote 95% confidence intervals. Asterisks indicate statistical significance, where * ≙ $p < .05$, ** ≙ $p < .01$ and *** ≙ $p < .001$

Alpha Power

We observed no orientation-related power fluctuations for the uncued sample orientation, nor for the cued sample orientation on the cued, right or the uncued, left side of the screen (all cluster *p's* ≥ .136). Shortly before the stimulus rotation on the cued, left side of the screen reached the cued sample orientation, however, right parieto-occipital electrodes showed a trend for low alpha (around 7-10 Hz) power decreases relative to baseline (*p* = .067, corresponding to a cluster starting around 220 ms before orientation onset; see Fig. 3). A similar decline around the cued sample orientation was observed over left parieto-occipital electrodes for stimuli presented on the right but uncued side of the screen, albeit in a lower frequency range around 5-8 Hz (*p* = .026, corresponding to a cluster from -230 to +100 ms around orientation onset).

This left-hemispheric, low-frequent power decrease around onset of the cued orientation on the uncued, right side of the screen was, however, not related to accuracy in either of the two tasks ($r_{counting}$ (27) = .15, *p* = .224; $r_{matching}$ (27) = .16, *p* = .203). Right-hemispheric alpha power reductions in preparation of the upcoming cued sample orientation on the cued, left side of the screen, in contrast, were marginally significantly correlated with performance in the following delayed match-to-sample task: Stronger alpha power decreases were, however, associated with impaired rather than improved matching performance thereafter ($r_{counting}$ (27) = .23, *p* = .111; $r_{matching}$ (27) = .28, *p* = .068). This effect was mainly driven by a poor matching performance for probes of the uncued sample orientation (r_{cued} (27) = .16, *p* = .208; r_{uncued} (27) = .33, *p* = .040), suggesting that participants who preferentially allocated attentional resources to locations and time points relevant to the current task at hand (i.e., counting) might have lacked attentional resources for events outside the current focus of attention, leading to worse matching performance for the previously uncued sample orientation thereafter.

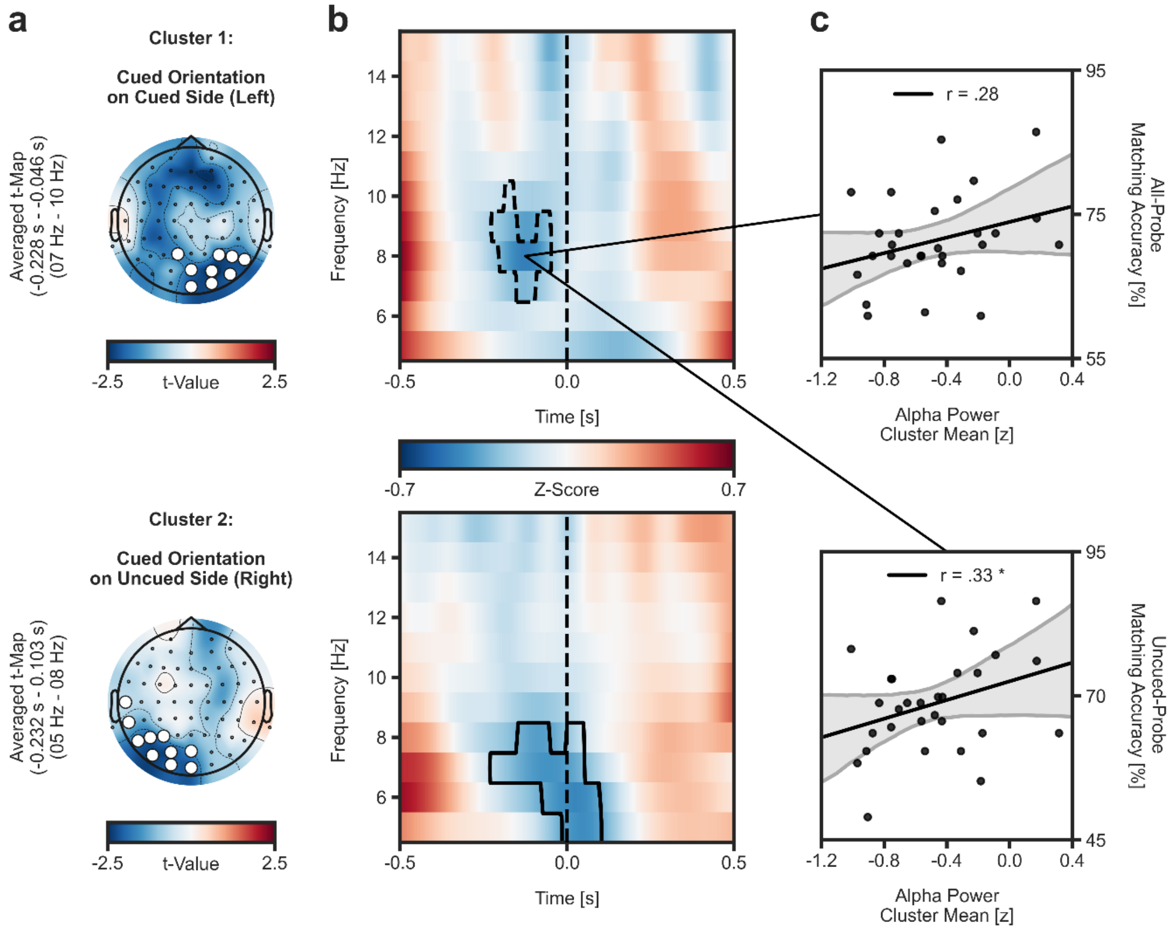

Fig. 3 Grand-average power modulations during the dynamic counting task **a** The topographic illustration of *t* values for each of the two identified clusters averaged across the respective time windows and frequency bands shows contralateral, parieto-occipital power decreases for the cued sample orientation on the cued, left and the uncued, right side of the screen **b** The corresponding time-frequency plots show that these power decreases were located in the alpha/theta frequency range and started around 230 ms before onset of the cued sample orientation **c** The correlation between the strength of right-hemispheric alpha power reductions shortly before onset of the cued sample orientation on the cued, left side of the screen (averaged across electrodes, frequencies and time points) and accuracy in the delayed match-to-sample task (separately for all vs. uncued-only probes) shows a decline in performance (primarily for probes of the uncued sample orientation) with increasing alpha power reduction. Note: Cluster electrodes are reflected by white circles, (marginally) significant clusters

by solid/dashed black lines and 95% confidence intervals by shaded areas in grey. Asterisks indicate statistical significance, where * ≙ $p < .05$, ** ≙ $p < .01$ and *** ≙ $p < .001$

Event-Related Potentials

We found no main effect of factors *Orientation* or *Side* on *Left-Right* difference waves (all cluster *p's* ≥ .166). Instead, we observed three significant *Orientation-by-Side* interaction clusters, all of which showed an increasing negativity towards the onset of the cued sample orientation on the cued side of the screen at centro-parietal electrodes primarily over the right hemisphere (p = .034/.007/.052, corresponding to clusters from -220 to -110 ms, -90 to +190 ms and +210 to +290 ms around onset of the cued sample orientation, respectively; see Fig. 4). No such effect was observed for the cued orientation on the uncued side of the screen, nor for the uncued orientation on either side of the screen.

This ERP interaction effect (i.e., an increasing negativity exclusively around the onset of the cued sample orientation on the cued side of the screen) was significantly but again positively correlated with performance in the following delayed match-to-sample task: Stronger ERP *Orientation-by-Side* interactions were associated with impaired rather than improved matching performance thereafter ($r_{counting}(27) = .19$, $p = .166$; $r_{matching}(27) = .35$, $p = .033$). As for alpha power decreases, this effect was mainly driven by a poor matching performance for probes of the uncued sample orientation ($r_{cued}(27) = .21$, $p = .141$; $r_{uncued}(27) = .29$, $p = .061$). This finding suggests that participants who accurately anticipated the location and onset of a task-relevant event while ignoring task-unrelated locations and time points might have missed information that became relevant at a later point in time, leading to worse matching performance for probes of the uncued sample orientation thereafter.

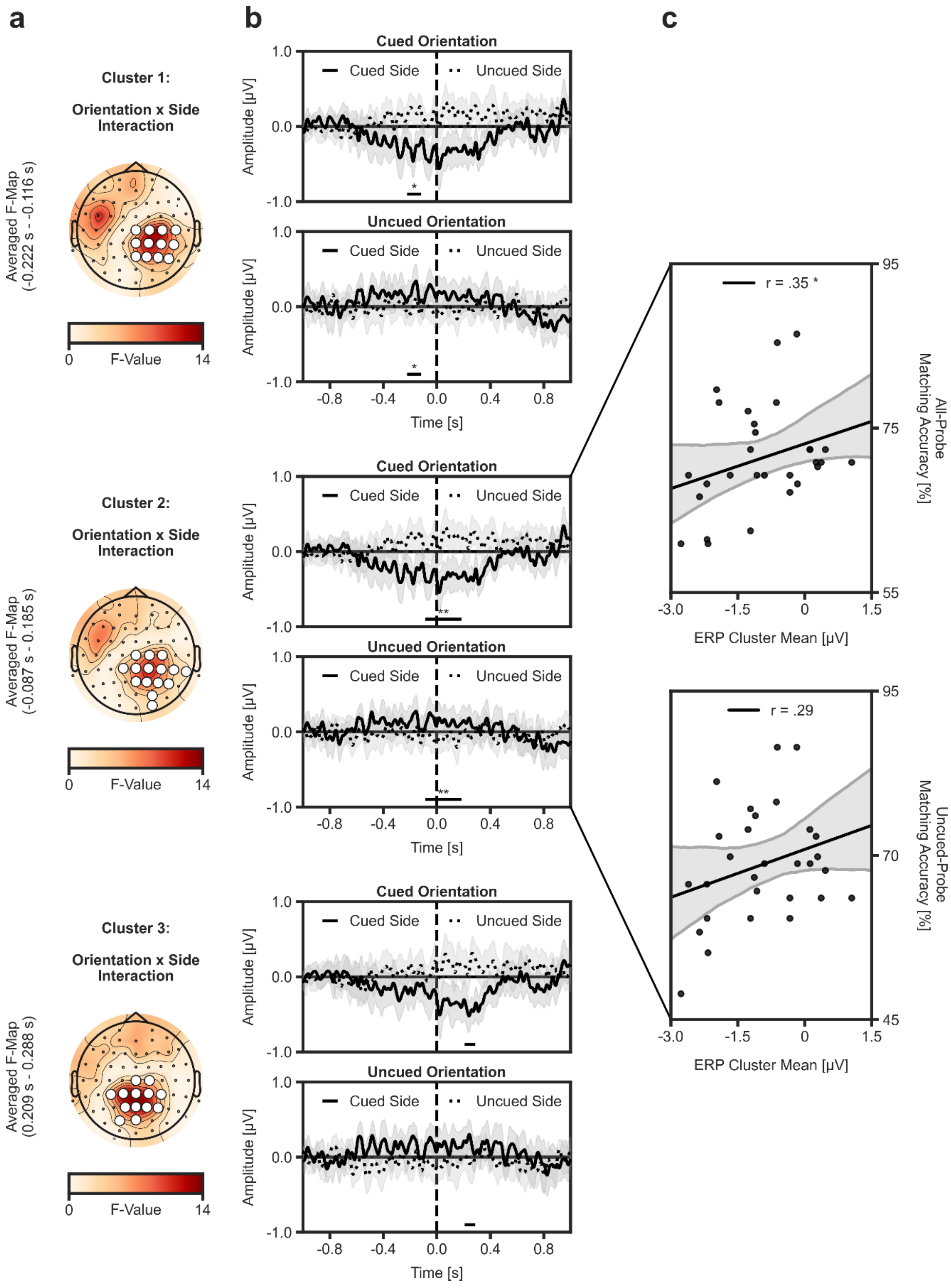

Fig. 4 Grand-average event-related potentials (ERPs) during the dynamic counting task **a** The topographic illustration of *F* values for each of the three identified clusters averaged across the respective time windows shows a significant *Orientation-by-Side* interaction of *Left-Right* difference

ERPs at centro-parietal electrodes primarily over the right hemisphere **b** The corresponding ERPs show an increasing negativity towards the cued sample orientation presented on the cued side of the screen **c** The correlation between the strength of the ERP *Orientation-by-Side* interaction around onset of the cued sample orientation on the cued side of the screen (averaged across electrodes and time points of the dominant, second cluster) and accuracy in the delayed match-to-sample task (separately for all vs. uncued-only probes) shows a decline in performance (primarily for probes of the uncued sample orientation) with increasing ERP negativity. Note: Cluster electrodes are reflected by white circles, cluster time points by horizontal black bars and 95% confidence intervals by shaded areas in grey. Asterisks indicate statistical significance, where * ≙ $p < .05$, ** ≙ $p < .01$ and *** ≙ $p < .001$

Discussion

Alpha power modulations and slow negative potentials have previously been associated with anticipatory processes in spatial and temporal top-down attention (Di Russo et al. 2021; Hanslmayr et al. 2007; Praamstra et al. 2006; Rohenkohl and Nobre 2011; Sauseng et al. 2005; Zanto et al. 2011). In the present study, we combined these two lines of research and investigated alpha power changes and slow negative waves during simultaneous shifts of attention in space and time while participants performed a dynamic target detection task. This paradigm was free from potentially confounding stimulus-driven alpha power fluctuations due to evoked neuronal activity and largely independent of decision- and motor-related processing enabling a confined analysis of preparatory processes on the perceptual level. We hypothesized that participants would naturally and dynamically guide attention to task-relevant moments in time (i.e., onset of the cued sample orientation) at task-relevant locations in space (i.e., in the cued hemifield); and that such spatiotemporal attention shifts would be reflected by dynamic alpha power decreases and slow negative potentials over posterior electrodes contralateral to the locus of attention.

In line with this hypothesis, we observed a trend for a reduction of alpha power shortly before the onset of the cued sample orientation on the cued, left side of the screen over right, parieto-occipital electrodes. Whereas this contralateral alpha power decrease in anticipation of task-relevant points in space and time was unrelated to accuracy in the dynamic target detection task (probably because it was too easy and did not require a high temporal precision of visual perception), we observed a trend for a correlation with accuracy in the following delayed match-to-sample task (which was rather difficult and potentially more sensitive to individual precision differences due to the small mismatch degrees). Although a strong reduction of alpha power was associated with impaired rather than improved memory performance, a separate analysis for probes of the cued versus uncued sample orientation revealed that this effect was primarily driven by an impairment of memory matching for the uncued sample orientation. This behaviourally relevant top-down modulation of neural oscillations was specific not only to the cued sample orientation and the cued side of the screen but also to the alpha frequency range, because the unexpected low-frequency power decrease around the onset of the cued sample orientation on the uncued, right side of the screen was not related to performance in either of the two tasks. Based on the evidence for a functional role of alpha power modulations in top-down attention and the associated behavioural costs for stimuli occurring outside the attentional focus (Popov et al. 2019; Posner 1980; Rohenkohl and Nobre 2011; Sauseng et al. 2005), we interpret this finding of alpha power decreases shortly before the onset of the cued sample orientation on the cued side of the screen as a preferential allocation of attention to task-relevant points in space and time at the expense of reduced attentional resources and impaired behavioural performance for information outside the current focus of attention.

Our results extend previous evidence for a functional role of alpha power modulations in spatial and temporal top-down attention and suggest that when humans direct their attention to one part of the visual field and herein expect the onset of a task-relevant event, alpha power gets dynamically and transiently suppressed over contralateral electrodes (at least when attention is explicitly cued and permanently allocated to the left or right visual hemifield during a perceptually demanding task using bilateral stimuli potentially facilitating hemisphere-specific processes, unlike other designs which have been associated with hemisphere-independent alpha power reductions through temporal expectations; Heideman et al. 2018; Rohenkohl and Nobre 2011). In previous studies, such short-term fluctuations of perception have mainly been associated with the phase of alpha oscillations (Busch and VanRullen 2010; Busch et al. 2009; Hanslmayr et al. 2011; Zauner et al. 2012), which reflects intrinsic, top-down attention-independent fluctuations between states of high versus low excitability thereby affecting subsequent information processing (Buzsáki and Draguhn 2004; Haegens et al. 2011; van Diepen et al. 2015; Zoefel and VanRullen 2017). When alpha power is suppressed, however, the inhibitory phase associated with impaired signal processing is shortened (Jensen and Mazaheri 2010; Mazaheri and Jensen 2010; Peylo et al. 2021) and the effect of oscillatory phase eliminated (Mathewson et al. 2009). A dynamic and transient reduction of alpha power shortly before the onset of a task-relevant stimulus might therefore help to suppress the involuntary effects of alpha phase, thereby stabilizing perception at relevant moments in time. A direct test of this interpretation, however, was beyond the scope of the present paper and remains a matter for future research.

In addition to alpha power modulations, we observed a *Left-Right* negative difference potential over right-lateralized, centro-parietal electrodes, which increased towards and then peaked around the onset of the cued sample orientation on the cued side of the screen. In contrast to the traditional view that slow negative potentials in anticipation of an upcoming, task-relevant event primarily reflect preparatory processes on the level of response decision and execution (Griffin et al. 2001; Miniussi et al. 1999), the observation of an anticipatory negative wave in a paradigm that was largely independent of decision- and motor-related processes argues in favour of temporal attention-driven modulations already on the perceptual level (Correa et al. 2006). Although we cannot entirely exclude the possibility that participants, even though not instructed to, made subtle movements during task-relevant events (i.e., onset of the cued sample orientation on the cued side of the screen) leading to the observed negative potential, this alternative explanation seems unlikely for the following reasons. Since potential auxiliary movements would have probably been executed either with the dominant or the task-related hand (both of which correspond to the right hand for the large majority of our sample and the present target detection task), effects of response preparation should have been elicited primarily over central electrodes of the left hemisphere independent of whether the event took place on the left or right side of the screen. Moreover, preparatory processes on the level of response decision and execution should have been unable to affect subsequent response accuracy. Instead we observed stronger contralateral negativity over right-hemispheric, centro-parietal electrodes, which was significantly correlated with accuracy in the following delayed match-to-sample task (though again with an adverse effect on performance, especially for probes of the uncued sample orientation). We interpret this finding in line with the alpha power reduction as an attention-driven preparation of task-relevant cortices including the visual hierarchy for relevant points in space and time at the cost of reduced attentional resources and impaired behavioural performance for information outside the current focus of attention.

Together, our findings of dynamic alpha power decreases and slow negative potentials towards task-relevant moments in time at task-relevant locations in space over electrodes contralateral to the locus of attention provide electrophysiological evidence for a close interaction between spatial and temporal top-down attention. Combined with the effect of attention-driven alpha power modulations and slow negative waves on subsequent memory performance, our results are in line with the suggestion that temporal attention might affect cognitive processes beyond the level of response preparation and an associated shortening of response times by exerting an indirect effect on behaviour through spatial attention, which itself has a direct impact on the retinotopically organized visual system (Correa et al. 2006; Doherty et al. 2005; Rohenkohl et al. 2014). Although some of our findings represent statistical trends (which is rather unsurprising in such a complex paradigm with multiple events taking place in close spatial and temporal proximity) and should thus be interpreted with caution, our study still highlights the important role of alpha power modulations and slow negative potentials for the interaction between spatial and temporal top-down attention.

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Declarations

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Competing interests

The authors have no competing interests to declare that are relevant to the content of this article.

Ethics approval

The study was approved by the Ethics Commission of the Faculty of Psychology and Education of the Ludwig-Maximilians-Universität München and was conducted in accordance with the Declaration of Helsinki.

Consent to participate

Informed consent was obtained from all individual participants included in the study.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Author contributions

C.P., C.R.-T. and P.S. conceptualized the experiment, which was programmed and carried out by C.P. with assistance from L.B. Preprocessing of the resulting EEG data (assisted by L.B.), analysis and visualization was performed by C.P. The results were interpreted and the manuscript written by C.P. under supervision from P.S., who acquired funding for the present study. C.R.-T. and L.B. reviewed and approved the manuscript.

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5. Project 3: Theta/Gamma Oscillations in Memory Matching

Following the evidence for a temporal tuning of spatial attention through dynamic alpha power modulations, the third project investigated theta:gamma phase-phase coupling and evoked gamma activity as potentially complementary signatures for cortical integration and memory matching in visual perception more specifically. The corresponding research article 'Theta:Gamma Phase Coupling and Evoked Gamma Activity Reflect the Fidelity of Mental Templates during Memory Matching in Visual Perception' (Peylo et al., 2022) was published in *Cerebral Cortex* and is presented in this chapter.

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Contributions:

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The author of this thesis is the first author of this manuscript. All authors conceptualized the experiment, which was programmed and carried out by CP. Target drawings were rated by EVCF and ALB, who provided research resources. Preprocessing of the resulting EEG data, analysis and visualization was performed by CP. The results were interpreted and the manuscript written by CP under supervision from PS, who acquired funding for the present study. TM and EVCF co-supervised the initial phase of the project and together with ALB reviewed and approved the manuscript.

Theta:Gamma Phase Coupling and Evoked Gamma Activity Reflect the Fidelity of Mental Templates during Memory Matching in Visual Perception

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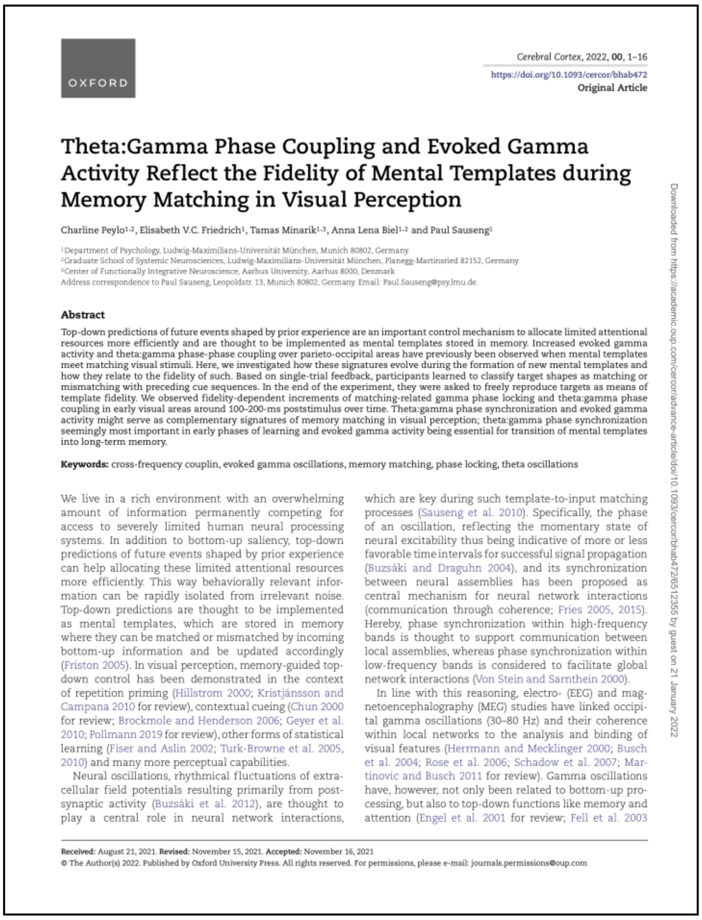

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Original Article

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Abstract

Top-down predictions of future events shaped by prior experience are an important control mechanism to allocate limited attentional resources more efficiently and are thought to be implemented as mental templates stored in memory. Increased evoked gamma activity and theta:gamma phase-phase coupling over parieto-occipital areas have previously been observed when mental templates meet matching visual stimuli. Here, we investigated how these signatures evolve during the formation of new mental templates and how they relate to the fidelity of such. Based on single-trial feedback, participants learned to classify target shapes as matching or mismatching with preceding cue sequences. In the end of the experiment, they were asked to freely reproduce targets as means of template fidelity. We observed fidelity-dependent increments of matching-related gamma phase locking and theta:gamma phase coupling in early visual areas around 100–200-ms poststimulus over time. Theta:gamma phase synchronization and evoked gamma activity might serve as complementary signatures of memory matching in visual perception; theta:gamma phase synchronization seemingly most important in early phases of learning and evoked gamma activity being essential for transition of mental templates into long-term memory.

Keywords: cross-frequency couplin, evoked gamma oscillations, memory matching, phase locking, theta oscillations

We live in a rich environment with an overwhelming amount of information permanently competing for access to severely limited human neural processing systems. In addition to bottom-up saliency, top-down predictions of future events shaped by prior experience can help allocating these limited attentional resources more efficiently. This way behaviorally relevant information can be rapidly isolated from irrelevant noise. Top-down predictions are thought to be implemented as mental templates, which are stored in memory where they can be matched or mismatched by incoming bottom-up information and be updated accordingly (Friston 2005). In visual perception, memory-guided top-down control has been demonstrated in the context of repetition priming (Hillstrom 2000; Kristjánsson and Campana 2010 for review), contextual cueing (Chun 2000 for review; Brockmole and Henderson 2006; Geyer et al. 2010; Pollmann 2019 for review), other forms of statistical learning (Fiser and Aslin 2002; Turk-Browne et al. 2005, 2010) and many more perceptual capabilities.

Neural oscillations, rhythmical fluctuations of extracellular field potentials resulting primarily from postsynaptic activity (Buzsáki et al. 2012), are thought to play a central role in neural network interactions, which are key during such template-to-input matching processes (Sauseng et al. 2010). Specifically, the phase of an oscillation, reflecting the momentary state of neural excitability thus being indicative of more or less favorable time intervals for successful signal propagation (Buzsáki and Draguhn 2004), and its synchronization between neural assemblies has been proposed as central mechanism for neural network interactions (communication through coherence; Fries 2005, 2015). Hereby, phase synchronization within high-frequency bands is thought to support communication between local assemblies, whereas phase synchronization within low-frequency bands is considered to facilitate global network interactions (Von Stein and Sarnthein 2000).

In line with this reasoning, electro- (EEG) and magnetoencephalography (MEG) studies have linked occipital gamma oscillations (30–80 Hz) and their coherence within local networks to the analysis and binding of visual features (Herrmann and Mecklinger 2000; Busch et al. 2004; Rose et al. 2006; Schadow et al. 2007; Martinovic and Busch 2011 for review). Gamma oscillations have, however, not only been related to bottom-up processing, but also to top-down functions like memory and attention (Engel et al. 2001 for review; Fell et al. 2003

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Peylo et al. (2022). Theta:gamma phase coupling and evoked gamma activity reflect the fidelity of mental templates during memory matching in visual perception. *Cerebral Cortex*, bhab472 by permission of Oxford University Press.

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Introduction

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In their match-and-utilization model (MUM), Herrmann and colleagues (Herrmann et al. 2004a, 2010) propose that the matching between bottom-up information and top-down expectations is reflected by evoked (i.e., phase-locked) gamma activity in early sensory cortices around 100-ms poststimulus, where memory-matching stimuli are thought to evoke stronger gamma responses due to synaptic strengthening between the involved neurons during preceding repeated encounters. This early gamma response is followed by induced (i.e., nonphase-locked) gamma activity around 300-ms poststimulus, indicating the utilization of the matching result for response selection and model updating. In line with this model, real-world objects with an existing representation in long-term memory have been found to elicit stronger gamma band responses than nonexistent, scrambled versions of the same objects in early visual areas around 100-ms poststimulus (Herrmann et al. 2004b; Morup et al. 2006; Fründ et al. 2008; Herrmann et al. 2010 for review), although inconsistencies have been noted as well (Martinovic and Busch 2011 for a critical review).

Despite the fair amount of evidence in support of the MUM, it has been argued that evoked gamma effects have primarily been found in the context of semantic long-term memory contents affecting feature binding (Holz et al. 2010; Sauseng et al. 2015). If, however, new mental templates were to be memorized and actively held in working memory, controlled by a distributed fronto-parietal network requiring global network interactions for the communication with distant visual cortices (D'Esposito and Postle 2015), local gamma oscillations alone might not be sufficient. An additional, slow oscillation, namely theta, might come into play. Theta oscillations (4-8 Hz) over frontal brain regions and their synchronization with parietal cortices have previously been associated with working memory encoding, maintenance and retrieval (Sauseng et al. 2005; Hsieh and Ranganath 2014 for review). Due to their versatile involvement in diverse memory functions and their co-variations not only with memory load (Jensen and Tesche 2002; Meltzer et al. 2007, 2008) but with task demands more generally (Sauseng et al. 2007), theta oscillations are widely believed to reflect executive control mechanisms underlying working memory, rather than memory contents *per se*. Theta oscillations have, for example, been proposed to organize individual memory items, stored in single gamma cycles, into one multi-item memory (Lisman and Idiart 1995; Jensen and Lisman 2005; Sauseng et al. 2009; Axmacher et al. 2010; Chaieb et al. 2015; Sauseng et al. 2019) and manipulations of individual theta frequencies have indeed been found to affect visual working memory capacity (Vosskuhl et al. 2015; Wolinksi et al. 2018; Bender et al. 2019), demonstrating the relevance of crossfrequency interactions for high-level cognitive processes including working memory.

Based on this evidence, Sauseng and colleagues (Sauseng et al. 2008, 2010, 2015) proposed an alternative model with theta:gamma phase-phase coupling as key mechanism for the matching between bottom-up visual information and top-down mental templates held in working memory. In their three-stage model, the authors suggest that the anticipation of a stimulus leads to a reactivation of its mental template in frontal brain areas, which is replayed back to early visual brain areas in parieto-occipital cortex, as reflected by an increase of fronto-parietal theta coherence. Around 100 ms after stimulus onset, theta oscillations in early visual brain areas are then supposed to undergo a phase reset, which allows for transient, matching-dependent phase-phase coupling between local theta oscillations (representing the top-down mental template) and local gamma oscillations (providing the bottom-up visual information) shortly after (around 150-ms poststimulus).

In line with this model, the authors observed increased theta:gamma phase-phase coupling in early visual cortices around 150 ms after the onset of a bar, which had to be classified as either long or short based on example stimuli presented and memorized at the beginning of the experiment, when it was presented at the cued location, that is when the mental template of an expected stimulus met a matching sensory input (Sauseng et al. 2008). Similarly, increased theta:gamma phase-phase coupling in parieto-occipital brain areas has been reported for matching compared to mismatching probes in a delayed match-to-sample task (Holz et al. 2010); and for single- compared to multi-item visual search (Biel et al. 2021), demonstrating the relevance of matching sensory information and concrete target expectations, respectively.

Despite the convincing evidence for the proposed role of evoked gamma and theta:gamma phase-phase coupling for template-to-input matching in visual perception, one important aspect to better understand naturalistic visual perception and its interaction with memory remains to be investigated: While previous studies relied on the matching between sensory information and preexisting mental templates (e.g. from long-term memory), in real life mental templates need to be gradually built through repeated exposure. Here, for the first time, we investigated the proposed signatures of template-to-input matching in visual perception, namely evoked gamma activity and theta:gamma phase-phase coupling, as complementary signatures of memory matching during the formation of new top-down mental templates and how they relate to the fidelity of such. Based on previous findings, we hypothesized that, if evoked gamma activity and theta:gamma phase synchronization indeed constitute signatures of memory matching in visual perception, they should increase with an increasing correspondence between bottom-up and top-down information, that is for template-matching compared to template-mismatching stimuli and for highly elaborated templates towards the end of the experiment compared to the nonexistent or very coarse templates at its beginning.

Materials and Methods

Participants

Thirty volunteers recruited at the Ludwig Maximilians University, Germany, participated in the experiment in exchange of financial compensation or lab tokens after having given written informed consent. Seven participants failed to improve their performance beyond chance level in the target identification task described below (final block's mean sensitivity *d'* < 0.51 corresponding to the 95th percentile of 1000 simulations of random guessing; see section *Behavioural Analyses* for the computation of sensitivity measure *d'*) and were excluded from all following main analyses. Another two participants had to be excluded due to an insufficient trial count following artefact rejection (*n* < 25 in at least one condition of interest; see section *EEG Recording and Preprocessing* and *EEG Analyses*). The final sample consisted of 21 participants (13 female, 8 male; 19 right-handed, 2 left-handed according to the Edinburgh Handedness Inventory; Oldfield 1971) and had a mean age of 22.43 years (SD = 3.08). All participants reported normal or corrected-to-normal vision and no history of neurological or psychiatric diseases. The study was approved by the local ethics committee and conducted in accordance with the Declaration of Helsinki.

Experimental Design

The experiment consisted of two parts. In the first and main part of the experiment, EEG was recorded (see section *EEG Recording and Preprocessing*) while participants performed a computerized target identification task. In this task, based on single-trial feedback participants were asked to classify a target shape as matching or mismatching with a preceding sequence of cue shapes by learning the initially unknown cue-target combinations over the course of the paradigm. In the second part of the experiment, participants were asked to freely reproduce the previously learned targets as means of template fidelity.

Stimuli in the target identification task were controlled using Presentation 0.71 (Neurobehavioral Systems®) and displayed on a central 17-inch Acer V176 monitor (1280 x 1024 resolution, 60 Hz refresh rate) placed in a dimly lit room. At a distance of about 80 cm from the monitor, participants were seated in a comfortable chair with a tray and computer mouse placed on their lap. Before the paradigm was started, participants were asked to place their right index and middle finger on the left and right mouse button, respectively, which were marked with colored stickers to remind them of the stimulus-response mapping throughout the task (left mouse button/green sticker = match, right mouse button/red sticker = mismatch).

Each trial started with the presentation of a black, central fixation cross (516 ms, ca. 1.5 x 1.5 cm; see Fig. 1) in front of a grey background, reminding participants to fixate the middle of the screen, where all stimuli were to be displayed. After a short blank-screen delay (516 ms), a sequence of three black cue shapes was presented (516 ms each, ca. 2 x 2 cm). This sequence of cue shapes was followed by another blank-screen break (1015 ms) and a single, purple target shape (until a response was made but not longer than 2013 ms, ca. 2 x 2 cm). Participants were asked to judge as accurately as possible whether the target shape matched (i.e., belonged to) the previously presented sequence of cue shapes or not by pressing the corresponding mouse button. Following their response and a short blank-screen delay (511 ms), participants were provided with visual feedback about their decision (1015 ms, ca. 1 x 9 cm). Participants were instructed to use this 100% reliable feedback to learn the initially unknown cue-target combinations to transform their random guesses at the beginning of the paradigm into informed decisions over time. After another blank-screen interval (randomly jittered between 615 and 1015 ms) a new trial was initiated. At the end of each experimental block, participants received feedback about their overall performance.

All presented cue and target stimuli were abstract shapes, which were chosen to be easy to distinguish but difficult to verbalize, encouraging participants to rely on their working memory to form new, visual target templates rather than drawing on pre-existing, verbal long-term memory concepts. Five cue-target combinations were created consisting of three unique cue shapes and one target shape each. Cue and target shapes were combined pseudo-randomly and independent of perceptual similarity, again requiring participants to base their decision on the provided feedback and the resulting mental templates rather than on perceptual decision criteria.

Depending on the presented combination of cue and target shapes, trials were divided into three conditions: In the *Match* condition, a correct cue-target combination was presented by pairing one of the cue sequences with its corresponding target shape (correct sequence, correct target). In the *Nonmatch* condition, an incorrect cue-target combination was presented by randomly pairing the cue sequence of one pre-defined cue-target combination with the target shape of another predefined cue-target combination (correct sequence, incorrect target). In the *Catch* condition, also an incorrect cue-target combination was presented. In contrast to the

Nonmatch condition, however, here the mismatch was achieved by pairing one of the cue sequences with its corresponding target shape but with the second shape of the cue sequence being replaced by a randomly selected equivalent of one of the other four sequences (incorrect sequence, correct target). While this condition was not the primary interest of the EEG analyses (because the predictability of the mismatch might have moved memory matching processes into a slightly earlier time window following cue presentation), it was introduced to discourage participants from using a strategy in which, instead of forming complex associations between targets and every shape of their corresponding cue sequences, they might simply link targets to their sequences' first or last element only. The three conditions were equiprobable (33%) with trials being presented in random order and each of the five targets being displayed equally often within each condition (20%). In total, the target identification task consisted of six blocks of 75 trials each (25 per condition) and took approximately 60 minutes.

In the second part of the experiment, participants performed an unannounced, paper-pencil, free-recall drawing task without EEG being recorded. This task was designed to test if and with which fidelity participants had established mental target templates over the course of the previous target identification task. In this task, participants were provided with a printout of the five previously learned cue sequences and were asked to draw the corresponding target shape as precisely as possible. The free-recall drawing task took approximately ten minutes adding up to a total experiment duration of about two hours including EEG preparation and breaks.

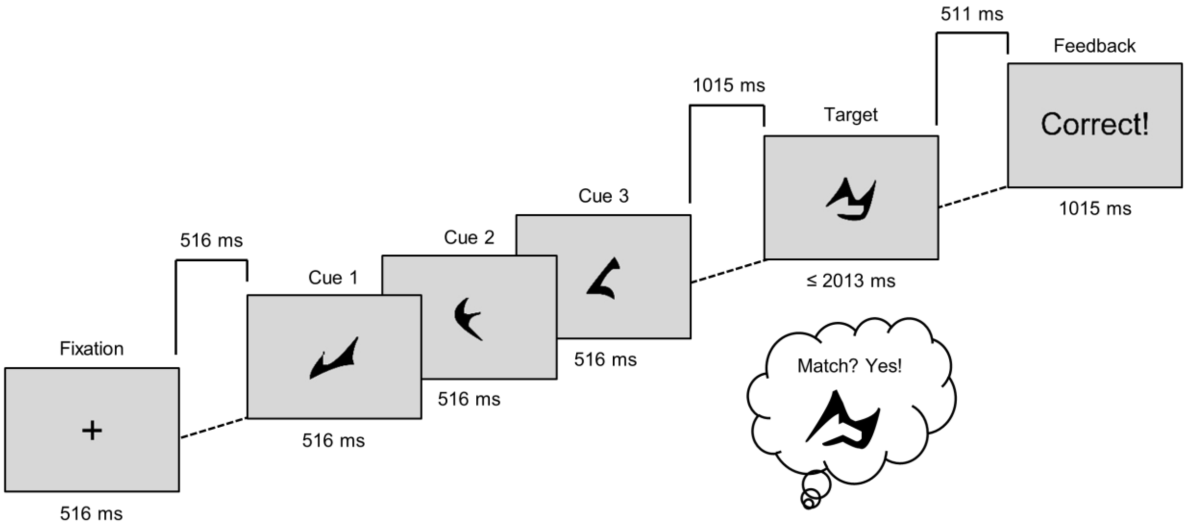

Figure 1. Example trial of the target identification task. In each trial, participants had to classify a target shape as matching or mismatching with a preceding sequence of cue shapes. Participants were instructed to use the following single-trial feedback to learn the initially unknown cue-target combinations (i.e., forming increasingly concrete mental target templates), which would help them to transform their random guesses at the beginning of the paradigm into informed decisions over time.

EEG Recording and Preprocessing

EEG was recorded from 62 scalp locations using passive Ag/AgCl electrodes mounted in an elastic cap (Easycap, Brain Products®), which was positioned in accordance with the extended 10-10 system. An electrode on the tip of the nose was used as reference and electrode position FPz served as ground. To correct for ocular artifacts later on, vertical and horizontal eye movements were recorded with two additional electrodes placed above the left eye and next to its outer canthus, respectively. Electrode signals between 0.016 and 250 Hz were digitized using a BrainAmp DC amplifier (1000-Hz sampling rate, 0.1-µV resolution, Brain Products®) and recorded using BrainVision Recorder 2.0.5 (Brain Products®). Electrode impedances were held below 10 kΩ throughout the recording.

EEG data was later offline preprocessed using BrainVision Analyzer 2.1.2 (Brain Products®). First, raw EEG data were filtered using a high- and low-pass filter (zero phase shift Butterworth filters with a slope of 48 dB/oct) with a cutoff of 0.1 and 100 Hz, respectively, and electrical line noise was removed using a 50-Hz Notch filter (with a slope of 96 dB/oct and a bandwidth of 5 Hz). Afterwards, noisy and slow-drift channels were visually identified and replaced using topographic interpolation by fourth-order spherical splines in affected blocks. EEG channels were then re-referenced using a common average reference, and large artifacts were visually identified and excluded from further processing. In the following semi-automatic Ocular Correction Independent Component Analysis (ICA), artifacts caused by eye movements and other systematic sources of interference, as well as channel-specific noise were removed. Lastly, small artifacts remaining after the Ocular Correction ICA were visually identified and excluded from all following EEG analyses.

To reduce the effects of volume conduction and the attenuation of high-frequency signals on the analyses of theta:gamma phase-phase coupling and evoked gamma activity (Buzsáki et al. 2012; Palva and Palva 2012), continuous, preprocessed scalp-level EEG data were projected into source space using the Low Resolution Electromagnetic Topography (LORETA) transformation in BrainVision Analyzer (Pascual-Marqui et al. 1994, 1999). This transform provides an estimate of the three-dimensional current density distribution within predefined regions of interest (ROIs) in a source space consisting of 2394 voxels at a 7-mm spatial resolution using template structural brain scans (Montreal Neurological Institute of McGill University©). Based on previous source loci of theta:gamma phase-phase coupling (Sauseng et al. 2008; Biel et al. 2021) and memory-related activity for abstract shape stimuli (Slotnick and Schacter 2004, 2006), we defined two symmetrical regions of interest comprising a voxel group within the left and right lingual gyrus of Brodmann area (BA) 18 (MNI voxel coordinate ranges: x = +/-[5;15], y = [-75;-90], z = [-5;-20]). This literature-driven choice was supported by a confirmatory, post hoc source localization of the observed ERP *Match-Nonmatch* difference between the two test halves (230-280 ms poststimulus) using the sLORETA software (Fuchs et al. 2002; Pascual-Marqui 2002; Jurcak et al. 2007), which revealed maximal activation within bilateral lingual gyrus of BA 18 (see Supplementary Fig. 1). For each of our two ROIs, we then extracted the current density (averaged across all voxels included within an ROI) along each of the three dimensions (x, y, and z) from the resulting three-dimensional current density vector and averaged those for both sources separately to compute the overall electrical current within the two sources used for all following source-level analyses.

Behavioural Analyses

Performance in the target identification task was quantified using response sensitivity and speed and was computed for each condition (*Match*/*Nonmatch*/*Catch*) and block separately, which were later averaged to test halves (first half = blocks 1 to 3, second half = blocks 4 to 6). Trials were considered correct if participants provided a single, valid response (*Match* trial = match response, *Nonmatch*/*Catch* trial = mismatch response) within 100 and 2000 ms after target onset, providing enough time for sufficient stimulus processing and response selection within the maximal limit triggering the learning-relevant feedback (Whelan 2008). Reaction times of correct trials were logarithmized and summarized by computing the median for each participant separately. To account for the unbalanced response probabilities (33% matches vs. 66% mismatches) and a potential resulting bias towards the more probable answer, the number of correct trials was transformed into sensitivity measure d' (Stanislaw and Todorov 1999). This was done by computing the difference between the z-transformed ratio of trials correctly classified as members of the current condition (hits, e.g., *Nonmatch* trials correctly classified as mismatch) and the z-transformed ratio of trials belonging to the other response category being incorrectly classified as members of the current condition (false alarms, e.g., *Match* trials incorrectly classified as *Nonmatch*). Sensitivity and reaction times were analyzed in two separate repeated-measures ANOVAs with factors *Test Half* (*Half1*/*Half2*) and *Condition* (*Match*/*Nonmatch*/*Catch*). Greenhouse-Geisser correction was applied where necessary. The following post hoc tests were carried out using Bonferroni-corrected pairwise *t* tests.

Performance in the target drawing task, serving as an index of template fidelity, was defined as the similarity between each target drawing (five per participant corresponding to the five targets previously learned in the target identification task) and the actual target (i.e., correct cue-target matching, overall shape, characteristic features) and was rated by three independent experts on a Likert scale ranging from 0 (no similarity) to 6 (perfect similarity). The resulting 15 rating scores (five targets rated by three experts each) were then averaged to achieve an overall target reproduction score, which was correlated with sensitivity in the target identification task using a one-tailed Pearson correlation. Because one participant was classified as outlier, this sensitivity-fidelity correlation was computed once with and once without the corresponding participant and both test results are reported.

All computations and statistical analyses (including behavioral and EEG data) were carried out in the Spyder 4.1.5 environment (Spyder Developer Team 2020) for Python 3.7.3 (Van Rossum and Drake 2009) using custom-written scripts and different open-source packages for script and data handling (EasyGUI 0.98.1, EasyGui Developer Team 2017; more-itertools 8.5.0, More-itertools Developer Team 2020; pandas 1.1.3, McKinney 2010; prettytable 0.7.2, Prettytable Developer Team 2013; termcolor 1.1.0, Termcolor Developer Team 2011), mathematical operations and statistical analyses (NumPy 1.19.2, Harris et al. 2020; pingouin 0.2.7, Vallat 2018; SciPy 1.5.4, Virtanen et al. 2020) and data visualizations (matplotlib 3.3.2, Hunter 2007; seaborn, Waskom 2021; statsmodels 0.9.0, Seabold and Perktold 2010).

EEG Analyses

All EEG analyses were carried out using custom-written Python scripts and the MNE-Python 0.21.0 package (Gramfort et al. 2013). First, preprocessed EEG data (from the 62 scalp locations and the two estimated sources) were segmented into clean epochs from -700 to +1000 ms around target onset for each of the two main conditions (*Match*/*Nonmatch*). Afterwards, epochs containing incorrect responses were removed and the remaining epochs were combined into test halves. Differences between the resulting number of available trials per condition and test half (*Half1 Match*: *M* = 43.76, *SD* = 9.86 vs. *Half1 Nonmatch*: *M* = 45.48, *SD* = 9.25 vs. *Half2 Match*: *M* = 56.52, *SD* = 12.34 vs. *Half2 Nonmatch*: *M* = 63.67, *SD* = 6.15), possibly affecting the trial count-sensitive indices in the following analyses (Cohen 2014; Luck 2014), were eliminated using pseudo-random epoch sub-sampling (minimizing timing differences between conditions while maximizing timing differences between test halves to account for inter-individual differences between learning curves). On average, 39.90 (*SD* = 8.94) trials remained per condition and test half for the following analyses.

Event-Related Potential Analyses

To relate our results to previous findings of memory matching on event-related potentials (ERPs; Biel et al. 2021), in addition to the proposed template-to-input matching signatures, we computed four separate ERP traces (*Match* and *Nonmatch* condition; first and second test half) by averaging across scalp-level epochs. The resulting ERPs were then averaged across all conditions and participants to compute an overall grand-average ERP, which was used to define one parieto-occipital electrode pool (comprising channels P7, P8, PO7, PO8, O1, and O2) exhibiting the overall highest peak amplitudes within the first 250 ms following target onset as determined by visual inspection. Afterwards, ERPs of each condition and test half were averaged across these six pool electrodes, cropped to the time window of interest (from -200 to +500 ms around target onset) and baseline-corrected using the 200-ms prestimulus interval. The resulting pooled ERPs were statistically compared between the *Match* and the *Nonmatch* condition in the first and the second test half followed by a comparison of the *Match-Nonmatch* difference between the two test halves using two-tailed cluster-based permutation tests (based on the cluster sum of sampling point-wise *t* values from -200 to +500 ms around target onset and 1024 permutations; Maris and Oostenveld 2007).

Cross-Frequency Phase Coupling Analyses

For theta:gamma phase-phase coupling analyses, source-level epochs of each condition and test half were transformed into time-frequency representations using 5-cycle Complex Morlet Wavelet analyses (to be able to detect transient gamma phase modulations). Based on the most recent findings of phase-phase coupling between gamma and relatively high (≥ 6 Hz) theta frequencies (Holz et al. 2010; Biel et al. 2021), we defined 7 Hz (+/- 1.4 Hz) as theta frequency band of interest. This literature-driven choice was further supported by power modulations in the predicted time window around 150 ms poststimulus being maximal across conditions (*Match*/*Nonmatch* in *Half1*/*Half2*) and sources (left/right) for the chosen 7-Hz center frequency within the theta frequency range (5-8 Hz; see Supplementary Fig. 2). Gamma center frequencies were defined as multiples of the chosen theta center frequency within the 30-80 Hz gamma frequency range (i.e., 35, 42, 49, 56, 63, 70, and 77 Hz). Time-frequency representations of the theta and gamma frequency bands of interest were then used to extract continuous phase values, which were used for the following computation of theta:gamma phase-phase coupling.

Phase coupling between theta and gamma oscillations was quantified using the phase synchronization index (PSI), which was used in similar variations in previous studies (Sauseng et al. 2008; Holz et al. 2010; Biel et al. 2021) and describes phase locking between two oscillations with an integer *n:m* frequency ratio (Palva et al. 2005; Schack and Weiss 2005). This cross-frequency phase locking is quantified for each point in time as the consistency of the phase difference across trials on a range from 0 (random fluctuations) to 1 (perfect stability) and can thus be used to identify transient, sub-cycle coupling processes. To compute the PSI, instantaneous theta and gamma phase values ($\Phi_{f_n,t}$ and $\Phi_{f_m,t}$, respectively) of each condition, test half, hemisphere, and theta:gamma frequency pair were multiplied with the opposite center frequency (m and n, respectively) to account for the frequency-dependent slope differences. Afterwards, the phase difference between the low and the high frequency at a certain point in time was computed for all epochs (k) and the resulting phase difference vectors were averaged to compute one mean vector. The PSI was then defined as the length of this average vector:

$$PSI(f_n, f_m, t) = \sqrt{\left(\frac{1}{k}\sum_{k=1}^{k}\cos\left(\left(m \times \Phi_{f_n,t}\right) - \left(n \times \Phi_{f_m,t}\right)\right)\right)^2 + \left(\frac{1}{k}\sum_{k=1}^{k}\sin\left(\left(m \times \Phi_{f_n,t}\right) - \left(n \times \Phi_{f_m,t}\right)\right)\right)^2}$$

Sampling point-wise PSI values were then cropped to the time window of interest (from -200 to +500 ms around target onset), cutting off any data potentially affected by edge artifacts (Cohen 2014), and combined into eleven discrete time windows (-200-0 ms, 0-50 ms, 50-100 ms, 100-150 ms, 150-200 ms, 200-250 ms, 250-300 ms, 300-350 ms, 350-400 ms, 400-450 ms, 450-500 ms). These were statistically compared between the *Match* and the *Nonmatch* condition in the first and the second test half followed by a comparison of the *Match-Nonmatch* difference between the two test halves using one-tailed cluster-based permutation tests (based on the assumption of matching-related increments over time and the cluster sum of window-frequency-wise *t* values and 1024 permutations; Maris and

Oostenveld 2007). To account for the hemisphere-specific effects reported in previous studies (Holz et al. 2010; Biel et al. 2021), all cluster tests were performed two times, separately for the left and the right hemisphere.

To test the specificity of high (7 Hz) theta:gamma phase-phase coupling for memory matching in visual perception and to rule out the possibility that any phase coupling results of the main analysis were in fact driven by effects in neighboring frequencies leaking into the frequency band of interest, we performed two control analyses in which we investigated whether neighboring frequency bands (i.e., low 5 Hz theta and low 9 Hz alpha) might show similar match- and/or time-dependent effects: Using the same procedure as described above, we computed and analyzed phase synchronization between the two new center frequencies of interest (5/9 Hz) and their multiples within the 30-80 Hz gamma frequency range (i.e., 30, 40, 50, 60, 70, and 80 Hz for low-theta:gamma coupling to reduce frequency overlap and to keep the number of gamma bands comparable across tests and 36, 45, 54, 63, 72, and 81 Hz for low-alpha:gamma coupling).

Lastly, we tested the functional relevance of theta:gamma phase synchronization by repeating all high (7 Hz) theta:gamma phase coupling computations from the main analysis with EEG data from five of the excluded, chance-level participants (two of which could not be analyzed due to an insufficient trial count following preprocessing in at least one of the four conditions of interest). If theta:gamma phase synchronization were indeed functionally relevant for the formation of mental target templates and their comparison with bottom-up information, any match- and/or time-dependent effects observed in the main analysis should be specific to those participants who improved beyond chance level (implying a formation of mental target templates) and should be absent (or at least less pronounced) for participants who failed to do so (suggesting difficulties with template formation).

Phase Locking Analyses

To estimate evoked gamma activity, source-level epochs of each condition and test half were transformed into time-frequency representations using 5-cycle Complex Morlet Wavelet analyses. Time-frequency decompositions were then used to compute for each hemisphere the inter-trial coherence, also known as phase locking factor (PLF; Tallon-Baudry et al. 1996; Schack and Weiss 2005). The PLF describes the amplitude-independent consistency of an oscillation's instantaneous phase with respect to an external event on a range from 0 (random jitter) to 1 (perfect synchronization) and was used as an index of evoked activity (e.g., evoked gamma band response) independent of potential background amplitude modulations. Similar to the PSI, the PLF is computed for each point in time as the length of the mean vector resulting from the instantaneous phase vectors across all trials.

The resulting PLFs were then cropped to the time window of interest (from -200 to +500 ms around target onset), again cutting off any data potentially affected by edge artifacts (Cohen 2014), and baseline-corrected (subtraction of the mean within the 200 ms prestimulus interval). Afterwards, PLFs were analyzed using cluster-based permutation tests (based on the cluster sum of time-frequency-wise *t* values and 1024 permutations; Maris and Oostenveld 2007), where we first compared for each hemisphere separately the *Match* and the *Nonmatch* condition in the first and the second test half followed by a comparison of the *Match-Nonmatch* difference between the two test halves.

Time-frequency decompositions and PLF computations were performed not only for the gamma frequency range but for all frequencies of interest (from a low 5 Hz theta frequency up to a high 80 Hz gamma frequency in 1 Hz steps). This was done because nonstationarities exhibiting a common drive on different spectral EEG components, like an external stimulus causing simultaneous phase locking of two *per se* unrelated oscillations, can lead to a spurious inflation of cross-frequency phase coupling, integrating both evoked and induced activity (Schack and Weiss 2005), without a genuine interaction between the two underlying oscillations (Aru et al. 2015; Palva and Palva 2018). The phase locking analysis thus did not only provide an index of evoked gamma activity but also served as control analysis for theta:gamma phase-phase coupling.

To quantify the degree to which any theta:gamma phase coupling effects might have been driven by simultaneous phase locking of the two underlying oscillations, we computed the cross-correlation (i.e., the similarity between two signals for varying time lags) between the respective phase locking traces: for each participant, baseline-corrected PLF time series of theta and gamma oscillations in the *Match* condition of the second test half (exhibiting maximal theta:gamma phase synchronization values most vulnerable to an artificial inflation caused by simultaneous phase locking) were correlated across the time window of interest (from -200 to +500 ms around target onset) with a maximum lag of 350 ms. We then identified the absolute latencies of cross-correlation maxima (indicating the time lag of greatest positive correlation between theta and gamma phase locking) separately for each source and gamma frequency. The resulting latencies were then averaged across gamma frequencies included in the observed theta:gamma phase coupling clusters (i.e., 35 and 42 Hz for the left source and 35, 42, and 49 Hz for the right source) and statistically compared against a time lag of zero (which were to be expected if theta and gamma oscillations indeed exhibited simultaneous phase locking) using two-sided one-sample t tests with p values Bonferroni-corrected for multiple testing.

Lastly, similar to the control analysis of cross-frequency phase coupling, we tested the functional relevance of evoked gamma activity by repeating all phase locking computations from the main analysis with EEG data from the five excluded, chance-level participants with sufficient trial counts. If evoked gamma activity were indeed functionally relevant for the formation of mental target templates and their comparison with bottom-up information, again, any match- and/or time-dependent effects observed in the main analysis should be specific to the above-chance participants (able to form concrete target expectations) and should be absent (or at least less pronounced) for chance-level participants (having difficulties with doing so).

Brain-Behaviour Correlation Analyses

To test the functional relevance of EEG parameters (i.e., ERP amplitude, theta:gamma phase-phase coupling and gamma phase locking as an index of evoked gamma activity) for template-to-input matching in visual perception, the mean for each parameter within significant clusters was computed for each participant. Afterwards, cluster means were correlated with performance (i.e., sensitivity in the two trial conditions (*Match/Nonmatch*) of the target identification task and target reproduction scores from the drawing task) using one-tailed Pearson correlations (with the assumption that matching-related EEG effects would be beneficial to performance and template fidelity). Each correlation with target reproduction scores was computed once with and once without the outlier and both test results are reported for the sake of transparency. All analyses (behavior, EEG parameters and brain-behavior correlations) were performed using an alpha level of $\alpha = 0.05$.

Results

Behavior

Overall, sensitivity (d') differed significantly between conditions ($F(2, 40) = 60.36$, $p < .001$, $\eta_p^2 = .751$) with scores being highest in the *Nonmatch* condition ($M = 1.62$, $SE = 0.18$) followed by the *Match* condition ($M = 1.16$, $SE = 0.16$; *Nonmatch-Match*: $t(20) = 8.32$, $p < .001$, $\eta^2 = .080$) and the *Catch* condition ($M = 0.81$, $SE = 0.17$; *Match-Catch*: $t(20) = 6.56$, $p < .001$, $\eta^2 = .052$; see Fig. 2A). Most importantly, however, participants significantly improved across all conditions from the first test half ($M = 0.51$, $SE = 0.13$)

to the second test half (M = 1.89, SE = 0.22; $F(1, 20) = 116.47$, $p < .001$, $\eta_p^2 = .853$). This improvement over time differed significantly between conditions ($F(2, 40) = 18.41$, $p < .001$, $\eta_p^2 = .479$) and was most pronounced in the *Nonmatch* condition (ΔM = 1.68, ΔSE = 0.13) followed by the *Match* condition (ΔM = 1.33, ΔSE = 0.12; *Nonmatch-Match*: $t(20) = 5.03$, $p < .001$, $\eta^2 = .082$) and the *Catch* condition (ΔM = 1.13, ΔSE = 0.16; *Match-Catch*: $t(20) = 3.00$, $p = .021$, $\eta^2 = .023$).

Similarly, reaction times decreased significantly from the first test half (M = 6.45 ≈ 632.70 ms, SE = 0.05) to the second test half (M = 6.18 ≈ 482.99 ms, SE = 0.06; $F(1, 20) = 72.99$, $p < .001$, $\eta_p^2 = .785$; see Fig. 2B). This decrease over time differed significantly between conditions ($F(2, 40) = 4.66$, $p = .024$, $\eta_p^2 = .189$) and was most pronounced in the *Catch* condition (ΔM = -0.34, ΔSE = 0.05; *Catch-Match*: $t(20) = -1.62$, $p = .364$, $\eta^2 = .036$) followed by the *Match* condition (ΔM = -0.26, ΔSE = 0.03; *Match-Nonmatch*: $t(20) = -1.50$, $p = .445$, $\eta^2 = .024$) and the *Nonmatch* condition (ΔM = -0.22, ΔSE = 0.03; *Nonmatch-Catch*: $t(20) = 2.93$, $p = .025$, $\eta^2 = .099$). Across test halves, however, reaction times did not differ significantly between the *Match* condition (M = 6.30, SE = 0.05), the *Nonmatch* condition (M = 6.36, SE = 0.04) and the *Catch* condition (M = 6.28, SE = 0.08; $F(2, 40) = 2.99$, $p = .088$, $\eta_p^2 = .130$).

In line with improved task performance in the second half of the target identification task, suggesting a formation of mental target templates over time, participants were able to draw the previously learned targets with moderate to high precision in the subsequent unannounced free recall drawing task (M = 3.84, SE = 0.26; see Supplementary Fig. 5). Larger performance improvements in the target identification task were associated with higher scores in the drawing task thereafter (with outlier: $r(19) = .60$, $p = .002$; without outlier: $r(18) = .56$, $p = .005$; see Fig. 2C).

Taken together, these results suggest that participants were indeed able to establish mental target templates over the course of the experiment, which helped them to improve their performance in the target identification task over time, with higher template fidelity being associated with steeper learning slopes and vice versa.

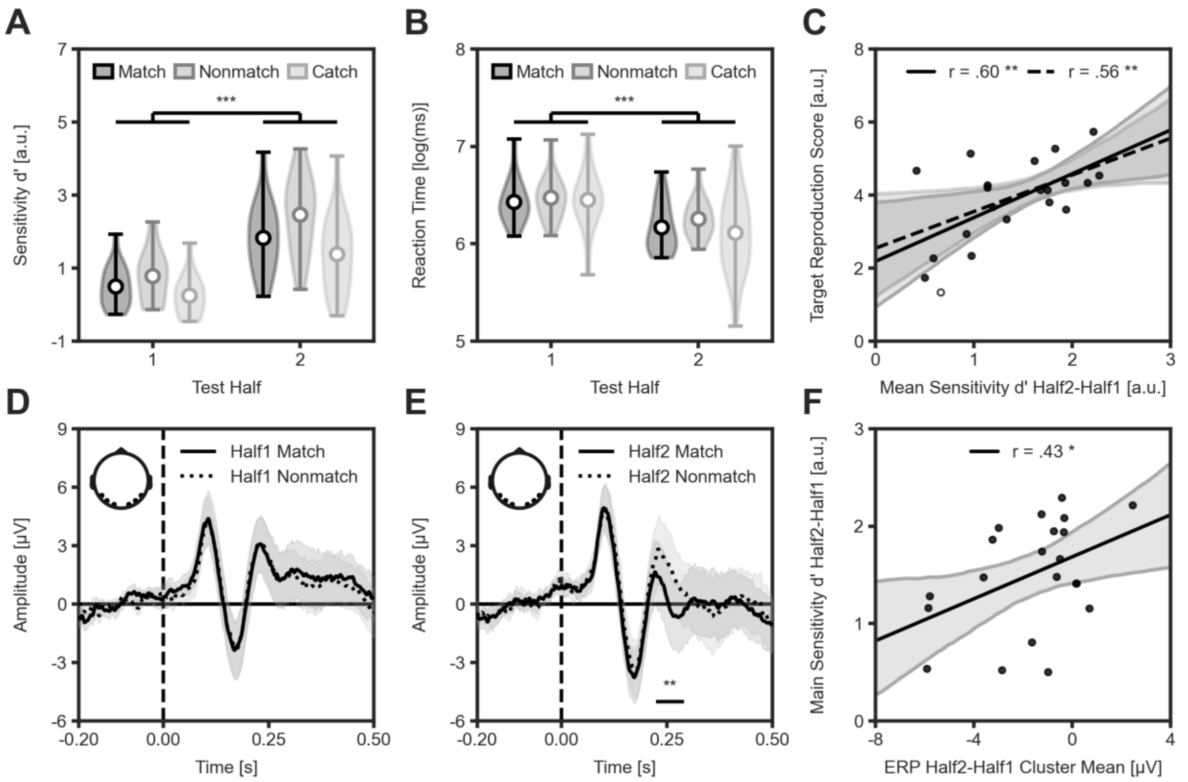

Figure 2. Performance and ERPs for the different conditions and test halves of the target identification task. Panels *A* and *B* show the significant improvement of performance (i.e., an increase of sensitivity d' and a decrease of reaction times, respectively) across conditions from the first to the second test half. Dots represent means across the sampling distribution illustrated by shaded areas and whiskers. In panel *C*, the correlation between sensitivity improvements in the target identification task and target reproduction scores as a proxy of template fidelity is displayed. Solid and dashed lines correspond to regression estimates with and without the target reproduction outlier (contoured dot). Panels *D* and *E* show the related increase of the grand-average (n = 21) ERP difference between the *Match* and the *Nonmatch* condition from the first to the second test half (averaged across electrodes P7, P8, PO7, PO8, O1, and O2). In panel *F,* the correlation between matching-related ERP increases from the first

to the second test half and sensitivity improvements in the target identification task is illustrated. Shaded areas denote 95% confidence intervals. Asterisks indicate statistical significance (for *A* and *B* only between test halves to improve visibility), where * ≙ $p < .05$, ** ≙ $p < .01$ and *** ≙ $p < .001$.

ERPs

In line with low performance in distinguishing between matching and mismatching cue-target combinations at the beginning of the experiment, parieto-occipital ERPs did not differ significantly between the *Match* and the *Nonmatch* condition in the first test half (all cluster p’s $\geq .394$; see Fig. 2D). In the second test half, however, in which participants were significantly better in distinguishing between matching and mismatching cue-target combinations, ERPs differed significantly between the *Match* and the *Nonmatch* condition ($p = .004$, corresponding to a cluster around 220-290 ms after target onset; see Fig. 2E). In addition to a descriptive, matching-independent difference between the two test halves (>300 ms poststimulus), this emerging *Match-Nonmatch* dissociation led to a significant matching-dependent difference between the first and the second test half ($p = .020$, corresponding to a cluster around 230-280 ms after target onset). The resulting ERP difference between test halves was significantly correlated with performance improvements from the first to the second test half of the target identification task ($r(19) = .43$, $p = .027$; see Fig. 2F). Target rating scores as an index of template fidelity, in contrast, were not significantly correlated with the ERP difference between test halves (with outlier: $r(19) = .10$, $p = .332$; without outlier: $r(18) = .12$, $p = .312$).

These results suggest that the increasing ability of distinguishing between matching and mismatching cue-target combinations from the first to the second test half can be reflected in parieto-occipital ERPs, which might, given the comparatively late time window around 250-ms poststimulus, however, be related to other task aspects than template-to-input matching *per se*.

Cross-Frequency Phase Coupling

In agreement with the low performance and the indistinguishable ERPs at the beginning of the target identification task, indicating an initial inability to differentiate between matching and mismatching cue-target combinations on the behavioral and cortical level, theta:gamma phase-phase coupling did not differ significantly between the *Match* and the *Nonmatch* condition in the first test half for any of the two hemispheres (all time-frequency cluster p's ≥ .463; see Fig. 3A and C). Consistent with the improved task performance in the second test half, however, theta:gamma phase-phase coupling in the left hemisphere was significantly higher in the *Match* condition compared to the *Nonmatch* condition (p = .019, corresponding to a cluster around 200-ms poststimulus in a low gamma frequency range around 40 Hz). This emerging *Match-Nonmatch* difference was, however, not significantly different from the first test half (all cluster p's ≥ .690; see Fig. 3D), nor did it correlate with performance in the second test half or template fidelity as indicated by target reproduction scores (*Half2 d'*: $r(19) = -.13$, $p = .283$; reproduction scores with outlier: $r(19) = -.16$, $p = .241$; reproduction scores without outlier: $r(18) = -.26$, $p = .139$).

In the right hemisphere, in contrast, the *Match-Nonmatch* difference was significantly higher in the second compared to the first test half (p = .007, corresponding to a cluster around 200-ms poststimulus in a low gamma frequency range around 40 Hz; see Fig. 3B). This difference between test halves was, however, not only driven by a descriptive trend of increased *Match-Nonmatch* theta:gamma phase-phase coupling in the second test half, but also by a nonsignificant reversal of this effect in the first test half (all cluster p's ≥ .463). In contrast to the left hemisphere, this right-hemispheric, matching-related theta:gamma phase-phase coupling difference between test halves was significantly, though, negatively correlated with performance improvements in the target identification task and target reproduction scores as a proxy of template fidelity (*Half2-Half1 d'*: *r*(19) = -.40, *p* = .036; reproduction scores with outlier: *r*(19) = -.41, *p* = .032; reproduction scores without outlier: *r*(18) = -.37, *p* = .053; see Fig. 3E and F); i.e., individuals with higher target reproduction scores demonstrated smaller theta:gamma phase-phase coupling increases from the first to the second test half. Importantly, no such match- and/or time-dependent effects were observed in any of the two control analyses of low-theta:gamma and low-alpha:gamma phase coupling (all cluster *p's* ≥ .102 and .171, respectively; see Supplementary Figs 3 and 4), nor for the excluded participants, who were unable to perform above chance by the end of the target identification task (implying difficulties with template formation; see Supplementary Fig. 6).

In line with the theoretical framework put forward by Sauseng and colleagues (Sauseng et al. 2008, 2010, 2015), these results suggest that (high) theta:gamma phase-phase coupling in early visual cortices reflects the interaction between bottom-up visual information and top-down mental templates, but might, unexpectedly however, be detrimental to performance on the long run.

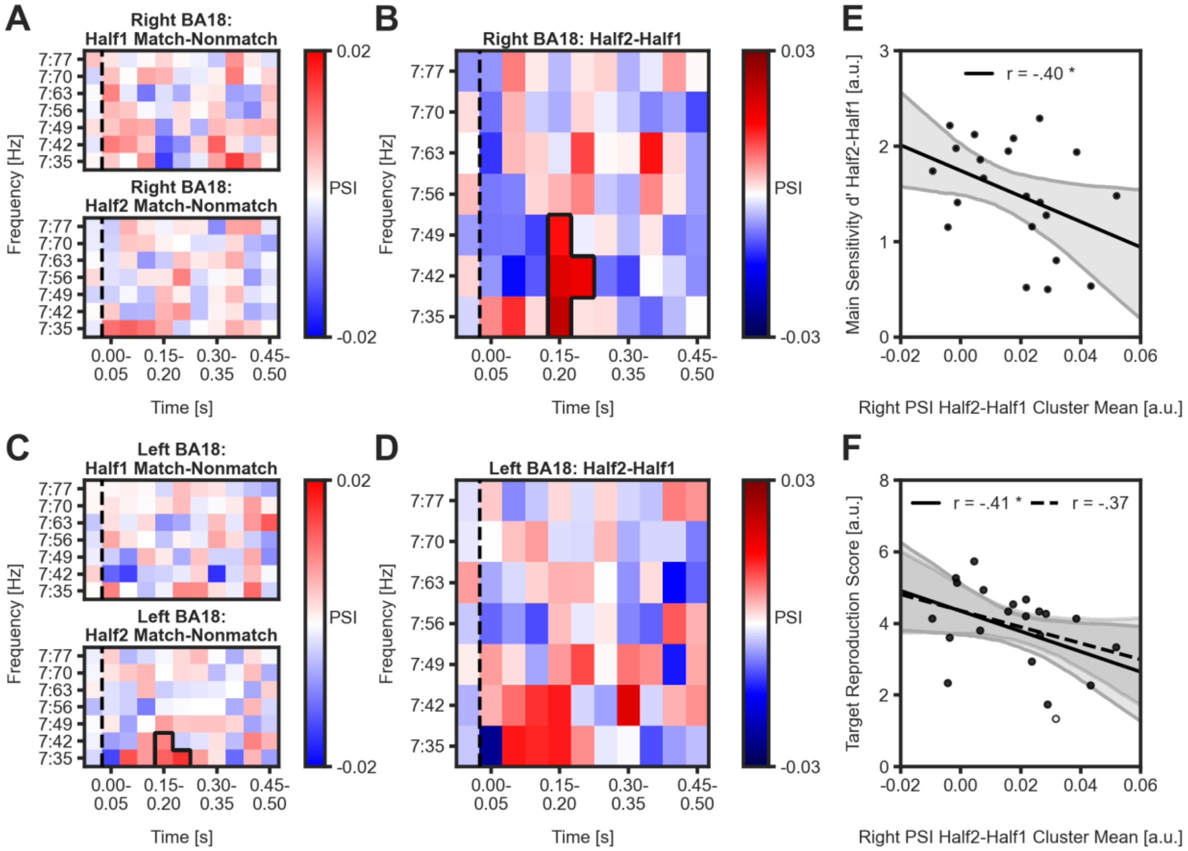

Figure 3. Theta:gamma phase-phase coupling (phase synchronisation index, PSI). Panels *A* and *C* show the grand-average (n = 21) difference between the *Match* and the *Nonmatch* condition for each test half of the target identification task separately for the right and the left source in BA18, respectively. In panels *B* and *D,* the corresponding difference between test halves for the two sources is displayed. Panels *E* and *F* show the correlation of right-hemispheric, matching-dependent increases of theta:gamma phase synchronization from the first to the second test half with performance improvements in the target identification task and target reproduction scores as a proxy of template fidelity, respectively. Solid and dashed lines correspond to regression estimates with and without the target reproduction outlier (contoured dot). Clusters highlighted with solid lines and correlations with asterisks are significant at $p < .05$.

Phase Locking

In each condition, test half, and hemisphere, we found significantly increased phase locking compared to baseline following target onset for a broad range of frequencies (all cluster *p's* < .001, corresponding to broad-band clusters up to around 400-ms poststimulus; see Fig. 4A and B). This effect was most pronounced for lower frequency bands (around 5-25 Hz) but extended into the gamma frequency range (around 30-70 Hz circa 100-ms poststimulus). In line with the MUM and the herein suggested role of evoked gamma activity for template-to-input matching in visual perception (Herrmann et al. 2004a, 2010), this gamma response was most evident (though only as a trend) in the *Match* condition, where it included high gamma frequencies (up to 80 Hz) in the first test half (*p* = .063 and *p* = .099 for the right and the left hemispheres, respectively) while being evident primarily in lower gamma frequency bands (up to around 40 Hz) in the second test half. In the first test half, matching-evoked high-gamma phase locking cluster means tended to correlate negatively with target reproduction scores as an index of template fidelity (*Half1 d'*: *r*(19) = -.11, *p* = .312; reproduction scores with outlier: *r*(19) = -.42, *p* = .031; reproduction scores without outlier: *r*(18) = -.28, *p* = .117; see Fig. 4E) in the left hemisphere. However, right-hemispheric high-gamma phase locking in the first test half was not related to behavior at all (*Half1 d'*: *r*(19) = .04, *p* = .439; reproduction scores with outlier: *r*(19) = -.15, *p* = .256; reproduction scores without outlier: *r*(18) = .11, *p* = .322).

The trend of increased gamma phase locking in the *Match* condition did not differ significantly from the *Nonmatch* condition in any test half for the right hemisphere (all cluster *p's* ≥ .146; see Fig. 4D), nor in the first test half for the left hemisphere (*p's* ≥ .107). In the second test half, however, in which participants were significantly better in distinguishing matching from mismatching cue-target combinations (presumably due to the formation of mental target templates), gamma phase locking in the left hemisphere was significantly higher in the *Match* condition than in the

Nonmatch condition (p = .009, corresponding to a cluster around 100 ms after target onset in a frequency range around 20-80 Hz; see Fig. 4C). Although this *Match-Nonmatch* difference was not significantly different between the two test halves for any of the two hemispheres (all cluster *p's* ≥ .385), this left-hemispheric matching-related increase of gamma phase locking in the second test half was significantly and positively correlated with target reproduction scores as an index of template fidelity (*Half2 d'*: $r(19) = .14$, $p = .272$; reproduction scores with outlier: $r(19) = .45$, $p = .021$; reproduction scores without outlier: $r(18) = .39$, $p = .046$; see Fig. 4F). Participants, who were excluded from the main analyses due to their lacking ability to perform significantly above chance by the end of the target identification task (presumably due to difficulties with template formation), in contrast, did not show any such gamma-related effects (see Supplementary Fig. 7).

Importantly, while lower frequencies including theta exhibited phase locking over an extended time interval up to around 400 ms after target onset, phase locking within the gamma frequency range was very restricted in time (around 100-ms poststimulus). While this latency is not only well in line with the MUM (Herrmann et al. 2004a, 2010), it also precedes the time window for which increased theta:gamma phase-phase coupling was found (around 200-ms poststimulus). This observation was further supported by cross-correlation analyses suggesting that theta and gamma phase locking in the *Match* condition of the second test half (exhibiting maximal theta:gamma phase synchronization values most vulnerable to an artificial inflation caused by simultaneous phase locking) were significantly separated by about 140 ms in both sources (left source: M = 135.41, SE = 14.17, $t(20) = 9.56$, $p < .001$, $\eta^2 = .521$; right source: M = 147.79, SE = 18.52, $t(20) = 7.98$, $p < .001$, $\eta^2 = .431$). Together, these findings argue against an artificial inflation of theta:gamma phase-phase coupling by simultaneous phase resetting of theta and gamma oscillations in the corresponding time window and suggest that cross-frequency phase coupling effects were driven by genuine interactions between theta and gamma frequencies.

In line with the MUM (Herrmann et al. 2004a, 2010), these results suggest that a match between bottom-up visual information and top-down mental templates (being maximal when an elaborated template meets memory-matching information, such as in the second test half and for participants with a detailed target template) is reflected by a relative increase of evoked gamma activity as indicated by higher phase locking in early visual areas.

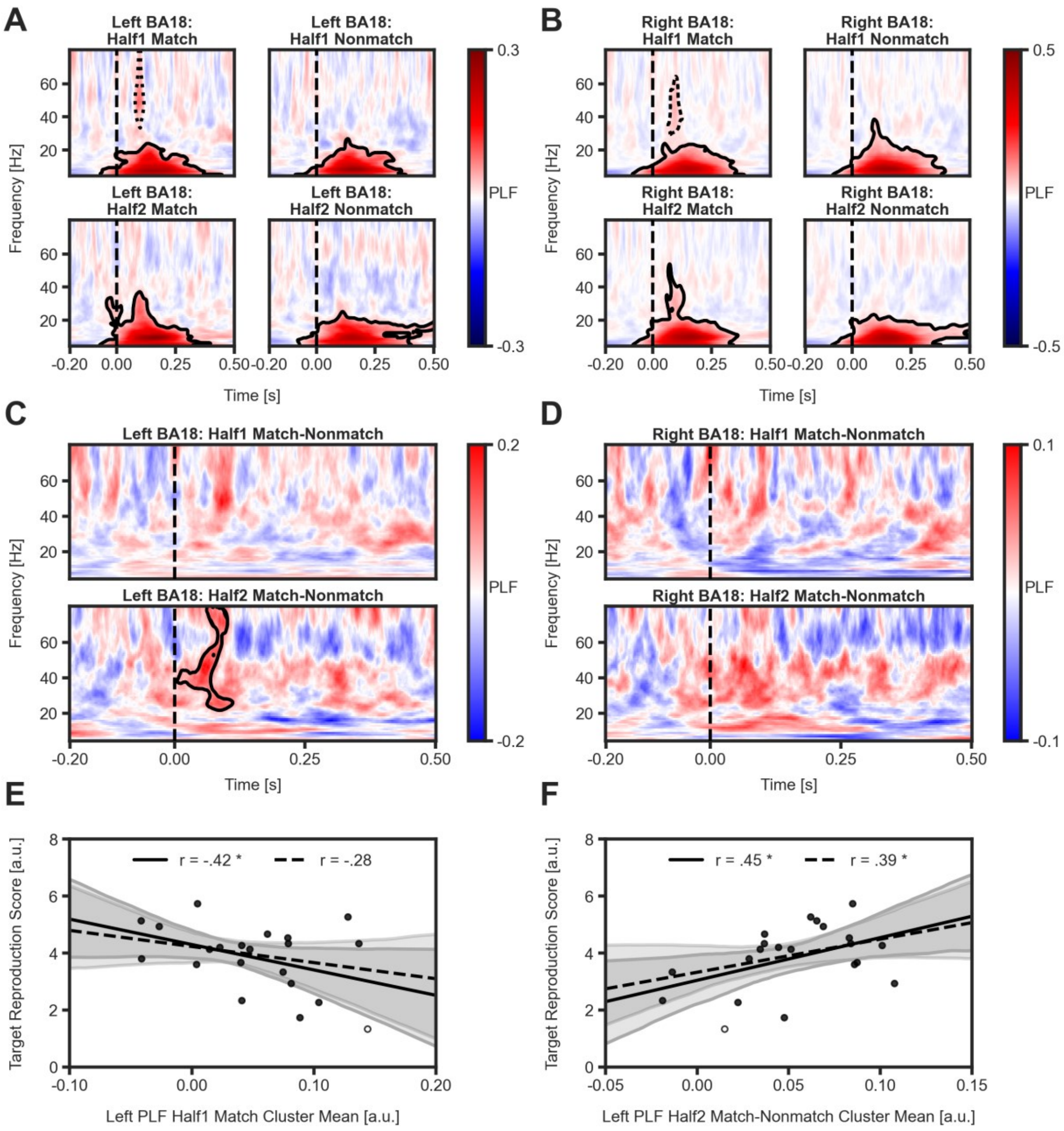

Figure 4. Broadband (5-80 Hz) phase locking to stimulus onset (phase locking factor, PLF). Panels *A* and *B* show grand-average (n = 21) phase locking for each condition and test half of the target identification task separately for the left and the right source in BA18, respectively. In panels *C* and *D,* the corresponding difference between conditions for the two test halves and sources is displayed. Clusters surrounded by solid lines are significant at $p < .05$; dashed lines indicate trend clusters with $p < .10$. Panels *E* and *F* show the correlation of left-hemispheric, matching-dependent gamma phase locking in the first and the second test half with target reproduction scores as a proxy of template fidelity, respectively. Solid and dashed lines correspond to regression estimates with and without the target reproduction outlier (contoured dot). Correlations with asterisks are significant at $p < .05$.

Discussion

Evoked gamma activity and theta:gamma phase-phase coupling in early visual cortices around 100-150-ms post-stimulus have previously been observed when a mental template meets a matching visual stimulus and have hence been proposed as signatures of template-to-input matching in visual perception (Herrmann et al. 2004a, 2010; Sauseng et al. 2008, 2010). Here, we investigated how these signatures evolve during the formation of new mental templates and how they relate to the fidelity of such. In line with our hypothesis that evoked gamma activity and theta:gamma phase synchronization should increase with an increasing similarity between bottom-up and top-down information (being maximal when a highly elaborated mental template meets a matching visual stimulus), we observed matching-related increments of both signatures over time, which were dependent on the fidelity of mental templates.

Supporting previous findings of matching-related evoked gamma activity (Herrmann et al. 2004b; Morup et al. 2006; Fründ et al. 2008), relative to baseline, we observed a tendency of increased gamma phase locking (around 30-80 Hz) in early visual cortices around 100 ms after onset of a template-matching target. This trend was significantly higher for matching compared to mismatching targets in the left hemisphere and the second test half, in which participants were also significantly better in distinguishing between matching and mismatching cue-target combinations (presumably due to the formation of mental target templates). Additionally, and in accordance with previous reports of increased theta:gamma phase synchronization for matches between bottom-up and top-down information (Sauseng et al. 2008; Holz et al. 2010; Biel et al. 2021), we observed a significant right-hemispheric increase of matching-dependent theta:gamma (ca. 7:40 Hz) phase synchronization in early visual areas around 200-ms poststimulus from the first to the second test half. Although we found a similar increase of matching-related ERP differences over time, they emerged in a later time window (around 250-ms poststimulus, similar to Biel et al. 2021) and were related to target identification improvements but not to target reproduction scores as a proxy of template fidelity. Gamma phase locking and theta:gamma phase-phase coupling, in contrast, were both significantly (though oppositely) correlated with the quality of target reproduction.

Interestingly, matching-related increases of theta:gamma phase-phase coupling from the first to the second test half were negatively correlated with target reproduction scores, as was gamma phase locking in response to template-matching stimuli in the first test half. However, matching-dependent increments of gamma phase locking in the second test half were positively correlated with target reproduction scores. Based on the proposed specialization of theta:gamma phase synchronization and evoked gamma activity for memory matching with templates stored in working and long-term memory, respectively (Holz et al. 2010; Sauseng et al. 2015), one could speculate that our results might reflect a switch between these two memory systems over time, which depends on how participants tried to solve the target identification task: The most straightforward strategy for a successful performance would be to directly focus on the actual targets and form corresponding mental templates, which would first be actively maintained in working memory and then slowly transferred into long-term memory over time. This approach would be beneficial to the quality of target reproduction later on and should be reflected by matching-related gamma phase locking being weak in the first test half but strong in the second test half (once stimuli are compared against the established target templates stored in long-term memory). At the same time there should be comparatively small increases of matching-dependent theta:gamma phase-phase coupling over time (as templates become more detailed but require less active maintenance in working memory).

In an alternative strategy, participants might not directly focus on the targets *per se* but rather link them to pre-existing long-term memory representations with a roughly similar shape. And only later they would form the actual target templates with all their details. This approach would be detrimental to the quality of target reproduction thereafter; and it should be mirrored by matching-related gamma phase locking (as a proxy for matching with long-term memory contents) being strong in the first test half but weak in the second test half (as matching to pre-existing long-term memory contents decreases) and rather large increments of matching-dependent theta:gamma phase-phase coupling over time (as the formation of actual target templates in working memory increases). This interpretation is supported by multiple participant reports following the experiment, according to which the unknown targets were initially remembered by the names of familiar, perceptually related long-term memory representations. This might also explain the observed lateralization of matching-dependent effects with stronger gamma phase locking in the left hemisphere and increased theta:gamma phase-phase coupling in the right hemisphere, thought to be specialized for verbal and visuospatial memory contents, respectively (Baddeley 2003 for review; Rossion et al. 2003).

These results are largely in line with the proposed models of template-to-input matching in visual perception (Herrmann et al. 2004a, 2010; Sauseng et al. 2008, 2010, 2015) and suggest that evoked gamma activity and (high) theta:gamma phase-phase coupling in early visual areas might indeed reflect matching processes between bottom-up and top-down information (although we do not assume these to be the only relevant signatures, frequencies or loci). ERPs, in contrast, seem to mirror other task components (e.g., model updating, in accordance with the time window and functional role proposed by the MUM and ERP models; Herrmann et al. 2004a, 2010, Polich 2007). Extending previous studies, here we show that these two phase-based signatures depend not only on the features of the visual stimulus, either matching or mismatching the internal model, but also on the fidelity of the corresponding mental template, formed and elaborated through repeated exposure.

Importantly, our findings are likely to reflect genuine memory matching processes and cross-frequency interactions. Compared to previous studies of matching-related gamma activity, which contrasted real and scrambled objects (Herrmann et al. 2004b; Morup et al. 2006; Fründ et al. 2008), thus leaving open the possibility that the observed condition differences were driven by a change of stimulus features and not purely by differences in memory matching (Martinovic and Busch 2011), here, targets were identical across conditions and only differed with respect to the preceding cue sequence. In addition to the correlation with target reproduction scores as a proxy of template fidelity and the specificity of matching-dependent gamma phase locking for above-chance participants (able to form concrete target expectations), this suggests that our phase locking effects are unlikely to reflect low-level confounds but rather interactions between bottom-up and top-down processes. Similarly, it is rather unlikely that our results of matching-related theta:gamma phase-phase coupling, which were not only specific to high (7 Hz) theta but also to those participants who improved beyond chance level in the target identification task (presumably due to the formation of mental target templates), reflect spurious cross-frequency synchronization due to simultaneous phase resetting (Aru et al. 2015; Palva and Palva 2018): Whereas theta oscillations exhibited increased phase locking around the same time for which we also observed increased theta:gamma phase coupling (around 200-ms poststimulus), gamma phase locking was temporally separated by about 140 ms and occurred before cross-frequency interactions.

It should be noted, however, that the target drawings that we used here as an index of template fidelity might have been affected by matching-unrelated factors like artistic skills and can therefore only serve as an approximation of such. Moreover, due to the necessarily low number of correctly answered trials at the beginning of the experiment and the resulting need to combine individual experimental blocks into test halves to achieve a sufficient trial count for cross-frequency coupling analyses (Cohen 2014), we cannot account for interindividual differences in learning curves; nor can we draw conclusions about the general trajectory of template formation. In future studies, it would be interesting to investigate these aspects in more detail to test if the generation of new mental templates constitutes a gradual process, and if evoked gamma activity and theta:gamma phase synchronization follow individual learning trajectories. Moreover, dynamic experimental designs free from evoked activity might prove particularly valuable for future investigations of theta:gamma phase-phase coupling by further excluding potential confounds caused by stimulus-related nonstationarities.

In summary, we found that matching processes between bottom-up visual information and top-down mental templates are reflected by increased left-hemispheric gamma phase locking and stronger right-hemispheric theta:gamma phase-phase coupling in early visual areas around 100-200 ms poststimulus. The matching result and the associated neural signatures hereby depend not only on the stimulus material, either matching or mismatching the internal model, but also on the fidelity of mental templates, formed and elaborated through repeated exposure. By combining these so far separate lines of research, we provide evidence for evoked gamma activity and theta:gamma phase synchronization as complementary signatures of template-to-input matching in visual perception, with a potential specialization for memory matching with templates stored in semantic long-term memory and visuospatial working memory, respectively.

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Notes

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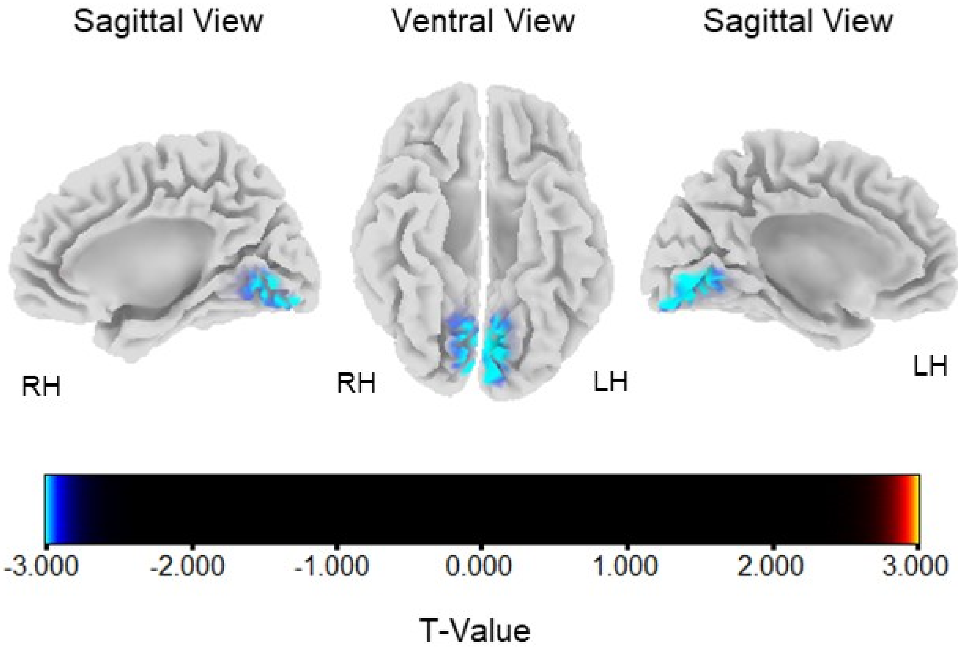
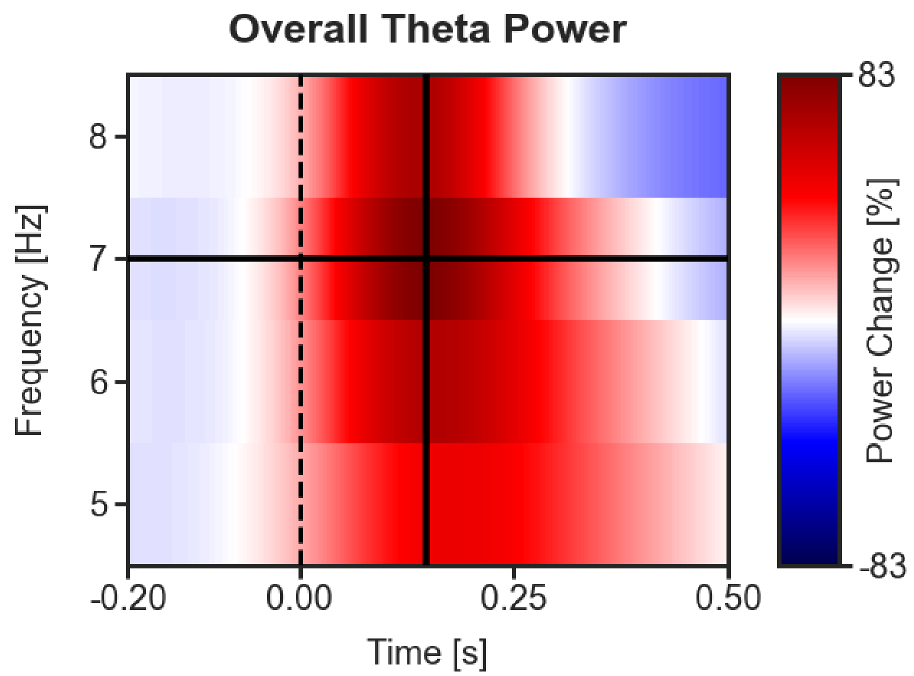
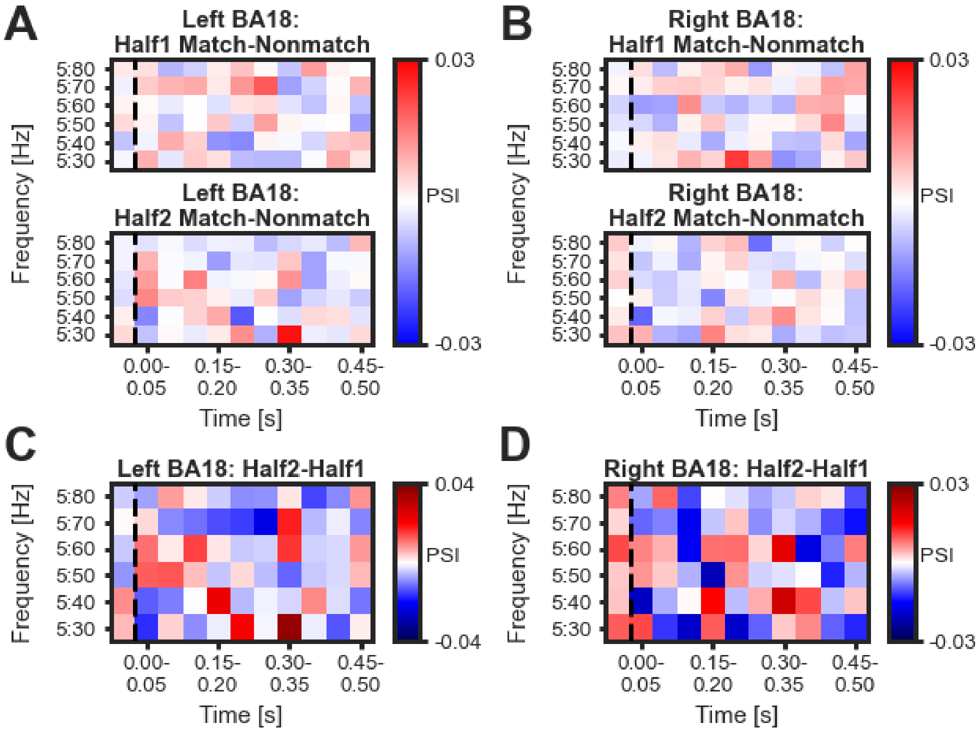
Supplementary Material



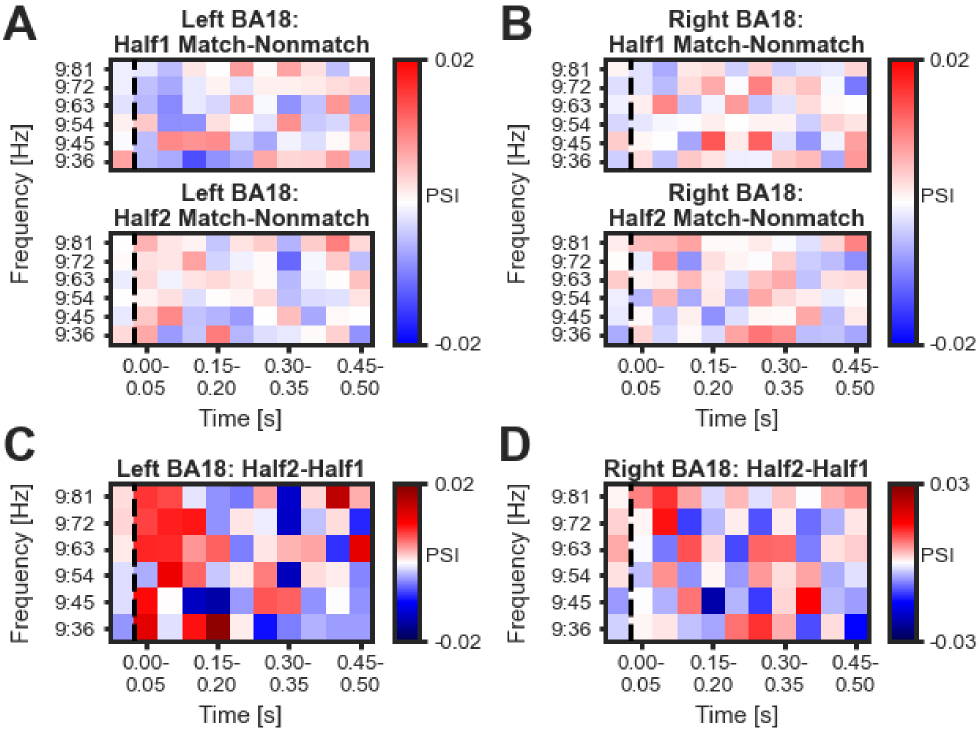
Supplementary Figure 1. Source localisation of the event-related potential (ERP) *Match-Nonmatch* difference between the two test halves (230-280 ms post-stimulus) showing maximal activation within bilateral lingual gyrus of Brodmann area 18.



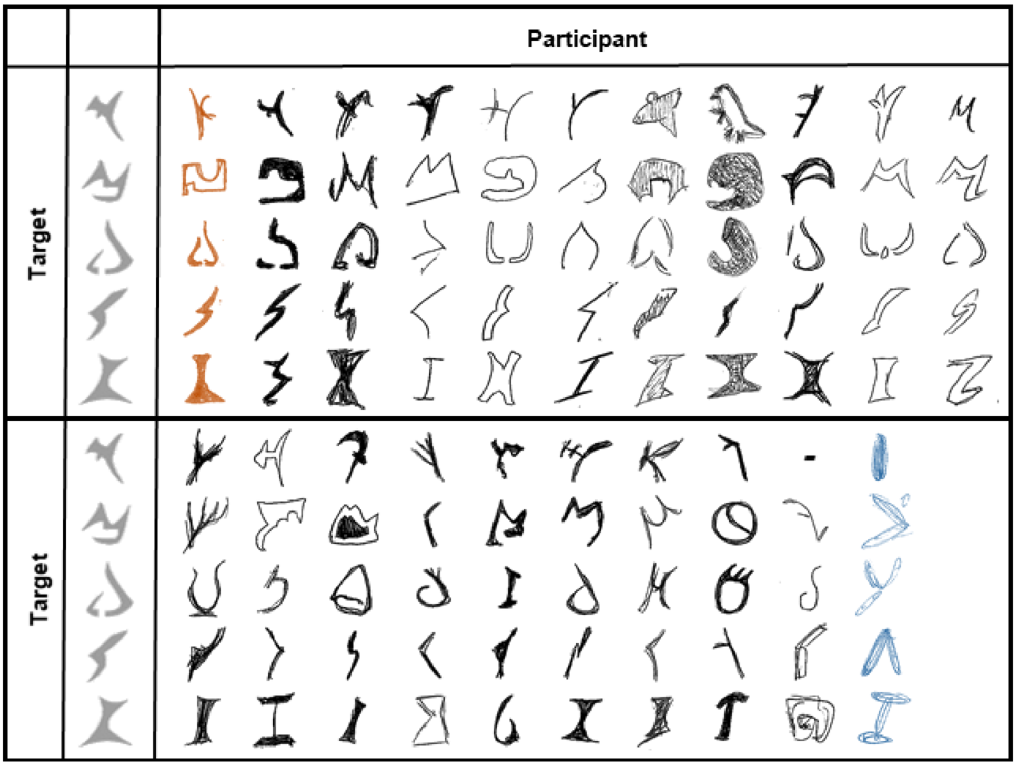
Supplementary Figure 2. Grand-average (n = 21) overall theta (5-8 Hz) power change (%) relative to pre-stimulus baseline across conditions (*Match*/*Nonmatch* in *Half1*/*Half2*) and sources (left/right). Cross hairs indicate the time point and frequency band of maximal post-target power change.



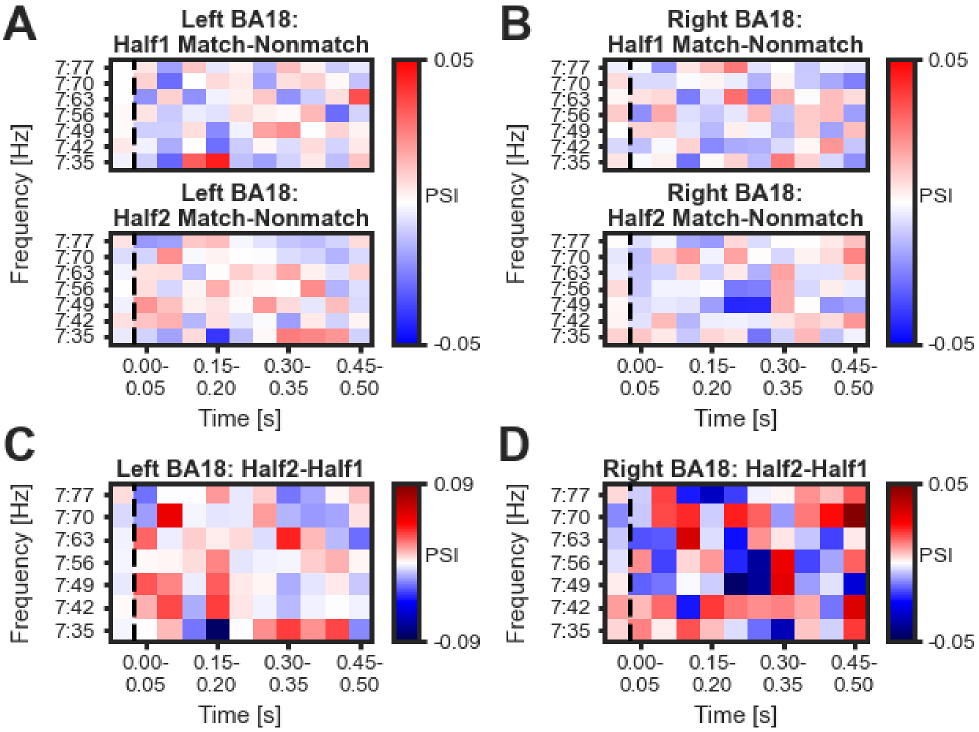
Supplementary Figure 3. Low-theta:gamma phase-phase coupling (phase synchronisation index, PSI). Panels *A* and *B* show the grand-average (n = 21) difference between the *Match* and the *Nonmatch* condition for each test half of the target identification task separately for the left and the right source in BA18, respectively. In panels *C* and *D,* the corresponding difference between test halves for the two sources is displayed.



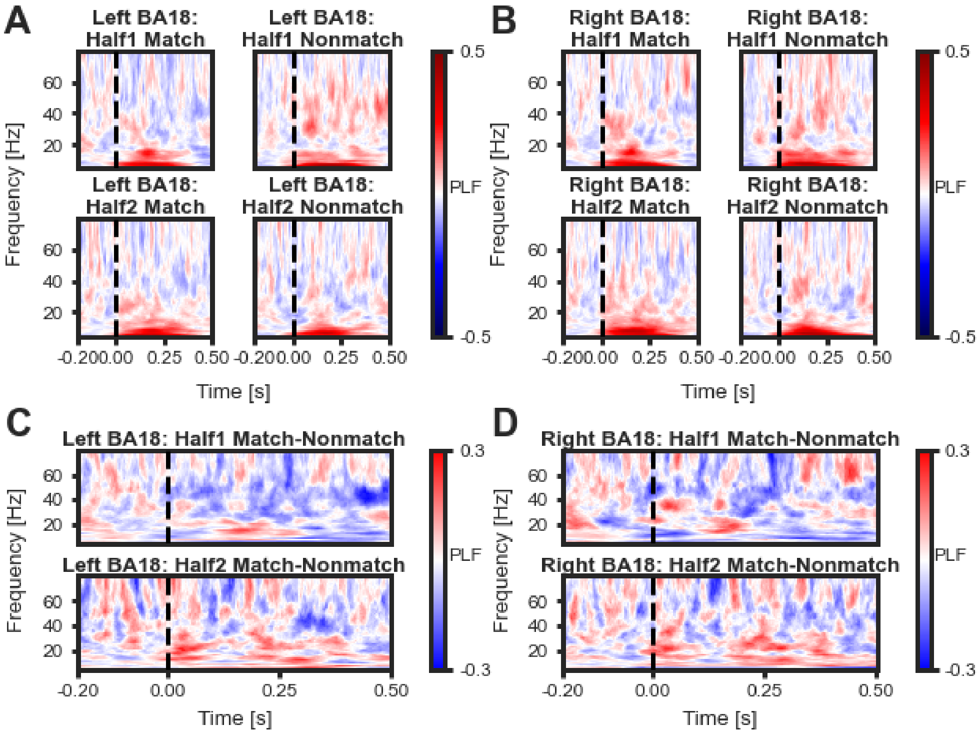
Supplementary Figure 4. Low-alpha:gamma phase-phase coupling (phase synchronisation index, PSI). Panels *A* and *B* show the grand-average (n = 21) difference between the *Match* and the *Nonmatch* condition for each test half of the target identification task separately for the left and the right source in BA18, respectively. In panels *C* and *D,* the corresponding difference between test halves for the two sources is displayed.



Supplementary Figure 5. Free recall drawings of all five targets (rows, original stimuli in grey) and all included 21 participants (columns) sorted from the highest (top left, orange) to the lowest (bottom right, blue) estimated template fidelity (i.e., overall rating score across all targets and experts).



Supplementary Figure 6. Theta:gamma phase-phase coupling (phase synchronisation index, PSI) for excluded, chance-level participants. Panels *A* and *B* show the grand-average (*n* = 5) difference between the *Match* and the *Nonmatch* condition for each test half of the target identification task separately for the left and the right source in BA18, respectively. In panels *C* and *D,* the corresponding difference between test halves for the two sources is displayed.



Supplementary Figure 7. Broad-band (5-80 Hz) phase locking to stimulus onset (phase locking factor, PLF) for excluded, chance-level participants. Panels *A* and *B* show grand-average (n = 5) phase locking for each condition and test half of the target identification task separately for the left and the right source in BA18, respectively. In panels *C* and *D*, the corresponding difference between conditions for the two test halves and sources is displayed.

6. Discussion

6.1. Summary of Results

The aim of this thesis was to investigate the potential of neural oscillations for the temporal coordination and integration of cognition. For this purpose, three projects were performed. The first project critically evaluated the causal relevance and potential mechanism of alpha oscillations for visuospatial attention. It was concluded that alpha amplitude modulations (i.e., contralateral power decreases and occasional ipsilateral power increases) might indeed be causally involved in visuospatial attention shifts. The effect of alpha oscillations on spatial attention seems to be achieved, however, not through top-down control of neural excitability in early visual cortices, but rather by gating information from low- to high-level visual areas. Based on this conclusion, the second project probed the dynamics of attention-driven alpha power lateralization during simultaneous shifts of attention in space and time. In line with our hypothesis, we found a dynamic decrease of posterior alpha amplitude (and slow negative potentials) towards task-relevant moments in time at task-relevant locations in space over cortices contralateral to the locus of attention. This finding suggests that alpha oscillations might reflect the dynamic tuning of attention to relevant points in space and time, demonstrating the potential of neural oscillations for the temporal coordination of individual cognitive processes.

The third and last project tested the suggested role of neural oscillations in creating time windows for cortical integration during cognitive interactions. To this end, theta:gamma phase-phase coupling and evoked gamma activity were investigated during interactions between bottom-up sensation and evolving top-down predictions in visual perception. We observed an increase of matching-related theta:gamma phase synchronization from the first to the second test half in early right-hemispheric visual cortices, which was, however, associated with lower template fidelity thereafter. Moreover, we found stronger match- than nonmatch-evoked gamma activity in the second test half in early left-hemispheric visual cortices, which, in contrast to theta:gamma phase coupling, was subsequently related to higher template fidelity. These results suggest that theta:gamma phase-phase coupling and evoked gamma activity might serve as complementary signatures of memory matching, with the former being most relevant in early WM-based phases of learning and the latter being important for the transition of mental templates into LTM. Together, these findings support the herein proposed role of neural oscillations for cortical coordination and integration.

6.2. Literature Synthesis

The above findings are well in line with previous theoretical considerations and empirical studies highlighting the importance of neural oscillations and their interaction across different spatial and spectral scales for successful neural communication, large-scale integration and high-level cognition, accordingly (Fries, 2005; Palva et al., 2005; Palva & Palva, 2018; Sauseng & Klimesch, 2008). Additionally, they provide new insights into the short- and long-term dynamics of oscillatory signatures, highlighting the outstanding ability of neural oscillations to flexibly adapt to the constantly changing requirements of the external world and the related adaptation of internal processes.

More specifically, our observation of posterior alpha power decreasing towards task-relevant points in space and time at electrodes contralateral to the locus of attention extends previous findings of alpha amplitude modulations during spatial (Barne et al., 2020; Popov et al., 2019; Sauseng, Klimesch, Stadler et al., 2005; Yamagishi et al., 2005) and temporal attention shifts (Praamstra et al., 2006; Rohenkohl & Nobre, 2011; Zanto, Pan et al., 2011) and hints at a joint effect of spatio-temporal top-down attention reflected by dynamic alpha power alterations. Although our study does not allow for the evaluation of any causal claims, this effect and its significant correlation with subsequent memory performance are well compatible with the suggested functional significance of alpha amplitude modulations for top-down attention.

In addition to the dynamic tuning of attention-related alpha activity, our results of late-stage theta:gamma phase-phase coupling and evoked gamma activity (associated with low versus high template fidelity, respectively) suggest a potential dynamic transition between these two oscillatory signatures as mental templates progress from WM to LTM. Whereas the importance of theta:gamma phase synchronization and evoked gamma activity for WM- and LTM-based template-to-input matching, respectively, has been suggested before (Holz et al., 2010; Sauseng et al., 2015), to our knowledge, the presented study is the first to directly compare these two signatures and their relation to template fidelity.

Our finding of stronger matching-related theta:gamma phase synchronization in early compared to later phases of the experiment (with a stronger dependence on WM processes) being beneficial for estimated template fidelity is well compatible with previous reports of increased theta:gamma phase-phase coupling for template-matching stimuli held in WM (Biel et al., 2021; Holz et al., 2010; Sauseng et al., 2008). Similarly, matching-related evoked gamma activity at later stages of learning (with templates slowly transitioning into LTM) being associated with better target reproduction thereafter is in good agreement with previous findings of increased evoked gamma activity for template-matching stimuli stored in LTM (Freunberger et al., 2007; Fründ et al., 2008; Herrmann, Lenz et al., 2004; Herrmann et al., 2010; Mørup et al., 2006). The combination of these so far largely independent lines of research constitutes an important extension to the existing literature on oscillatory signatures of cognitive integration and highlights their temporal flexibility, which is of central relevance for understanding everyday behavior in a dynamic and multi-dimensional world such as ours.

Importantly, even though the presented studies highlight the importance of dynamic alpha power modulations for spatio-temporal attention, as well as the relevance of theta:gamma phase-phase coupling and evoked gamma activity for memory matching in visual perception, they are not meant to suggest that these are the only relevant oscillatory signatures involved in these cognitive processes, nor are they assumed to be exclusively involved in only these cognitive operations. As discussed in the first project, although selective attention does affect the amplitude of steady-state visually evoked potentials (indicative of sensory gain modulation in early visual cortices), this effect seems to be largely independent of alpha oscillations (Antonov et al., 2020; Gundlach et al., 2020; Keitel et al., 2019), which are likely to operate at higher stages of the visual hierarchy. Accordingly, one would expect the existence of at least two complementary mechanisms underlying top-down attention; one modulating the sensory gain in early visual areas and the other (presumably reflected by alpha power changes) gating information from low- to high-level visual cortices.

Similarly, WM-based processes have been associated with cross-frequency interactions not only between theta and gamma oscillations but also across other frequency bands (Maris et al., 2011; Palva et al., 2005; Schack et al., 2005), with the exact coupling frequencies changing in a task-dependent manner (Voytek et al., 2010). Conversely, theta-gamma interactions have been implicated for a variety of cognitive processes beyond memory matching in visual perception (Sauseng et al., 2015), including the above introduced temporal order maintenance and single-item integration in WM (Axmacher et al., 2010; Kamiński et al., 2011; Lisman & Idiart, 1995; Lisman & Jensen, 2013; Sauseng, Klimesch, Heise et al., 2009) or the dynamic (de-)coupling of neural synchrony required for scene exploration and stimulus selection in visual perception (Fries, 2009). Thus, modulations of neural oscillations and their interaction across different spatial and spectral scales seem to constitute universal mechanisms for cognitive coordination and integration, with the exact signature and involved frequencies depending on the particular cognitive process currently in action.

6.3. Open Questions & Future Directions

Whereas the presented studies focused on neural oscillations for attention allocation and memory matching in the visual domain, our multi-modal world requires the precise coordination of multiple sensory systems and successful integration across such. This raises the question whether the herein investigated oscillatory signatures generalize to other sensory modalities (e.g., when tuning attention to relevant acoustic information) and if they allow for cross-modal interactions (e.g., when comparing a visual template against an auditory stimulus). Alpha power lateralization has indeed been associated with attentional tuning to speech in space and time (Kerlin et al., 2010; Wöstmann et al., 2016), as well as with improved vibro-tactile discrimination performance (Haegens et al., 2012; Haegens, Händel & Jensen, 2011). Alpha amplitude modulations might thus constitute a supra-modal oscillatory signature of selective attention.

Similarly, increased evoked gamma activity has been found for rare targets held in memory compared to frequent standard stimuli in an auditory oddball paradigm (Debener et al., 2003), suggesting that evoked gamma oscillations might reflect memory matching not only in the visual but also in the auditory domain. Gamma activity has further been implicated for audio-visual interactions in multi-sensory matching processes, with sounds confirming image-based expectations eliciting stronger gamma band responses than sounds that mismatch expectations (Schneider et al., 2008; Widmann et al., 2007). In future studies, it would be interesting to investigate if theta:gamma phase-phase coupling enables a similar integration of bottom-up sensation and top-down prediction within but also across other sensory modalities and if the suggested role of theta:gamma phase synchronization and evoked gamma activity for WM-and LTM-based template-to-input matching, respectively, generalizes to such non-visual and cross-sensory contexts.

Moreover, whereas the majority of previous studies investigating cross-frequency coupling has primarily focused on oscillatory interactions between two frequencies of interest, neural oscillations have been suggested to form a large-scale interaction hierarchy, spanning the entire frequency range from slow delta to fast gamma oscillations (*oscillatory hierarchy hypothesis;* Lakatos et al., 2005). In this oscillatory hierarchy, lower-frequent oscillations (adaptable to external temporal structure) are thought to phase-modulate higher-frequent oscillations, which ultimately tune neural activity to achieve optimal timing of information processing with respect to external task demands. The oscillatory hierarchy has even been proposed to include not only brain but also body oscillations resulting from rhythmic cardiac or respiratory activity (Klimesch, 2018). Oscillatory cross-spectral interactions might thus serve as general organization principle for signal coordination and integration (Sauseng et al., 2010).

Simultaneous phase resetting across the oscillatory hierarchy and subsequent cross-frequency phase alignment have further been implicated as important factors for the generation of early ERPs (*phase reset model*; Gruber et al., 2005; Makeig et al., 2002). These findings (although a matter of ongoing research) highlight not only the importance of neural oscillations and their interaction across multiple frequency bands even for basic cognitive processes, but also the potential for a closer collaboration between these two research fields in future studies (e.g., ERP latency informing about potential time windows for oscillatory cross-spectral interactions; Sauseng, Klimesch et al., 2007). Together, ERP-informed investigations of oscillatory interactions across multiple spectral scales and the brain-body barrier might constitute the next important step towards revealing the full impact of biological oscillations on signal transmission and the guidance of everyday behavior, accordingly.

7. Conclusion

In this thesis, it was argued that neural oscillations, which reflect fluctuations of neuronal network excitability (thus creating more of less favorable time windows for successful information transmission), are ideally suited to coordinate the timing of individual cognitive processes and their interaction. In line with this hypothesis and the suggested functional significance of alpha oscillations for top-down attention, we observed dynamic alpha power reductions towards task-relevant points in space and time over electrodes contralateral to the locus of attention, which were predictive of subsequent memory performance. This finding implicates a flexible and functionally relevant tuning of spatio-temporal attention reflected by dynamic alpha amplitude modulations and demonstrates the potential of neural oscillations for the precise control of cognitive timing, which constitutes a highly relevant mechanism for successful interactions with a constantly changing world.

In addition to the temporal coordination of individual cognitive processes, we observed increased theta:gamma phase-phase coupling and evoked gamma activity in early visual cortices for matches between bottom-up sensation and top-down prediction in visual perception, highlighting the relevance of neural oscillations in creating time windows for cortical integration during cognitive interactions. Our finding of late-stage theta:gamma phase-phase coupling and evoked gamma activity (associated with low versus high template fidelity, respectively) further points to a potential dynamic transition between these two oscillatory signatures as mental templates progress from WM to LTM. Together, the presented projects suggest that neural oscillations and their interaction across different spatial and spectral scales constitute an important and dynamic mechanism for cognitive coordination and integration as central components of the mental clockwork underlying everyday behavior.

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