UNIVERSITÄTSKLINIKUM HAMBURG-EPPENDORF

Institut für Systemische Neurowissenschaften

Prof. Dr. med. Christian Büchel

Rhythms of Association: Pre-stimulus Brain States and the Formation of Multisensory Memory

Dissertation

zur Erlangung des Doktorgrades Dr. rer. biol. hum.
an der Medizinischen Fakultät der Universität Hamburg.

vorgelegt von:

Jan Ostrowski

aus Lwow, Ukraine

Hamburg, 2025

Betreuer:in / Gutachter:in der Dissertation: Prof. Dr. Michael Rose

Gutachter:in der Dissertation: Prof. Dr. Andreas Engel

Vorsitz der Prüfungskommission: Prof. Dr. Michael Rose

Mitglied der Prüfungskommission: Prof. Dr. Andreas Engel

Mitglied der Prüfungskommission: PD Dr. Patrick Bruns

Datum der mündlichen Prüfung: 12.03.2026

Table of Contents

1 Synopsis

1.1 Introduction

Human behavior and development are shaped by emergent cognitive functions that enable action and conscious experience. If one were to ask several cognitive scientists what they consider the most fundamental aspect of cognition, one would likely receive a different set of answers. While there is little doubt that functions of executive control, attention, inhibition, or object recognition are crucial for goal-directed behavior (Corbetta & Shulman, 2002; Toba et al., 2024), the ability to memorize and learn from experiences enables humans to develop representations of the world around them and predict future events based on these past experiences. Episodic memory, in particular, can be considered critical for the human condition, as it is the aspect of memory specifically responsible for storing past events and unique personal experiences (Baddeley et al., 2002; Piolino et al., 2009) and thus may contribute substantially to the development of self-identity and a sense of personal continuity (Haslam et al., 2011; Markowitsch & Staniloiu, 2011; Nichols, 2014; Vandekerckhove, 2009).

Memory has been the focus of psychological research in all its facets since the beginning of the 20th century (Ebbinghaus, 1948; Murdock, 1985), and a multitude of insights have been gained in the last decades. Importantly, research has established that cognitive functions are linked to the activation of individual brain areas as well as networks composed of several brain regions working in concert. In the case of episodic memory, its neural correlate is thought to originate primarily in structures of the hippocampal network with strong structural and functional connections to several neocortical areas (Buzsáki & Moser, 2013; van Strien et al., 2009). It is assumed that memory traces are formed and consolidated through the dynamic interaction between these areas (Nadel & Moscovitch, 1997; Squire, 1992; Tse et al., 2007). This dynamic interaction occurs because neural populations exhibit electrophysiological activity by which they "communicate" with each other. Depending on the purpose and the type of information being transmitted, the communication can happen at different speeds, which can be mathematically described as the frequency spectrum of the communication signal. This oscillatory activity, measurable using electroencephalography (EEG), constitutes a central aspect of the neural correlate of cognition. In the context of memory, evidence suggests that activity on the lower end of the frequency spectrum plays an important role, specifically activity in the theta (3 – 7 Hz) and alpha range (8 – 12 Hz; Herweg et al., 2020; Klimesch, 2012)). While theta activity is thought to serve as a guiding rhythm for concatenating sensory information (e.g. Clouter et al., 2017), alpha activity is proposed to support the flow of information by inhibiting unwanted interference (e.g. Payne et al., 2013).

Although much has been learned regarding the oscillatory correlates of episodic memory from both human and animal research, some aspects remain unclear. First, a majority of studies investigating the mechanisms of memory formation base their evidence and conclusions on experimental designs with unisensory stimulus material. In a classic memory task, the participant is instructed to memorize visually presented words or images, usually followed by a recall task (e.g. Addante et al., 2011; Schneider & Rose, 2016)**.** While the insights gained are important, one could argue that this approach may lack ecological validity because the information that is encoded to episodic memory outside of the laboratory setting rarely consists of only one sensory modality but rather forms an amalgamation of several sensory streams. If a person experiences a remarkable natural phenomenon, such as a great waterfall, and recalls the event later in life, the image of the running and falling water will be closely associated with the soundscape and the corresponding smell. Its subsequent recall typically involves information from multiple sensory modalities rather than one isolated from the other. This should be considered in memory research, for example, by using multisensory stimulus material that more closely resembles the real-world environment. Second, neurocognitive research has primarily focused on the processes that happen during – or sometimes after – the presentation of the relevant stimuli. However, the brain exhibits ongoing activity not only during the processing of relevant stimuli but also before. These brain states could potentially affect how subsequent information is processed (Bengson et al., 2014; D. M. Roberts et al., 2014; Salari et al., 2014; Van Dijk et al., 2008). In the context of memory, this implies that the encoding of episodic experiences into memory might not only be affected by the brain states during the experience itself, but also by the oscillatory patterns the brain exhibited immediately before the episode occurred.

This dissertation aims to elucidate the role of pre-stimulus oscillations in the encoding of multisensory information into memory. In the first study, I investigated whether the neural correlates of successfully encoded multisensory associations recorded before stimulus presentation differed from those associated with encoding. Furthermore, connectivity patterns between sensory areas were analyzed to determine whether successful encoding was associated with increased interareal connectivity. To this end, a Subsequent Memory Effects paradigm (SME) was used, in which participants were instructed to memorize audiovisual associations. The second study built upon the findings from the first study and used a modified version of the experimental paradigm to infer the functional relevance of the previously identified neural correlates. In this experiment, oscillatory activity was modulated through sensory rhythmic stimulation to clarify the effects observed in the first study. In the third study, we employed a different variation of the SME paradigm to examine the neural correlates of encoding in the context of multisensory sequences.

On the following pages, I will present relevant background information on mechanisms of episodic memory and its oscillatory correlates, and introduce theoretical frameworks regarding the involvement of oscillations in the shaping of memory content. This will be followed by a detailed presentation of the goals of this work, as well as a summary of the methods used, and the results obtained in each study. Finally, the evidence will be discussed in the context of previous literature and theory, as well as potential practical implications and future directions. The physicist and philosopher Thomas Kuhn once said that most scientists in a field at any given time conduct what he calls "normal science", that is, a process of puzzle-solving under the guiding principle of an overarching paradigm (Kuhn, 1962). Although psychology and neuroscience are relatively young and still in the process of developing such a paradigm, I hope that this dissertation will contribute an additional piece of the puzzle that is higher cognition and memory.

1.2 Background

1.2.1 Taxonomy and the memory network

According to established theories on the structure of human memory, episodic memory is thought to be part of the declarative domain of long-term memory (Squire & Zola-Morgan, 1991). All information about the world that can be considered factual as well as past experiences, i.e. that which is retained in the brain for longer than several minutes, can be assigned to that domain. This type of information can usually be accessed consciously and even be reported verbally (Tulving, 1972). Notably, the memorization of episodes strongly relies on the ability of the brain to form and save associations between elements of sensory information that compose the memorized episode. While associations can be created in memory between different types of semantic content (Eichenbaum, 1997), they must still be learned through some form of personal experience. The core aspect of this associative memory is the ability of the brain to bind different bits of information from either the same stream of sensory input, or from different sensory modalities, and encode it so that it can be recalled at a later point in time. This mechanism enables us to solve problems and adjust to new situations in a more flexible way, using the knowledge and experiences of the past to either seek out more desirable situations or being able to avoid situations known to have negative consequences (Kadwe et al., 2022). Associative memory can either take the form of connections between individual items (e.g. pairing the visual percept of a dog with its bark) or embedding an item in a specific context (e.g. associating the context of a specific location with a particular individual). While the former provides the basis for learning about individual objects and entities, the latter crucially affects our ability to navigate in space and time (Robin, 2018).

Furthermore, models such as Baddeley's working memory framework and Tulving's conception of episodic memory highlight how maintenance and manipulation of information enable durable associations (Baddeley et al., 2002), and how recalling them leads to the subjective, autonoetic awareness of the individual (Tulving, 1972, 1985).

The formation of associative memories relies on a complex network of interconnected brain regions, consisting mainly of the hippocampus (Rugg et al., 2002; Tulving & Markowitsch, 1998), the medial temporal lobe (MTL; Danieli et al., 2023; Hasselmo, 2012), and several other neocortical areas (e.g. sensory cortices, and parts of the prefrontal cortex; Danieli et al., 2023; Ranganath & Knight, 2002). Sensory information is transmitted from the sensory organs to the corresponding sensory cortices for initial processing. Most neural correlates of sensory modalities consist of several tiers of processing, starting with representations of basic features like contrast or color at a low level of abstraction. The information passes through these processing tiers, each associated with a progressively higher degree of abstraction, until a high-level representation of the perceived objects is reached (Brincat et al., 2018). The representations are then transmitted further to the perirhinal and posterior parietal cortices, where a more complex, non-spatial representation of an object is formed (Bussey et al., 2005). The perirhinal cortex has been associated with the unification of simultaneously present items (Haskins et al., 2008), and is thought to be involved in episodic recognition through the concept of familiarity and the corresponding strength of encoding traces (Diana et al., 2007; Eichenbaum et al., 2007). At this point, the representation is based on a multimodal aggregation of information about the object, combining higher-order sensory representations from several sensory modalities into one with an even more elevated degree of abstraction, i.e. the object identity. This is then transmitted to the parahippocampal cortex, along with information from the dorsal visual stream, the MTL, and the parietal cortex (Born & Bradley, 2005; Rauschecker, 2018). Spatial properties are added to the representation, e.g. the location of the object in the visual field, its position in relation to other objects, and its movement speed. These assessments are not only based on the visual domain, as other modalities also contribute to accurate computation (e.g. auditory information; Bizley & King, 2008; Shamma, 2001). Early spatial processing strongly ties into contextual representations, as the parahippocampal cortex is involved in spatial but also non-spatial context-associations (Aminoff et al., 2007, 2013). Subsequently, the information is diverged again in the entorhinal cortex (EC) which functions as an intermediary between the hippocampus and the neocortex (Danieli et al., 2023). Information on object identity and other non-spatial features is routed to the lateral entorhinal cortex (LEC), and supplemented by signaling from the perirhinal cortex, the anterior cingulate cortex (ACC), and the medial prefrontal cortex (Deshmukh et al., 2012). The LEC, specifically, is involved in associative recognition (Wilson et al., 2013), and acts as a relay between the hippocampus and the ACC (Weible et al., 2009, 2012). Conversely, the spatial aspect is handled by the medial entorhinal cortex (MEC), which contains grid cells that act as a precursor to the place cells found in the Cornu Ammonis 1 (CA1) region of the hippocampus and function in a similar way (Giocomo et al., 2011; Rowland et al., 2016). Importantly, it has been suggested that the grid cells may be crucial for the oscillatory rhythm that functionally connects the MEC to the hippocampus, and subsequently in processing temporal information for episodic memory (Schlesiger et al., 2015). At the end of the encoding stream, the information reaches the hippocampus, whose primary functions are spatial navigation, long-term memory processing, and the structural binding of multimodal information in the associative network (Buzsáki & Moser, 2013; Cooper & Ritchey, 2020; Danieli et al., 2023). Subsequently, the created multisensory associations are consolidated through an interplay between the hippocampus and several cortical areas, including the prefrontal cortex (Holleman & Battaglia, 2015; Preston & Eichenbaum, 2013; Squire et al., 2015), and become long-term semantic representations (Skelin et al., 2019).

1.2.2 Oscillatory correlates of associative memory

The network of brain areas contributing to the emergence of associative memory is complex, and it is imperative for information to be transmitted from one node of the network to the next. One of the key mechanisms enabling the transmission of information is oscillatory synchronization, in which brain rhythms coordinate the timing of signal transmission (Pariz et al., 2021; Saalmann et al., 2012). These oscillatory rhythms can be recorded in a noninvasive manner using EEG. Previous research has shown that distinct brain oscillations can be tied to a multitude of cognitive functions, including attention (Friese et al., 2016; Knudsen, 2018), sensory processing (Hanslmayr et al., 2007), language processing (Beese et al., 2017), motor control (Fetz, 2013), and social interaction (Buidze et al., 2025; Kawasaki et al., 2013; Kinreich et al., 2017). In the following paragraphs, I will review the literature demonstrating how distinct oscillatory states relate to the formation of associative memory.

Theta oscillations – a binding rhythm

The theta band has been one of the most promising candidates for the coordination of the memory network, specifically within the hippocampus as well as between the hippocampus and the neocortex (Herweg et al., 2020; Luo & Guan, 2018). First characterized in the hippocampus of the rabbit in the first half of the 20th century (Jung & Kornmüller, 1938), the definition of the corresponding frequency range has varied over time. Importantly, there is a discrepancy between theta oscillations found in the rodent model and those found in human brain research. Theta signatures in rodents have usually been reported for a frequency range of 4 to 12 Hz (Vanderwolf, 1969), often subdivided into the lower (4 – 7 Hz) and upper interval (7 – 12 Hz; Luo & Guan, 2018). In humans, studies sometimes refer to the frequency range of 4 to 8 Hz as theta (Kahana et al., 1999; B. C. Lega et al., 2012), but 4 to 7 Hz or 3 to 7 Hz are also frequently used (e.g. Cantero et al., 2003; da Silva, 1992; Sarnthein et al., 1998). Importantly, these definitions provide a clear distinction to the alpha rhythm which is commonly thought to range from 8 to 12 Hz.

Traditionally, theta oscillations originating in hippocampal place cells have been the mechanistic focus of animal research on spatial navigation (O'Keefe & Dostrovsky, 1971; O'Keefe & Recce, 1993). It has been shown that the hippocampus is involved in two distinct types of navigation, dead reckoning as well as map-based, each relying on the activation of unidirectional or omnidirectional place cells in the CA1 layer, respectively. In this context, theta oscillations have proven to be critical for establishing temporal associations between stimuli, as the firing rate of the event- and place-coding cells is embedded in an ongoing theta rhythm (Buzsáki, 2005; Buzsáki & Moser, 2013). Researchers soon drew the analogy to episodic memory (Andersen, 2007), as personal experiences are similarly characterized by spatiotemporal information (Frackowiak, 2004; Tulving, 1972).

The Temporal Encoding Model was an attempt to explain how the mechanisms primarily associated with visual navigation could give rise to episodic memory (Buzsaki, 2011; Buzsáki, 2005; Buzsáki & Moser, 2013). According to the model, the theta rhythm is aligned with the phase of the signal present at the onset of a stimulus. While the amplitude of a signal represents its intensity at a specific point in time, the phase describes how far along its cycle is from its start. Depending on the timing of activation of a single cell relative to the firing of surrounding cells in the local population, the result is a temporal compression of the firing sequence. This process is called phase precession (Jaramillo & Kempter, 2017; O'Keefe & Recce, 1993). Place cells whose receptive fields are tuned to a specific location thus fire progressively earlier relative to the ongoing theta rhythm as the organism crosses that location. In this way, a sequence of visited locations can be efficiently represented within cycles of theta oscillations. The model posits that map-like representations of physical space are established in the brain by repeated encounters with the same stimuli. Similarly, it can be assumed that episodic memory is based on repeated sequences of temporal distances between personally experienced events rather than physical distances between places (Buzsaki, 2011; Buzsáki, 2005). Thus, via the process of phase precession, the hippocampal network may create associations between components of episodic memory (Yamaguchi, 2003). In broader terms, input from sensory areas is compressed by theta oscillations, which may provide conditions under which associations can be formed in the MTL network (Herweg et al., 2020).

In an influential study, Terada and colleagues (2017) provided empirical support for the idea that the Temporal Encoding Model might apply to non-spatial memory encoding as well.

The authors further argued that theta sequences during spatial navigation might reflect a general integration of multiple types of information, including external cues, locomotion, and internal metrics (Feng et al., 2015). In the experiment, rats were trained in a cue-combination task that required the integration of sound and odor cues. Correct responses were determined by a combination of both modalities. While the cues were presented sequentially, there was a period in which they overlapped and the animal perceived both sensory modalities simultaneously. The results showed that hippocampal CA1 neurons exhibited stimulus-related activity in a non-spatial learning task. The neurons also showed transient phase precession following the onset of stimuli, becoming locked into early theta phases for the remainder of stimulus presentation, suggesting that stimulus-specific neurons formed both segmented and discrete representations. Furthermore, the results suggested that neurons whose receptive fields were tuned to a specific combination of cue might represent the conjunctive information linking cue combination and the corresponding behavior. The authors concluded that the hippocampus may organize relational networks in support of episodic memory, and that this mechanism is not limited to spatial memory but instead supports a generalized cognitive map model. In this, the theta rhythm might serve as a substrate for the representation of discrete events, and their associative connections.

These insights from animal research inspired investigations into the role of theta oscillations for associative memory in humans. Systematic reviews suggest that most studies report a positive correlation between cortical theta activity and memory success, i.e. increases in theta power are generally measured alongside better performance in memory tasks (Hanslmayr & Staudigl, 2014; Herweg et al., 2020). Specifically, this has been observed in studies utilizing traditional SMEs in their experimental designs (Addante et al., 2011; Fellner et al., 2013; Hanslmayr, Volberg, et al., 2011; Khader et al., 2010; Osipova et al., 2006). However, similar patterns were also reported in studies that compared neural correlates of trials in which correct retrieval was recorded but the degree of associative strength differed. Stimuli that were deemed closer in terms of semantic or temporal distance were more often accompanied by increased theta power compared to stimuli with a weaker association, even though both types of stimuli were correctly retrieved (Herweg et al., 2016; Kaplan et al., 2012; Staudigl & Hanslmayr, 2013). Previous studies from our own laboratory support the notion of a positive correlation, as increases in theta power were consistently observed in relation to memory success not only in unisensory experimental paradigms (Schneider & Rose, 2016), but also in experiments examining the role of context for multisensory encoding (Scholz et al., 2017; Winterling et al., 2019).

Beyond oscillatory power changes in local neural populations, successful associative encoding has also been linked to functional synchronization of neural activity across distributed cortical and hippocampal networks, particularly within the theta frequency range. Early evidence suggests that cortical synchronization during encoding as well as during retrieval might be positively correlated with memory performance (T. Gruber et al., 2001; Klimesch et al., 1997; Sato & Yamaguchi, 2007; Summerfield & Mangels, 2005). Specifically in the context of encoding information, the alignment of oscillations between frontal and posterior brain regions to the same phase was shown to be beneficial (Summerfield & Mangels, 2005). Similarly, theta synchrony between subregions of the MTL was found to be associated with successful memory encoding (Solomon et al., 2019), and synchronization in the theta band may be the mechanism that enables interactions between cortical brain areas and the hippocampal complex (Nyhus & Curran, 2010). One study in particular highlights how the functional coordination between different sensory areas could be specifically crucial for encoding multisensory associations. In their experiments, Clouter and colleagues (2017) manipulated the degree of synchronization between visual and auditory areas noninvasively using sensory entrainment. Participants were required to memorize associations between short videos and semantically unrelated snippets of sound. Importantly, the luminance of the visual stimuli as well as the sound amplitude oscillated according to specific frequencies, eliciting steady-state potentials in the corresponding sensory areas that mirrored the external rhythm. Crucially, different degrees of phase offset between the visual and auditory stimulus oscillations were introduced. The results indicate that increased synchronization between visual and auditory areas was strongly associated with better memory performance. However, this effect was specific to theta stimulation, as using other frequencies did not yield significant changes in performance. In a follow-up study, it was further shown that success in encoding audiovisual associations could even be predicted on a trial-to-trial basis by using theta phase-synchronization as the outcome measure (Wang et al., 2018). The authors of both studies concluded that these effects are unlikely to be driven solely by perceptual binding. Rather, theta phase may provide discrete temporal windows for synaptic plasticity. Accordingly, the coincident timing of multisensory inputs during theta cycles may facilitate associative binding through phase-dependent neural communication.

Taken together, the literature positions theta oscillations as the temporal currency for binding in the brain. Beyond their hippocampal origins, theta rhythms compress and order event representations, and — in humans — greater theta power and phase synchronization reliably predict successful memory. Crucially, theta appears to coordinate communication within the MTL and between frontal, posterior, and modality-specific cortices, offering an oscillatory mechanism for how multisensory associations are formed and encoded in the brain.

Alpha oscillations – regulation of information flow

While theta oscillations are considered crucial for binding information in the formation of multisensory memories, this neural rhythm is not the only contributor. The alpha rhythm (8 – 12 Hz) is another component of the oscillatory landscape of the brain strongly associated with different aspects of cognition. Alpha oscillations are most commonly associated with attentional processing and sensory suppression (Foxe & Snyder, 2011), facilitating perceptual processing by suppressing irrelevant information. The inhibition of irrelevant perceptual and semantic information constitutes an active form of information processing that helps to increase the signal-to-noise ratio in cognitive computations (Knyazev, 2007). This ties into processes of cognitive control, wherein alpha activity appears to be involved in the top-down modulation of moment-to-moment control of cognitive processes (Sadaghiani & Kleinschmidt, 2016). Importantly, alpha oscillations have been shown to facilitate controlled access to internal knowledge, as well as enabling semantic orientation in time, space, and context via the underlying mechanisms of attentional suppression and selection (Klimesch, 2012).

Notably, research suggests that alpha oscillations may play an important role in the process of forming complex episodic and associative memory content as well. Previous literature suggests that one of the ways that alpha oscillations may contribute to memory formation is through the inhibition of task-irrelevant processes (Bonnefond & Jensen, 2013; Klimesch et al., 2011; Minarik et al., 2018; Payne et al., 2013; Strunk & Duarte, 2019). Specifically, there is evidence indicating that increases in alpha activity that are observed with concurrent increases in performance during SME tasks may reflect the suppression of already encoded information in favor of the current encoding task (Hanslmayr et al., 2012; Jensen et al., 2002; Meeuwissen et al., 2011). While not directly posited as a mechanism of binding, alpha oscillations may therefore facilitate the encoding of information into episodic memory by managing intrusive associative information. Importantly, inhibition is only one part of the mechanism. Alpha oscillations may also be involved by modifying preparatory attentional states (Strunk & Duarte, 2019). Supporting evidence comes from studies investigating incidental versus accidental memory encoding suggesting that changes in patterns of alpha activity may indicate the reallocation of attentional resources, subsequently leading to attentional engagement (Schneider & Rose, 2016; Uncapher et al., 2011). The allocation of resources for attentional engagement may affect oscillatory patterns, hinting at the importance of incidental engagement with information for encoding.

However, while there appears to be consensus regarding the cognitive mechanism of alpha oscillation involvement, it is not entirely clear whether this mechanism is associated with increased alpha synchronization, or rather with a decrease in power due to desynchronization. Notably, several sources report evidence supporting the latter, as successful encoding in semantic and non-semantic memory tasks has been shown to be associated with decreases in alpha power (Griffiths, Martín-Buro, Staresina, Hanslmayr, et al., 2021; Hanslmayr et al., 2009, 2012). Furthermore, studies have shown that hippocampal theta-gamma activation follows decreases in neocortical alpha power, suggesting that this temporal dissociation might reflect a functional dissociation in which cortical alpha oscillations support the processing of incoming information relevant to memory, while hippocampal theta-gamma activity corresponds to the binding of this information into a coherent trace (Griffiths, Martín-Buro, Staresina, & Hanslmayr, 2021). The information-via-desynchronization-hypothesis attempts to explain the observations of alpha power decreases during encoding by proposing that memory formation may require the brain to shift from synchronized towards desynchronized states that can support the encoding of rich and unique episodic memories (Hanslmayr et al., 2012, 2016). The hypothesis is grounded in insights from information theory, based on the principle that the more predictable an event is, the less information it carries, and the more redundant it is (Shannon & Weaver, 1949). This appears to hold true for neural activity as well, as evidence suggests that synchronized neural firing, which can be seen as more regular and therefore more predictable, might carry redundant information (Schneidman et al., 2011). Given that one of the crucial features of episodes can be considered their uniqueness (Tulving, 1972), it follows that unique codes must be created for each episode. This is often referred to as the problem of pattern separation (Alvarez & Squire, 1994; Marr, 1971; Norman, 2010). Alpha band desynchronization that is often observed alongside increased memory performance may constitute a solution to this problem, as an infinite number of unique firing patterns might be generated by a population of neurons not firing in a steady rhythm but in a “chaotic” concert of individual rhythms.

In sum, the formation of multisensory associative memories appears to rely on the coordinated interplay of theta and alpha oscillations, each contributing distinct, complementary functions. Theta rhythms, originating primarily within the hippocampal–cortical network, are proposed to provide the temporal structure necessary for binding distributed sensory inputs into coherent episodic representations. They synchronize neural activity across regions, compress temporal information, and enable communication among sensory, cortical, and hippocampal areas — mechanisms that have been linked to successful associative and multisensory memory formation. Alpha oscillations, in contrast, modulate the attentional and inhibitory landscape that supports this binding process. Through dynamic shifts between synchronization and desynchronization, alpha rhythms regulate the flow of information by suppressing irrelevant inputs and facilitating cortical processing of novel sensory combinations. Together, these oscillatory mechanisms provide a dual framework in which theta governs associative binding, while alpha shapes selective, flexible processing that enables the encoding of complex multisensory experiences into memory.

1.2.3 How pre-stimulus brain states affect subsequent information processing

While most research has focused on oscillatory activity during stimulus processing, recent evidence indicates that brain states preceding stimulus onset — reflected in spontaneous fluctuations of theta, alpha, and beta power — may critically shape how incoming information may be processed. These findings invite a more dynamic view of the involvement of oscillations in cognition, emphasizing preparatory mechanisms that configure neural systems before the event occurs.

Ongoing brain activity in perception and attention

It is important to recognize that the brain is always active, even during periods of rest and during sleep (Wamsley, 2013). External stimulation, i.e. incoming sensory information, changes its activity patterns, so one could argue that the observable patterns in the absence of stimulation may represent the brain's ongoing state. Of course, the brain is hardly ever completely isolated from stimulation, but researchers can attempt to learn about the ongoing state by employing experimental designs that leave "breathing room" for the brain, translated into the absence of target stimuli. Although researchers have mostly focused on the mechanisms related to stimulus-evoked activity and how it interacts with measures of cognition, a growing number of studies have emerged over the last two decades proposing that ongoing brain activity may not just represent noise but rather play a larger role in how perception and cognition are shaped (Britz & Michel, 2011). Notably, it is important not to conflate resting-state activity with ongoing brain states, as the former implies the absence of any task-related activity, while the latter describes "idle time" between periods of explicit stimulation.

In most studies, pre-stimulus brain states have been investigated in the context of lower-level cognition. These states have been deemed essential for the deployment of attentional resources, as studies have found that preparatory attentional states in the alpha band might activate selective neurons in the visual cortex before the onset of task-relevant stimuli (Battistoni et al., 2017; Bengson et al., 2014). The authors suggested that this effect may reflect a general mechanism that may be observable at multiple levels of the cognitive hierarchy, and across several modalities of brain activity, including BOLD signals. One explanation is that alpha oscillations not only serve an inhibitory function during stimulation, but also in the period preceding it if the task demands top-down regulation (Hummel et al., 2002; Jensen & Mazaheri, 2010; Klimesch et al., 2007). Furthermore, pre-stimulus alpha states have been shown to relate to manifestations of cognitive control (Coste et al., 2011), working memory (Klein et al., 2016), as well as sensory detection and discrimination (D. M. Roberts et al., 2014; Salari et al., 2012), with lower power generally correlated with better performance (Ergenoglu et al., 2004; Hanslmayr et al., 2005, 2007). Notably, even stimuli that share similar physical traits can be processed differently and subsequently produce differences in their corresponding percepts based on the state of pre-stimulus alpha activity (Britz & Michel, 2011). It was argued that states with increased pre-stimulus alpha activity may point towards an internal orientation that reduces the probability of interference from internal stimuli. Conversely, lower activity could indicate an external orientation, reflecting a bias where external information from sensory processing areas is favored (Hanslmayr, Gross, et al., 2011). The phase of the alpha band, however, might represent the temporal dimension of internally or externally oriented alpha oscillations, as evidence suggests that visual stimuli are more likely to be perceived if presented at the peak of the alpha rhythm compared to the trough (Hanslmayr, Gross, et al., 2011; Mathewson et al., 2009).

Pre-stimulus states and memory encoding

Although the majority of research into ongoing brain states has focused on low-level processes such as attention and visual discrimination, the results and interpretations suggest that these states might also affect higher-order cognition. Investigations have shown that successful encoding of experiences can be highly dependent on the context in which the episode is encoded (e.g. Scholz et al., 2017), and that episodes can be reinstated more effectively by reactivating the associative link between context and episode (Staudigl et al., 2015). If one assumes that internal oscillatory states can serve as contextual factors in encoding, one can conclude that variations in pre-stimulus states may also affect subsequent encoding in similar ways as their effects on subsequent visual discrimination or attentional reallocation.

However, there is only scarce evidence on the role of pre-stimulus oscillations in associative memory formation. One early study investigated the dynamics of event-related potentials (ERPs) in the context of ongoing brain states and found that negative activity spikes approximately 250 ms before stimulus presentation could predict successful encoding of visually presented words (Otten et al., 2006). The authors argued that these pre-stimulus effects might reflect the generation and maintenance of specific sets of tasks, closely related to the engagement of working memory control processes. Other studies focused on time-resolved frequency analyses to allow insights into the involvement of specific pre-stimulus oscillations. For instance, it was shown that successful memory formation might be associated with increased pre-stimulus theta power (M. J. Gruber et al., 2013; Guderian et al., 2009; Merkow et al., 2014), and that the corresponding sources might be situated in parts of the MTL (Guderian et al., 2009; B. C. Lega et al., 2012). These results suggest that theta oscillations during and before encoding may play an equally important role, although it is not clear yet what kind of process pre-stimulus theta oscillations reflect. On a related note, SMEs have also been reported in the alpha frequency range (Fell et al., 2011; Park et al., 2014; Park & Rugg, 2010). However, it has been difficult to determine conclusively whether these pre-stimulus SMEs reflect general memory-promoting states, as research in the domain of visual perception might suggest, or whether they are specifically related to memory-focused mechanisms.

One important limitation in the majority of studies investigating episodic memory, including work that focused on pre-stimulus states, is the use of predominantly unimodal stimulus material. Visually presented verbal stimuli (Addante et al., 2011), objects isolated from their associated environments (Hornstein & Mulligan, 2001), or even abstract patterns have often been used to study episodic memory (Bellhouse-King & Standing, 2007). Even if the focus of the investigation was how associations are formed in memory encoding, the experimental designs often used unimodal pairings of visual stimuli. While the use of visual stimuli allows for a high degree of control in the laboratory environment due to the accumulated knowledge about the visual system, human experience – and, subsequently, its encoding – is rarely unimodal. This impacts the ecological validity of these studies. However, one way to approach this problem is to investigate the interplay between contextual information and individual stimuli, considering the corresponding neural correlates that accompany the association of several pieces of information with different contexts. While the underlying mechanisms of source memory have been of interest in memory research for a while (e.g. Addante et al., 2011; B. M. Roberts et al., 2018; Staudigl & Hanslmayr, 2013), only a few studies have implemented multisensory information in their SME paradigms. In a previous study from our laboratory, Scholz and colleagues (2017) investigated whether SMEs may depend on the modality of the to-be-encoded stimuli. Participants were shown either visually presented verbal stimuli or sounds of a person speaking them. Simultaneously, one of several images was presented on-screen in each trial as a visual source of context. In a subsequent surprise recognition task, participants indicated recognition of the stimulus and, if recognized, the source image as well. It was found that pre-stimulus theta power was higher for trials in which the source image was also successfully encoded, and when the encoding involved binding an auditory item to the source image. This suggests that theta oscillations before encoding might reflect a preparatory state that facilitates the associative binding of item and source, thereby highlighting the involvement of theta oscillations in the integration of information across modalities.

Open questions

The reviewed literature presents a multifaceted perspective on the role of low-frequency oscillations like theta and alpha band activity in the process of encoding new information to episodic memory. Theta oscillations organize event timing, compress sequences, and synchronize distributed regions so that multisensory inputs can be linked into coherent episodic traces, as greater theta power and synchrony reliably track successful associative encoding. Alpha, by contrast, shapes the informational landscape: through dynamic shifts between synchronization and desynchronization, it regulates access to and competition among representations by gating irrelevant input and enhancing cortical processing of novel, task-relevant features. However, gaps remain. Most studies reviewed here use unimodal stimuli for memorization. Although this practice improves controllability and practicality in the laboratory setting, it does not correspond to the multisensory nature of information that is encoded in real-world settings. Moreover, most studies investigated memory with single, discrete stimuli, rather than presenting associative information. In the few cases where associations were investigated, the focus was on context-item associations, rather than the mechanisms underlying the encoding of individual associations. Finally, while research on oscillatory mechanisms during encoding has yielded many insights into how episodic – and specifically associative – memory is realized, the role of ongoing brain states and pre-stimulus activity has not been a priority. I believe that closing this gap will broaden our understanding of how multisensory associations are formed and ultimately how memories are created.

1.3 Research Goals

Previous literature indicates that low-frequency oscillations within the hippocampal and cortical memory networks are crucial for our ability to form complex memories of experiences. However, it also reveals that there are gaps in our understanding of the underlying mechanisms, particularly regarding how ongoing, non-stimulus-induced oscillations may affect the subsequent encoding of multisensory information. The three empirical studies outlined in this dissertation aim to address these gaps by elucidating the neurophysiological correlates of multisensory memory encoding and by investigating the contribution of preparatory states.

Theta and alpha oscillations are strongly implicated in the formation of multisensory memories within the episodic memory system. Both local theta and alpha power, as well as oscillatory synchronization between relevant sites in these frequency bands have been frequently observed to correlate with associative memory. Thus, in Study 1 we tested whether features of spontaneous pre-stimulus oscillations can be used to differentiate between later remembered and forgotten audiovisual associations, i.e. successful and unsuccessful encoding. Furthermore, we investigated whether phase-based connectivity between sensory areas before stimulus presentation could contribute to crossmodal binding. To this end, an SME paradigm was employed that specifically separates the memory of associations from the encoding of individual items, thus permitting the investigation of individual item-to-item links in a multisensory domain. EEG recordings during encoding and retrieval were used in combination with measures of memory performance to address the research questions.

While Study 1 provided novel insights into the neural correlates of associative memory and encoding, the results did not permit to infer a causal link. Effects occurred across several parts of the frequency spectrum, but it remained unclear which neural correlate drove them. Thus, based on the results from Study 1, the aim of Study 2 was the assessment of the functional role of pre-stimulus oscillatory states. Specifically, we asked which pre-stimulus state identified as relevant in Study 1 was causally related to the encoding of multisensory associations and thus influenced subsequent recognition. To address this question, a sensory entrainment procedure was implemented within the SME paradigm from Study 1, introducing visual stimulation during the pre-stimulus interval of the encoding task. Participants viewed an image oscillating rhythmically at one of two frequencies (theta or alpha), or received arhythmic stimulation, depending on the experimental group. Importantly, all other aspects of the experimental paradigm were kept identical to those in Study 1, enabling the inclusion of Study 1 data as an additional control condition. EEG recordings were mainly used to validate the stimulation procedure, and behavioral measures were used to assess whether theta or alpha stimulation may be functionally relevant for subsequent encoding.

One of the defining features of episodes and associations that are encoded into memory is that the information is often experienced in a fixed temporal order of events. However, little is known about whether the order of information across different sensory modalities affects the encoding and subsequent retrieval of multisensory content. Thus, the goal of Study 3 was to investigate how the temporal sequence of different sensory modalities during encoding influences associative memory formation, treating order as a form of intrinsic contextual information. Furthermore, we sought to elucidate how the sequential presentation of multisensory associations is manifested in the neural correlates during encoding and retrieval. To this end, the encoding task of the SME paradigm from Study 1 was modified so that audiovisual item pairings were presented sequentially rather than simultaneously. Importantly, the overall task of association memorization remained the same, and the retrieval phase of the paradigm was identical to that employed in Studies 1 and 2. Univariate as well as multivariate analyses of the recorded EEG and behavioral data were conducted to address this research question.

1.4 Methods

All three studies presented in this work share the same basic experimental paradigm, the SME task. It is particularly useful when investigating mechanisms that pertain to the encoding of information into memory, as it enables the analysis of corresponding neural and behavioral measures based on the responses in the retrieval task. A large body of evidence has been generated by behavioral and neurocognitive studies using the SME across data modalities, including EEG (e.g. Addante et al., 2011; M. J. Gruber & Otten, 2010; Otten et al., 2006; Scholz et al., 2017), magnetoencephalography (MEG; e.g. Hanslmayr et al., 2012), and functional imaging (Addante et al., 2015; Park & Rugg, 2010). In the task variation used in the studies presented here, participants were required to memorize individual audiovisual associations, and perform in a cued retrieval task in which memory performance was assessed. While the general task structure was identical for all three studies, the encoding period was modified according to the respective research questions. In the following sections, the task, its modifications, and study-specific design considerations will be presented.

1.4.1 Subsequent memory effects and general procedure

In each study, the SME paradigm consisted of three separate experimental runs. Each run consisted of an encoding task, an intermission, and a subsequent recognition phase. During the encoding phase, participants were presented with pairs consisting of one image and one sound and were required to judge whether both stimuli could be categorized as an animal or not (see **Figure 1** for a schematic overview). Simultaneously, participants were instructed to memorize the association of both stimuli for a subsequent test of their memory. It was highlighted that participants should not focus on individual stimuli, but rather on the association as a whole. The encoding phase was followed by a short intermission of approximately three minutes during which participants were required to count numbers in reverse order. Thus, information represented in the working memory system was less likely to introduce a confound in the measurements, and recency effects were minimized (Oberauer & Bartsch, 2023). In the subsequent recognition task, participants were presented with the same audiovisual pairs that were used during encoding, as well as the same number of additional pairs. These consisted of the same individual images and sounds as the originals, but the pairings had been shuffled randomly to create new associations from the same stimuli. Participants were instructed to indicate whether a pair as a whole had been present during the encoding task or not. In all three studies, participants completed a total of 141 encoding trials and 282 recognition trials in one experimental session. Furthermore, EEG data were recorded during encoding and recognition runs, but never during the intermissions. All images used in the experiments showed photographs or realistic depictions of natural scenes, landscapes (natural and urban), tools and items. Similarly, the sounds contained animal calls, natural noises, or noises from man-made environments (e.g. honk of a car). The pairings were pulled from the stimulus database randomly and created to make certain that semantic congruency effects within pairs were avoided, ensuring that a-priori confounds of semantic information for the retrieval performance were minimized.

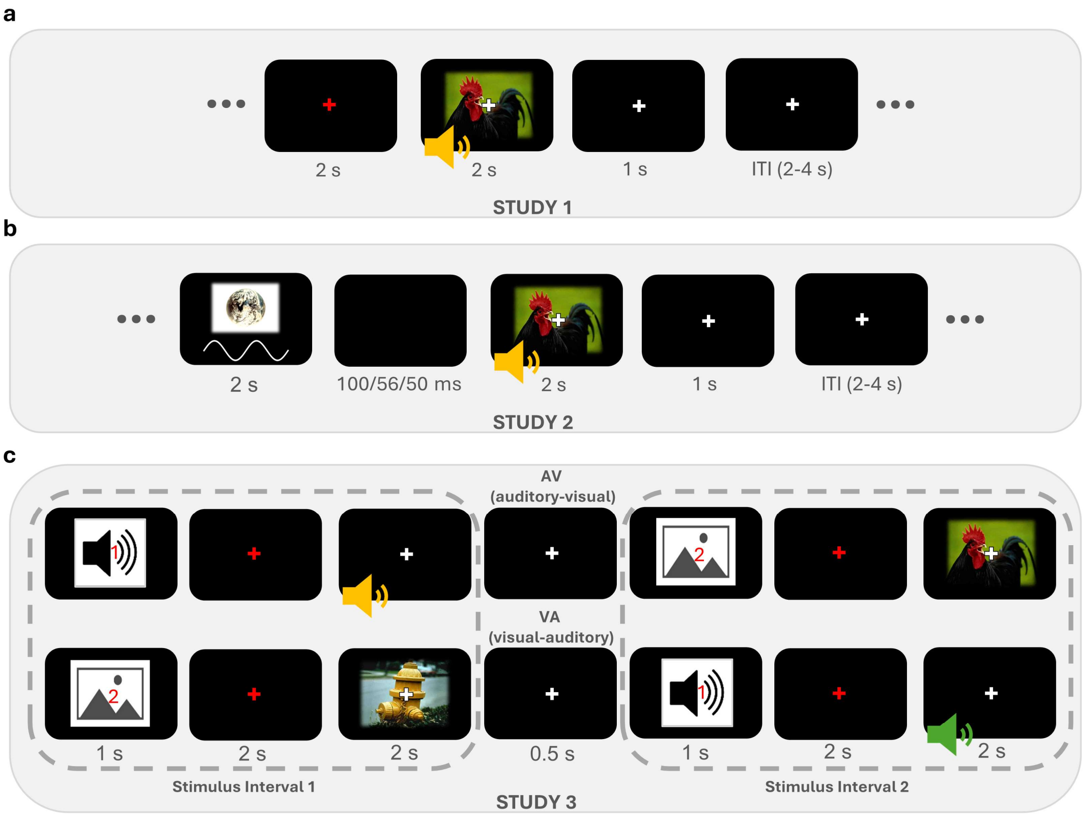


Figure 1. Encoding trial structure. The figure shows schematic representations of the encoding trial structure from every study. **(a)** Trial structure for Study 1. The stimulus onset is preceded by a pre-stimulus period marked by the red fixation cross. **(b)** Trial structure for Study 3. Visual stimulation is followed by a black screen whose duration depended on the stimulation condition. The subsequent stimulus pair is presented in rhythm with the entraining stimulus for the theta and alpha conditions. **(c)** Trial structure for Study 3. Trials were characterized by two stimulus intervals consisting of the modality cue, the pre-stimulus interval, and item presentation. Modality sequence was balanced across trials.

In the encoding task from Study 1, the audiovisual pairs were presented for 2 s, with a white fixation cross overlaid in the middle of the image. Before stimulus presentation, a red fixation cross was shown for 2 s, marking the pre-stimulus period. After stimulus offset, the white fixation cross remained on the screen for the rest of the response window (1 s) and the subsequent inter-trial interval (2 to 4 s). In trials from the recognition task, old and new pairings were again presented for 2 s, with a white fixation cross overlaid in the middle. The response window ended 1 s after stimulus offset. However, the inter-trial interval was set to a fixed duration of 4 s.

1.4.2 Study-specific modifications

Although the general task design was the same in all three studies, modifications were made to accommodate the corresponding research goals of the experiment. Importantly, only the procedure of the encoding task was modified in Study 2 and Study 3, as the recognition task remained identical to the original design in from Study 1.

Study 2 – Visual sensory entrainment

The goal of Study 2 was to elucidate whether low-frequency oscillations before stimulus onset functionally affect the encoding of multisensory associations. Thus, we modified the pre-stimulus interval of the encoding trial structure to incorporate a form of signal entrainment and directly enhance specific narrow-band frequencies. In accordance with our preregistered hypotheses, the experimental design followed a between-subjects structure with three entrainment conditions serving as the independent variable: rhythmic visual stimulation at **theta (5 Hz), alpha (9 Hz)**, or an **arrhythmic control** condition comprising randomized frequencies between 13 and 24 Hz. Due to the identical task structure, the data from Study 1 were considered as an additional control condition in Study 2 and will be referred to as the NE group (no entrainment).

The principle of signal entrainment has been used in a multitude of studies to investigate the functional involvement of brain oscillations in cognition (Herrmann et al., 2016; Lakatos et al., 2019), and memory in particular (Hanslmayr et al., 2019; Wang et al., 2024). By applying an external signal with a specific frequency to an internal oscillating system, the difference in phase between the external signal and the internal system decreases over time, as more and more neurons begin to fire in synchrony (Hanslmayr et al., 2019; Thut, Veniero, et al., 2011). The end state of the entrainment process is characterized by the phase difference approaching zero, as the internal system oscillates at the same rhythm as the external signal. Importantly, activity in the to-be-entrained frequency needs to be already present in the internal system for the entrainment to succeed (Miller et al., 2009; Watrous et al., 2018). However, the Arnold tongue principle posits that given a difference in frequencies between the external signal and the internal system, an increase in stimulation intensity may alleviate these constraints and lead to successful entrainment (Pikovsky et al., 2003; Tass et al., 1998).

Adhering to the principles of signal entrainment, participants were exposed to a 2-second visual entrainment stimulus before the onset of the audiovisual pair in each encoding trial (see **Figure 1b**). As the entraining stimulus, a photographic depiction of Earth with an inverted color scheme was used to increase contrast and thereby its stimulation intensity. The luminance of the entrainment image oscillated sinusoidally at the target frequency, and stimulus presentation was synchronized to the phase of the entrainment signal through a brief delay (100 ms for theta, 56 ms for alpha, 50 ms for control). For the theta and alpha groups, this constituted half of an oscillatory cycle in the respective frequency, which ensured that the main stimulus pair was always presented at the peak of the oscillation curve for the theta and alpha conditions. Notably, the entire experiment was presented on a display with a framerate of 240 Hz and a single-frame duration of 4.2 ms, ensuring high temporal precision of the sinusoidal luminance modulation.

Study 3 – Multi-sensory sequences

The objective of study 3 was to explore how sequences of information from different modalities may serve as a contextual feature for the encoding of associations. While the overall structure of the experiment remained consistent with that of Study 1 and Study 2, the structure of the encoding trials was changed to adhere to the research question of Study 3 (see **Figure 1c**). Each trial commenced with a modality cue represented by an icon bearing a red numeral. The cue indicated which sensory modality – visual or auditory – would appear first. Subsequently, a red fixation cross was displayed for a duration of 2 s, which served as a preparatory signal. Then, the initial stimulus (either image or sound) was presented, followed by a 500-ms inter-stimulus interval and a second cue that predicted the upcoming complementary modality. After another fixation period, the second stimulus appeared, thereby completing the pair. The subsequent inter-trial interval varied randomly from 3 s to 5 s. Participants were explicitly instructed to memorize the *association* between the two stimuli rather than the individual items, ensuring that recognition performance reflected associative rather than item memory. Notably, the participants were not required to indicate whether both stimuli could be categorized as an animal, as was the case in Studies 1 and 2. To control for order effects, the design was counterbalanced so that each participant was presented with an equal number of auditory-visual (AV) and visual-auditory (VA) trials. The sequential presentation of the stimuli prevented the immediate integration of audiovisual information, enabling the investigation of whether the temporal order of the modalities themselves constituted a contextual feature within the memory trace.

1.4.3 Data processing and analysis

Memory performance and response time

Despite its simplicity in design, the SME task enables an examination of memory-related behavior from a unique perspective. The task can be characterized as a 2-alternatives forced-choice task (2AFC) in its fundamental structure. This resulted in four distinct response categories: correctly remembered old pairs (hits), forgotten pairs (misses), correctly rejected new pairs (correct rejections), and old pairs erroneously categorized as new (false alarms). Consequently, computations within the framework of the Signal Detection Theory proved to be applicable (Pastore & Scheirer, 1974; Stanislaw & Todorov, 1999).

In all three studies, the sensitivity index *d'* was employed as the primary metric to assess memory performance. The sensitivity index is defined as the difference between the z-transformed hit rate and the z-transformed false alarm rate. In Studies 1 and 3, the analysis of memory performance was supporting the analysis of oscillatory measurements. Group memory performance was evaluated in a frequentist framework, employing a one-sample *t*-test to rule out the possibility of random response patterns. Furthermore, memory performance in Study 3 was compared between the two sequence conditions to assess whether the order of the modalities influenced memory success (paired-samples *t*-test).

In Study 2, memory sensitivity was established as the primary behavioral metric. This approach was adopted to ascertain whether different stimulation frequencies would yield disparate performance outcomes. However, it was also utilized as the main criterion for the incremental accumulation of evidence employed in the study. Due to the absence of prior studies from which to estimate appropriate samples for this between-subjects design, an incremental evidence-gathering approach within the Bayesian framework was adopted to determine the necessary sample size. Upon reaching a group size of $k = 15$, Bayesian versions of *t*-tests were carried out to test our hypotheses. This process was repeated every time k increased by 1 in all groups. In the corresponding pre-registration, it was posited that data collection would stop either when evidence in favor of the null- or alternative hypothesis reached a moderate level, or when group size reached $k = 35$ independent of the actual effect size. Depending on the hypothesis, one-sided or two-sided versions of the Bayesian *t*-test were used to estimate the effect. A Cauchy distribution of medium width ($r = \sqrt{2}/2$) was used as prior in these tests.

In all three studies, response times (RTs) were utilized as secondary measures of behavioral performance in the memory task. In Study 1, only an ancillary analysis of RTs was conducted. RTs from the encoding task that corresponded to later remembered and not remembered stimuli were contrasted to assess potential differences during the categorization task (paired-samples *t*-test). To assess the effects of RT during the recognition task, a repeated-measures ANOVA was conducted, with the factors *type of pairing* (old vs. new) and *type of response* (correct vs. incorrect). This analysis was also conducted in the context of Study 3 and expanded upon by investigating differences in RTs between modality sequences using paired-samples *t*-tests. In Study 2, the Bayesian version of a one-way ANOVA was employed to assess differences in RTs during encoding between all four groups. This analysis was also conducted for every response category from the recognition task, including subsequent post-hoc tests. Furthermore, the difference in RT between correct and incorrect responses was calculated and submitted to a group analysis to explore how entrainment (or the absence thereof) might influence implicit measures of encoding.

In addition, a brief self-report questionnaire on entrainment perception was incorporated into the paradigm in Study 2. The objective was to establish a metric to control for confounding effects associated with entrainment salience and fatigue, given the expectation that groups receiving visual stimulation would not demonstrate variations in these variables. Accordingly, the participants were instructed to rate the *pleasantness* of the oscillating image, the degree of *distraction* it induced, their state of *attention*, and their current level of *fatigue*. The ratings were collected after each encoding block. For each survey item, a Bayesian version of a mixed-design ANOVA with the between-subjects factor *pre-stimulus condition* (theta, alpha, control) was conducted. The within-subjects factor *block* (A, B, C) was incorporated to the model to account for changes in ratings over the course of the experiment.

Oscillatory data (EEG)

Raw EEG data was recorded in the same laboratory setting for all three studies using the Brain Vision Recorder software (Brain Products GmbH, Gilching, Germany). Separate recordings were made for each encoding and recognition run. The main portion of the data processing was conducted using the Fieldtrip toolbox (Oostenveld et al., 2011) for MATLAB (Study 1: v2021a; Study 2: v2023a, Study 3: v2022a; The MathWorks Inc., Natick, Massachusetts, USA). The configuration of the preprocessing pipeline was maintained as a consistent framework across all studies. Initially, the data was filtered and segmented into discrete epochs corresponding to each trial. This was followed by the rejection of trials containing major artifacts from the data, and the subsequent application of Independent Component Analysis (ICA) for the purposes of removing eye-movement components and large-scale artifactual noise related to muscle activity. In Studies 1 and Study 3, trial and component rejection were done by visually inspecting the data and removing noisy segments manually. Importantly, because of the sequence manipulation in the encoding phase of Study 3, the data underwent further segmentation into visual/auditory and auditory/visual subsets for subsequent analysis following pre-processing. In Study 2, however, a data-driven, automated approach was selected. This approach utilized algorithms from the Fieldtrip toolbox based on z-standardization (Oostenveld et al., 2011). It also employed a classification tool for automatically identifying and rejecting artifactual independent components (Pion-Tonachini et al., 2019). Additionally, resting-state data was recorded before and after the experiment in Study 2. This data was then used to explore oscillatory effects related to the entrainment procedure. The recordings obtained from the pre- and post-paradigm periods were subjected to separate preprocessing steps but processed in a manner analogous to that of the experimental data, undergoing the same calculations to remove artifacts.

Then, the pre-processed data was decomposed into the time-frequency domain using a multitaper approach. The decomposition procedure incorporated the same parameters for all three studies except for parameters controlling the padding for the convolution window, as that depended on trial length which differed between the studies. For univariate statistical analysis, the data from the encoding as well as recognition task was averaged across trials within the respective subsets for each participant. In Study 1, the data was then divided into two conditions corresponding to the primary contrast: later remembered (REM) and later forgotten (NOTREM). As we also hypothesized about effects in phase-based connectivity, single-trial cross spectral densities in the theta band were extracted from the pre-processed data in a separate analysis pipeline. Functional connectivity was then estimated using the weighted Phase Lag Index (wPLI; Vinck et al., 2011). The subsequent statistical analysis was constrained to the connectivity between occipital and frontocentral locations. In Study 2, the experimental data was not split between REM and NOTREM conditions, as the group-specific contrasts between entrainment conditions were of primary importance. The resting-state data was decomposed into stationary power spectra due to the absence of event-related activity, and a grand-average spectrum was calculated for subsequent statistical computations. The decomposed experimental data from Study 3 was split into four conditions for each participant and then averaged across the respective trials.

The decomposed data from the encoding task was then used as the basis for subsequent statistical computations in all three Studies. Contrast effects between conditions or groups were estimated using a non-parametric approach based on cluster-based permutation as implemented in the Fieldtrip toolbox (Oostenveld et al., 2011). In this approach, individual statistical tests based on the corresponding contrast were computed for each channel–time–frequency data point across participants. Contiguous data points exhibiting significant differences between conditions were aggregated into clusters based on temporal, spatial, and spectral adjacency. For each cluster, the sum of test statistics was calculated to yield a cluster-level statistic, and the largest of these served as the main test statistic for the condition or group comparison. A Monte Carlo permutation approach was then employed to estimate the null distribution. All trials from both conditions were pooled and randomly divided into two groups, after which the same point-wise comparisons and cluster-level calculations were repeated. This resampling procedure was performed multiple times, and for each iteration, the maximum cluster-level statistics for positive and negative clusters were recorded to construct the cluster-level null distribution. Finally, p-values were derived by determining the proportion of random partitions producing a larger test statistic than the observed one. This process was repeated for all clusters, resulting in a p-value for each cluster identified in the data. While the adjacency and resampling parameters slightly differed between Studies, this approach was utilized for statistical EEG analyses in most cases. In instances of within-subjects contrasts, paired-samples *t*-tests were used on sample level, whereas *F*-tests were utilized for between-subjects contrasts. Furthermore, correlation coefficients were used to estimate correlation effects between oscillatory data and third variables.

1.5 Results Summary

1.5.1 Study 1: Increases in pre-stimulus theta and alpha oscillations precede successful encoding of crossmodal associations

This study focused on the assessment of pre-stimulus oscillatory states in the context of crossmodal associative memory. The goal was to ascertain how these states might influence subsequent integration and encoding of individual associations between auditory and visual information. The SME paradigm utilized in this study permitted the examination of associative memory performance and its neural correlate, disentangled from markers of individual item memory (see **Figure 1a**). This was achieved by instructing participants to memorize the pairings of stimuli rather than individual items. We hypothesized that oscillatory power prior to the onset of the crossmodal pairs would allow for a differentiation between later remembered (REM) and later not remembered (NOTREM) pairs. Furthermore, we expected that synchronization between the relevant sensory areas in the theta band would enhance the binding of sensory information and might also differentiate between REM and NOTREM trials. The results of this study are based on data obtained from a sample of n = 51 individuals.

First, it was imperative to validate the behavioral performance in the SME task to establish a robust foundation for subsequent analyses of oscillatory data. Participants demonstrated a high level of above-chance performance in the categorization task during encoding, indicating a high degree of engagement with the memory task. Additionally, no significant variations in RTs between REM and NOTREM trials. In the subsequent recognition task of the paradigm, participants showed a high hit rate, which was contrasted by a relatively low false alarm rate. This finding suggests good overall recognition performance in distinguishing between old and new pairs, as we found that the sensitivity index differed significantly from chance level. The analysis of response times during recognition trials revealed that participants generally responded more rapidly on trials with a correct response than on trials with an incorrect response, and that the discrepancy between correct and incorrect responses was greater for new pairs than for old ones.

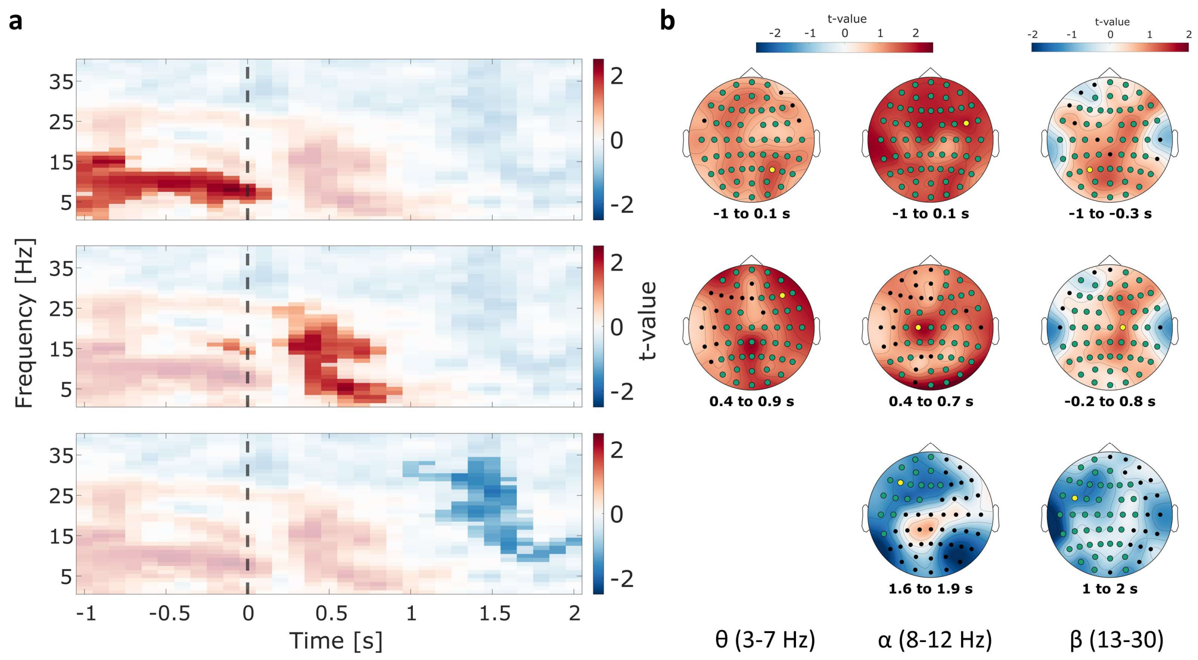


Figure 2. SMEs in time-frequency power. (a) Time-frequency plots depicting the statistical results of the SME over time and frequency (REM-NOTREM). The vertical line marks the onset of the stimulus pair. Positive *t*-values signify greater oscillatory power for REM trials. Opaque data points show the boundaries of the significant effect ($p < .05$, corrected). **(b)** Topographical distributions of the statistical SME for each cluster. The columns denote the distributions for the respective frequency bands. Channels marked in green are contribute to the respective cluster. Yellow markers show the channel with the maximum effect. Figure adapted from Ostrowski & Rose (2024).

The primary focus of this study was the analysis of neural SMEs in oscillatory power, with a particular emphasis on effects in the pre-stimulus period. Contrasting the oscillatory power from REM trials with NOTREM trials revealed several significant clusters in the data (**Figure 2**). Notably, a positive cluster ranging from 1 to 18 Hz was observed in the pre-stimulus interval, indicating increased ongoing theta and alpha power for REM trials as compared to NOTREM trials. This effect was centered around right parietal locations. A second positive cluster was found in the initial phase of the stimulus presentation window, with a third negative cluster at the end of the window. These results suggest that REM trials were accompanied by increased theta, alpha, and beta activity during early stimulus presentation as compared to NOTREM trials, while exhibiting lower alpha and beta power at the end of the stimulus window.

The effects were centered around central and right frontal areas for the positive cluster and left frontal areas for the negative cluster.

In light of these findings, we were interested whether the extent of memory sensitivity might be reflected in the power disparity between REM and NOTREM correlates. A correlation analysis yielded a positive cluster primarily in the alpha band that spanned the entire pre-stimulus analysis window, with the effect centered around left parietal and right anterior-frontal regions. The cluster further encompassed part of the theta band, showing significant correlations in the early pre-stimulus window, most prominently around parietal and anterior-frontal regions that later shifted to frontline midline areas. These results suggest that enhanced memory sensitivity was generally accompanied by increased power disparities between REM and NOTREM trials, thereby confirming that memory performance may be contingent on SME magnitude.

To test whether theta band synchronization between auditory and visual areas might similarly differentiate between successful and unsuccessful encoding, phase-based connectivity in REM trials was compared to the connectivity in NOTREM trials using the wPLI metric. Notably, no significant differences were detected either prior to stimulus onset or during stimulus presentation, indicating that intersensory phase-based connectivity in the theta band may not reflect the encoding outcome in a similar way as oscillatory power.

1.5.2 Study 2: Disentangling the Functional Roles of Pre-Stimulus Oscillations in Crossmodal Associative Memory Formation via Sensory Entrainment

The primary goal of Study 2 was to assess the functional relevance of the oscillatory patterns identified in Study 1 in the development of crossmodal associations that extend beyond the covariation of activity. Addressing this question, however, required a method to modulate pre-stimulus activity and selectively amplify individual frequencies. Thus, sensory entrainment was utilized to target specific narrow-band power in the visual domain by presenting rhythmically oscillating stimuli preceding each encoding trial. Participants were assigned to receive either 5 Hz (theta) or 9 Hz stimulation (alpha) in experimental conditions, while randomly generated arhythmic stimulation was used in the control group. The following results are derived from a final sample of n = 105 participants, with a group size of k = 35 for each group. Given the congruence in the experimental design, the sample from Study 1 was used as an ancillary control condition without any form of visual stimulation during the pre-stimulus period (k = 45; NE group).

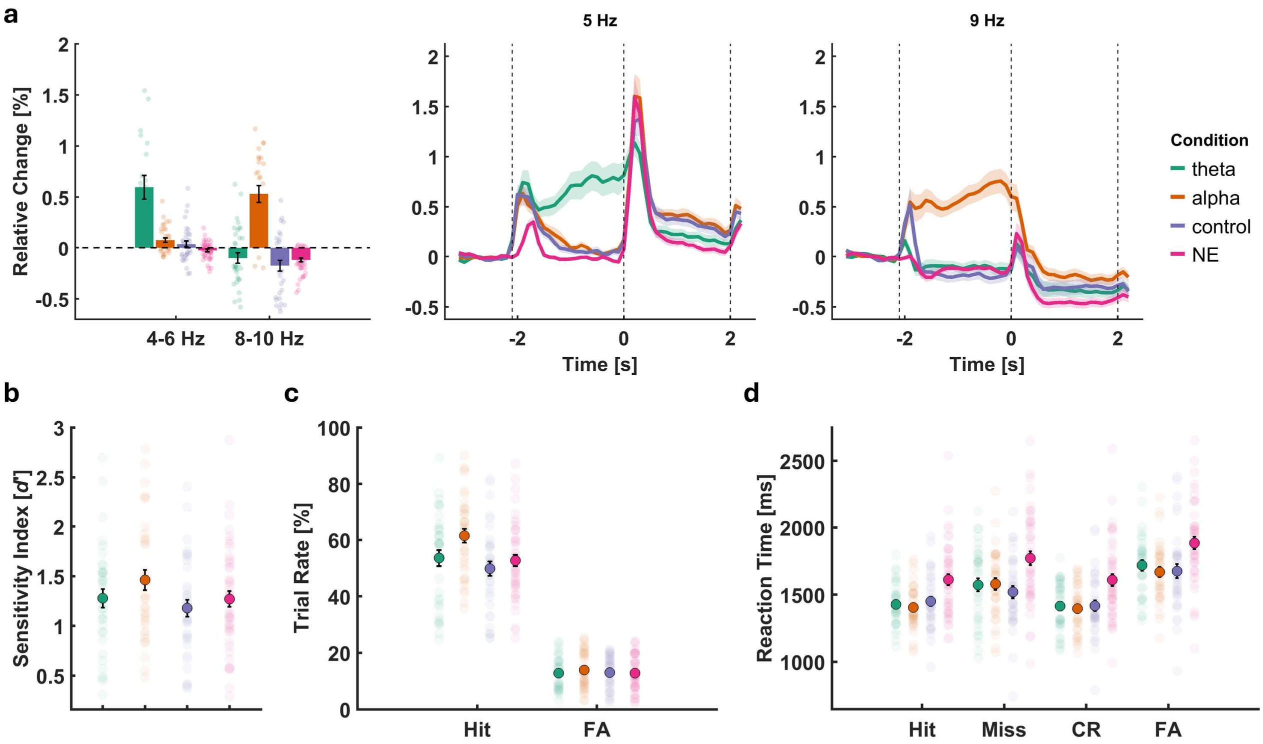


Figure 3. Effects of visual stimulation on oscillations and performance parameters. (a) *Left* shows the average relative change in power of the respective narrow-band envelope for every group. Each data point denotes the respective mean value for one participant. The black error bars depict the standard error of means. *Right* shows the average time courses of relative change in power for 5 Hz and 9 Hz narrow-band frequencies for every group. The shadings represent the standard error of means across participants. The first dashed line marks entrainment onset, while the other two lines mark the main stimulus presentation window. Data from all three figures is derived from the mean of occipital electrodes *O1, O2,* and *Oz*. **(b)** Mean memory sensitivity with standard error of means for all groups. **(c)** Average trial rates for the proportion of remembered old pairs (Hit) and falsely remembered new pairs (false alarm, FA) across individuals for each group. Black error bars mark the standard error of means. **(d)** Group means of response times for all response categories from the recognition phase. In addition to Hits and FAs, the figure includes response time for forgotten old pairs (Miss) and correctly rejected new pairs (CR).

As a first step, it was necessary to validate that the stimulation procedure indeed resulted in signal entrainment. We hypothesized that visual stimulation through oscillating images would effectively modulate activity in the target frequency, resulting infrequency-specific increases in power. Thus, oscillatory power recorded during the latter half of the entrainment period from the theta and alpha group was statistically compared to recordings during arhythmic stimulation in the control group, but also to ongoing activity in the absence of visual stimulation (NE group). The effects that were observed to be common to both the control as well as the NE comparison were found to overlap only in the theta band around 5 Hz for the theta group and in the alpha band around 9 Hz for the alpha group (**Figure 3a**). Moreover, the stimulation effects were most prominent in occipital and parietal regions, with a progressive decline in effect sizes towards the frontal portion of the brain. Our results indicate that relative change in oscillatory power in the theta and alpha groups was significantly higher than in the control and NE groups, and that this effect was specific to the respective target frequencies. Consequently, the stimulation procedure was successful in manipulating the pre-stimulus oscillatory state in the intended frequency space.

The Arnold tongue principle posits that a mismatch between internal and external signal frequency may result in diminished entrainment effects, which could be circumvented by either matching the external signal to the individual peak frequency or by augmenting the intensity of the entrainment stimulus (Hanslmayr et al., 2019; Pikovsky et al., 2003; Tass et al., 1998). Given that the entrainment frequencies used in this study were constant within each group, we were interested whether the degree of overlap between the target frequency and individual peak frequencies would correlate with the strength of the power modulation induced by the entrainment. Therefore, individual peak theta and alpha frequencies were extracted from the pre-experiment resting-state activity for every participant and subtracted from the group-specific target frequency. This individual frequency distance was then correlated with the maximum value of relative change in power during entrainment. The findings suggest that the frequency distance in the alpha group was not significantly associated with entrainment magnitude. However, a significant correlation was observed for the frequency in the theta group, suggesting that theta frequency distance might have influenced how the entrainment effect manifested in the modified brain state.

The primary goal of this study was to investigate whether changes in pre-stimulus oscillations might be functionally relevant for the encoding of crossmodal associations, and whether these changes could lead to measurable differences in memory performance. We hypothesized that both theta and alpha entrainment would result in better performance as compared to the control group. Moreover, performance in both theta and alpha groups was expected to supersede performance in the NE group. The results demonstrated that participants exposed to alpha stimulation performed significantly better than participants in the control group as well as the NE group (see **Figure 3b**). However, we found no evidence indicating that theta entrainment improved memory performance beyond was observed in the control and NE groups, despite targeted power increases from visual entrainment. This indicates a frequency-specific benefit of pre-stimulus alpha oscillations for crossmodal memory formation, but not of theta oscillations. In addition, it was hypothesized that memory performance would likely differ between the theta group and the alpha group. Our results, however, could not support this hypothesis, as both groups exhibited comparable performance throughout the experiment.

The impact of visual entrainment on processing speed was assessed by estimating differences in response times during both the encoding and recognition phases. For the categorization task during encoding, we observed a significant variation in RTs among the entrainment conditions. Interestingly, participants in the NE group were significantly slower to respond as compared to the other groups where visual stimulation occurred. However, the three entrainment groups did not show any differences in response times. For the recognition phase, response times were analyzed separately for each of the four response categories (hit, miss, correct rejection, false alarm). The analysis yielded substantial evidence for differences between conditions across all response categories. The pattern of differences mirrored the results from the encoding phase, as participants from the NE group responded significantly slower than participants in the three entrainment groups. Similarly, no differences among the entrainment groups were observed across all response categories. These findings indicate that visual entrainment may potentially enhance processing speed in relation to memory tasks. However, the observed acceleration might reflect a generalized mechanism rather than enhanced performance accuracy.

To further explore the effects of sensory entrainment, two additional analyses were conducted. First, resting-state recordings were obtained before and after the experiment to explore potential baseline changes resulting from the entrainment procedure. The statistical comparison of pre- and post-experiment resting-state power changes across the entrainment group revealed no significant differences. This suggests that any alterations in baseline oscillations were not confined to a specific type of entrainment but rather pertained to more general shifts. Second, we could explore potential confounds due to stimulation quality by having participants rate their current perceived state of fatigue and attention, as well as the pleasantness and the distracting qualities of the entrainment procedure. The analysis revealed a substantial decline in perceived attention, accompanied by an increase in perceived fatigue over the course of experiment. Importantly, these changes were consistent across different entrainment conditions, indicating that the subjective experience of the entrainment procedure and the level of task engagement were comparable across conditions.

1.5.3 Study 3: The order of multisensory associative sequences is reinstated as context feature during successful recognition

In this study, we investigated how the sequential order of sensory modality information might affect the encoding and recognition of crossmodal associations. While the main objective was to elucidate whether modality sequence could be utilized as a contextual feature from encoding to recognition, the analyses also yielded notable insights into the neural correlates of the encoding process. The findings of this study are derived from a sample of n = 32 participants who completed a modified version of the original SME paradigm from Study 1. Audiovisual pairings were presented in a sequential manner during encoding, rather than simultaneously, while the subsequent recognition task was identical to the one employed in Studies 1 and 2.

The results demonstrated that participants effectively memorized the associations, as evidenced by their high recognition performance and a consistent improvement over the course of the experiment, irrespective of the modality order conditions. Consistent with previous studies, participants responded faster on trials where old pairings were presented, and generally on trials where correct responses were recorded. A comparison of the neural correlates for remembered and forgotten pairs from the recognition task revealed differential effects that depended on the modality order in which the stimuli had been presented during encoding. Alpha and beta band power was reduced during the successful recognition of pairs that were previously presented in the VA condition as compared to forgotten pairs. For the AV condition, successful recognition was instead found to be associated with reduced theta and alpha power in comparison to forgotten pairs. Importantly, a multivariate classifier that was trained on the neural correlates of the recognition task was able to robustly differentiate whether a stimulus pair had been presented in the VA or AV condition during encoding, with peak classification accuracy observed in the theta band. This finding suggests that the memory trace might carry the modality order as a contextual feature which is then reinstated during recognition.

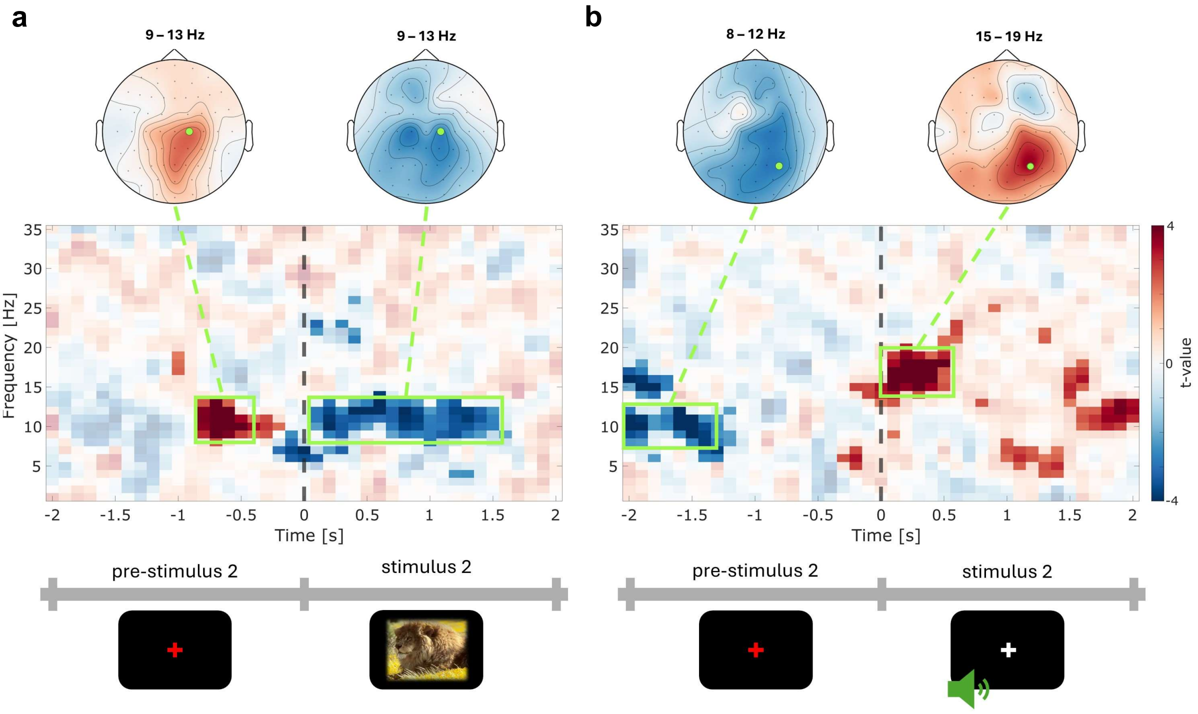


Figure 4. Differential effects of modality order on the correlation of SMEs and memory performance. (a) The correlation of REM-NOTREM power differences with memory sensitivity at channel *C2* for the AV condition. Topographies show the distribution of the correlation across the hemisphere for the respective cluster, with the green marker denoting *C2*. Opaque data points denote the space of significant correlation, corrected for multiple tests. **(b)** Same as (A), but for the VA condition. The time-frequency plot shows the effects for channel *P4*.

As in Study 1, we were interested in whether oscillatory dynamics during encoding might be related to subsequent recognition, and how the sequential presentation of the sensory information potentially affects these dynamics. We conducted correlational analyses in which the discrepancy in oscillatory power between REM and NOTREM trials was related to subsequent memory sensitivity during recognition. This procedure was repeated for each of the two stimulus presentation windows and both modality order conditions. While no effects were identified in the first stimulus window, significant correlations were observed in the second stimulus window for both the AV and VA conditions (see **Figure 4**). Increases in pre-stimulus alpha activity were significantly associated with improved memory performance, but only when the second stimulus was visual (AV). In contrast, in the VA condition and prior to the onset of the auditory stimulus, we observed that increases in pre-stimulus alpha power correlated with decreases in memory performance. During stimulus presentation, however, the effects were reversed. In the AV condition, significant negative correlations were observed in the alpha and low beta bands, while the VA condition exhibited positive correlations in the beta band only. Notably, no effects were found in the theta band. The findings indicate that neural activity elicited exclusively during the second stimulus is associated with subsequent success in the recognition task. Crucially, the nature of this association may be contingent upon the modality order in which the associations were presented and encoded.

1.6 Discussion

The objective of this dissertation was to explore the involvement of electrophysiological correlates in the process of encoding complex multisensory associations to memory, and thereby broaden our understanding of how the brain enables remembering experiences from the past. In this context, the manner in which pre-stimulus or ongoing brain states influence subsequent encoding was a subject of particular interest. In pursuit of this objective, I attempted to explore potential answers to these questions over the course of three studies. Study 1 was centered on the characteristics of spontaneous oscillatory activity and its function in the encoding of individual audiovisual associations. Study 2 expanded upon the insights gained from Study 1, investigating whether pre-stimulus brain states held any functional significance in the encoding process beyond mere correlation. Study 3 explored how the sequential influx of associative information might affect the encoding and retrieval processes under the assumption that the order of modality input carries intrinsic contextual information. The results from this work suggest that pre-stimulus oscillations are intrinsically linked to the process of encoding multisensory associations. Specifically, theta and alpha power were shown to correlate with memory success and found to differentiate between later remembered and not remembered stimuli. Importantly, the use of non-invasive sensory stimulation revealed a functional connection between changes in pre-stimulus alpha power and subsequent memory success, as augmenting alpha but not theta activity resulted in significantly better memory performance as compared to controls. Moreover, if multisensory associative information is encoded sequentially rather than concurrently, alpha activity preceding the onset of the second stimulus was found to differentiate between remembering and forgetting. Taken together, these results underscore the notion that memory might not begin with the sensory input, but rather with consistent preparatory states. In the following sections, I will discuss these findings and how they align with theories on memory formation, identify the limitations of this work, and point out potential implications for future work.

1.6.1 Division of labor: Binding and inhibition

The evidence presented here is largely in line with prior research on the role of low-frequency oscillations in the formation of associative memory. In Study 1, we were able to replicate the positive relationship between theta power and memory performance before and during stimulus presentation. This phenomenon has been documented in several articles published in recent years, with an increasing number of researchers focusing on the neural correlates during encoding (Herweg et al., 2020). However, studies have also demonstrated that SMEs can be observed in the pre-stimulus theta range in designs that investigate source memory as a form associative encoding (Merkow et al., 2014, 2014; Scholz et al., 2017). The present findings build upon this notion and suggest that increased theta activity before encoding benefits not only the associative binding of context and item (Scholz et al., 2017; Staudigl & Hanslmayr, 2013), but also the formation of individual associations between single pieces of information from different sensory modalities. While the notion of contextual or source-based associations is paramount to the effectiveness of episodic memory, it can be posited that individual associations between discrete items constitute the basic building blocks of episodic memory, and that theta oscillations not only coincide with encoding the overall structure of an episode but may also be involved in the encoding on the lowest level of information binding.

Moreover, the results presented here suggest that pre-stimulus alpha oscillations may play an equally important role in the encoding of individual multisensory associations. Although alpha power during stimulus presentation has been positively associated with encoding success in previous work (Hanslmayr et al., 2012; Jensen et al., 2002; Meeuwissen et al., 2011), less effort has been invested into investigating how pre-stimulus alpha activity is related to memory, as the majority of research associates pre-stimulus alpha activity with benefits to perceptual discrimination and learning (Battistoni et al., 2017; Bengson et al., 2014; Michael et al., 2022). The results from Studies 1 and 2 now suggest that pre-stimulus alpha oscillations may offer a functional advantage in the subsequent encoding of multisensory associations that extends beyond the contribution of pre-stimulus theta activity. Specifically, enhancing frequency-specific power in the alpha band resulted in significant increases in memory performance, while the same procedure in the theta band revealed no notable behavioral effects. This is supplemented by evidence from Study 3, where SMEs in the alpha range before the presentation of the second stimulus were found to correlate with later memory performance. It is reasonable to assume that the mechanisms involved in the formation of associations would only become relevant before or during the input of the second set of information, as only then could an association between items be created.

Despite the notable overlap in the evidence with reports from previous studies, some of it does not necessarily align with expected outcomes. While increased theta power was found to accompany later remembered associations in Study 1, visual stimulation of pre-stimulus theta power did not affect memory performance in Study 2. In addition, there was no indication that phase-based connectivity between sensory areas in the pre-stimulus theta range might contribute to subsequent encoding, although previous evidence suggests that enhanced theta synchronization during encoding and retrieval may positively affect memory performance (T. Gruber et al., 2001; Klimesch et al., 1997; Sato & Yamaguchi, 2007; Summerfield & Mangels, 2005). In light of the findings on alpha oscillations in the present work, the evidence may suggest a functional organization in the brain that is characterized by differential theta and alpha activations which depend on the time interval of the encoding process. Specifically, I suggest that these results indicate a division of labor in the encoding process. In this scenario, the functional contribution of theta oscillations would happen during stimulus processing, while alpha oscillations would assume a preparatory role, gating and inhibiting unwanted information, and establishing the optimal conditions for the subsequent binding and encoding.

According to the temporal encoding model, theta oscillations are referenced to the phase of the signal that is detected when a stimulus appears (Buzsáki, 2005; Buzsáki & Moser, 2013; Terada et al., 2017). In this scenario, phase precession in the theta band is the mechanism that functionally enables spatial memory and the binding of information to memory in general (Terada et al., 2017). This mechanism may not be triggered in the absence of stimuli that require encoding, thereby suggesting that the functional significance of theta oscillations for crossmodal binding is confined to the actual encoding window (Hsieh & Ranganath, 2014; Nyhus & Curran, 2010). While the functional contribution of theta activity to the encoding of associative information during stimulus presentation is well documented (Clouter et al., 2017; Köster et al., 2019; Wang et al., 2018, 2024), its role in preparatory processes is not fully understood. To the best of my knowledge, Study 2 was the first attempt at investigating a potentially causal relationship between pre-stimulus theta oscillations and subsequent encoding success. Contrary to previous assumptions that posited pre-stimulus theta activity as an important correlate of memory formation (Addante et al., 2011; Hanslmayr, Volberg, et al., 2011; Otten et al., 2006), the current findings contend against a causal role of cortical pre-stimulus theta oscillations in the formation of crossmodal associations.

According to previous literature, the function of alpha oscillations in crossmodal encoding is thought to involve the suppression of irrelevant information and the management of attentional resources (Klimesch et al., 2011; Minarik et al., 2018; Strunk & Duarte, 2019). The present results support this notion, as patterns of alpha synchronization before stimulus onset were consistently observed to be associated with successful encoding, while stimulus presentation was accompanied by alpha synchronization as well as desynchronization. However, these observations partially oppose the widespread assumption that alpha oscillations contribute primarily due to mechanisms of desynchronization. The information-via-desynchronization hypothesis posits that desynchronized states are less predictable and can subsequently carry more information (Hanslmayr et al., 2012, 2016). This increased capacity for information could explain the frequent observation of decreases in alpha power in conjunction with successful encoding (Griffiths, Martín-Buro, Staresina, Hanslmayr, et al., 2021; Hanslmayr et al., 2012). While alpha desynchronization during stimulus presentation was also found to be associated with successful encoding in Study 1, the bulk of the remaining evidence points towards an opposite effect for the pre-stimulus period. This pattern could indicate that the function of alpha oscillations in the context of crossmodal encoding may change depending on the period of the encoding process. Insights from Study 3 further imply that this may even be contingent on the combination and order in which the sensory information arrives in the brain. While this proposition can be reconciled with the notion that fluctuations of alpha oscillations reflect inhibitory processes in the context of memory, it could also indicate that the mechanistic manifestation of inhibition may depend on the current cognitive demands. As negative alpha SMEs were observed during stimulus presentation in Study 1, one could argue that the encoding process of multisensory associations may benefit from an oscillatory state in which more complex information can be taken in. In contrast, large-scale pre-stimulus synchronization could be indicative of the allocation of attentional resources (Schneider & Rose, 2016; Uncapher et al., 2011), preparing the system by creating favorable conditions for integrating sensory information.

1.6.2 Complementary learning systems and access to knowledge

The proposition that theta and alpha oscillations during and prior to encoding may reflect a mechanistic division of labor in the processing of multisensory content for memory appears to be consistent with recent frameworks that emphasize the interaction between cortical and hippocampal memory systems. For instance, the Complementary Learning Systems framework (CLS) proposes a reconciliation of synchronization discrepancies observed in the literature within and between frequency bands, as well as subsequently between processing locations. According to this framework, the cortex is characterized by the representation of information in a rich and integrated manner, where the representations are refined over several experiences. Conversely the hippocampus is noted for its relatively sparse representation of information (McClelland et al., 1995; Norman, 2010; O'Reilly et al., 2014). Hanslmayr and colleagues (2016) expanded on this theory, proposing that sensory stimulation may induce a reduction in alpha oscillations so that neural populations in the cortex could encode the information by increasing their firing rate (Jensen & Mazaheri, 2010; Klimesch, 2012). This, in turn, would cause phase precession of the hippocampal neurons down the line, initiating a temporal segregation into cycles of high-frequency gamma activity (> 30 Hz) that may explain how the coupling between theta and gamma activity is usually observed to correlate with memory formation as well as the binding of individual items with context information (B. Lega et al., 2016; Staudigl & Hanslmayr, 2013; Tort et al., 2009). Consequently, stimulation-sensitive neurons in the hippocampus would become interconnected, thereby encoding a memory based on the sensory information. This association of sensory information would further facilitate the retrieval of information at a later point in time.

The CLS framework integrates theta and alpha mechanisms into a comprehensive system of complex encoding, yet its emphasis remains on the processes initiated in response to the onset of a stimulus. However, the present findings indicate that alpha oscillations prior to sensory input appear to affect the efficacy of subsequent encoding. In order to understand how this might be integrated into the CLS framework, it is necessary to reflect on the general role of alpha oscillations in the brain. In the literature review, I established that alpha oscillations have been found to be associated with multiple cognitive domains. Therefore, it can be posited that the reason underlying these observations is that alpha oscillations reflect a distinct category of processes related to the regulated access to a general knowledge system (Klimesch, 2012). Importantly, the knowledge system in this context refers to a representation of information storage that incorporates any type of knowledge, including procedural and implicit (Klimesch, 2012). The inhibitory functions of the alpha band can manifest in two distinct forms: event-related synchronization (ERS) or desynchronization (ERD). Whereas ERS is associated with inhibition, ERD, on the other hand, would be associated with the release from inhibitory states. As oscillations are indicative of rhythmic changes in neural activity, changes in alpha may equally reflect changes between minimal and maximal inhibition. Thus, if the primary effect of alpha oscillations is inhibitory, it is reasonable to assume that it underlies attention. Conversely, the central function of attention is to sharpen or to suppress representations, where the former is largely associated with ERD and the latter with ERS

(Klimesch, 2012; Klimesch et al., 2007, 2011). While anticipatory ERD is concurrent with good performance in most cognitive domains (Ergenoglu et al., 2004; Hanslmayr et al., 2005), the pattern is reversed for the memory domain: Larger pre-stimulus alpha ERS correlates with good memory performance (Klimesch, 2012). Conceptually, this would translate to an attentional mode before stimulus onset that blocks the processing of distracting information. This, in turn, reflects the prevention of access to the knowledge system, thereby enabling selective access during subsequent stimulus presentation.

Taken together, the present findings could be interpreted as evidence that the CLS framework has been missing a vital component to fully describe how complex memories are formed. Based on the present work, I view the role of pre-stimulus activity and the importance of preparatory states for subsequent encoding as a useful extension to the framework, reflecting the view that the brain is not merely a reactionary system. The CLS framework posits that cortical processing is characterized by rich and integrated representations being refined over several experiences. One could argue that access to the knowledge system as described by Klimesch (2012) may be crucial for this refinement process. Anticipatory alpha states could represent a way to prepare the system for knowledge access, as evidenced by the functional relevance of pre-stimulus alpha ERS reported in this work. Therefore, within the CLS framework, the mechanism of access control can be conceptualized as a moderator of the subsequent cortical alpha ERD during encoding, influencing the cortical pattern for the hippocampal system to bind. I suggest pre-stimulus alpha activity effectively functions an upstream mechanism, preparing and constraining cortical inputs that drive the theta-dependent formation of hippocampal representations.

1.6.3 Reflections on neural entrainment

It is imperative to deliberate on methodological aspects that underpin research on oscillatory mechanisms, in addition to their theoretical ramifications. Choices in experimental design and signal analysis can affect the drawing of conclusions, which is why I would like to outline some methodological considerations relevant to the present work. In Study 2, ongoing theta (5 Hz) and alpha (9 Hz) oscillations were effectively manipulated to investigate the functional relevance of pre-stimulus activity for crossmodal memory formation. Our analyses validated the entrainment procedure, confirming targeted power increases in the form of steady-state visually evoked potentials (SSVEPs), and replicating previous findings on the entrainment of theta and alpha activity (Clouter et al., 2017; Hanslmayr et al., 2019; Köster et al., 2019; Michael et al., 2022).

One important methodological consideration pertains to the frequencies at which sensory stimulation occurred. In the present work, the stimulation was administered at a fixed frequency across participants for both the theta and the alpha condition. Although this approach may guarantee experimental consistency, it prompts the question of stimulation efficacy, especially in comparison to methods that adapt the stimulation to each participant's intrinsic peak frequency. Researchers have been debating whether extracting individual peak frequencies is more advantageous for experimental paradigms involving sensory entrainment, as it might improve experimental outcomes substantially by accounting for naturally occurring variations (Michael et al., 2022; Romei et al., 2016). The Arnold tongue principle posits that a growing difference between the internal and external signal would require a proportionally higher intensity of the external signal, otherwise potentially limiting or preventing entrainment. Thus, targeting individual peak signals seems a plausible option to account for interindividual differences in baseline oscillatory spectra, as research has shown that peak frequencies may vary from person to person for the theta band (Irmiš et al., 1971; Schulz et al., 2011) as well as the alpha band (Haegens et al., 2014; McLain et al., 2022; Tarasi & Romei, 2024). However, there is evidence in prior work demonstrating that employing a fixed-frequency approach can also yield substantial entrainment effects, resulting in subsequent changes in behavioral variables associated with perceptual learning (Gregorio et al., 2022; Janssens et al., 2022; Nelli et al., 2021) and memory (Williams, 2001). This is corroborated by the present results, which demonstrated that the distance between individual peak alpha frequency and the target frequency was not associated with entrainment strength. Conversely, our findings indicated that this was indeed the case for the entrainment magnitude in the theta band, suggesting that the efficacy of fixed-frequency methodologies may be mediated by the frequency of interest. A potential explanation for this phenomenon could be found in the inherent nature of the frequency spectrum usually observed in human EEG signals. Peaks in alpha activity are typically readily extractable from resting-state activity (Michael et al., 2022; Nelli et al., 2021), while theta activity is highly stimulus-dependent and therefore difficult to separate from background activity (Buzsáki & Moser, 2013; Hsieh & Ranganath, 2014; Nyhus & Curran, 2010). Consequently, the fixed-frequency approach may be a viable option if the choice of target frequency can be derived from theory or prior evidence, or if data on stimulus-evoked activity is available for the same sample of participants (Köster et al., 2019).

Beyond the selection of target frequency, it is important to deliberate on the potential of visual stimulation to offer insights on the causal relationship between oscillations and behavior. Previous evidence shows that a stream of rhythmic visual stimulation can elicit substantial enhancements in various cognitive functions, including perception (Mathewson et al., 2012; Spaak et al., 2014) or memory (Clouter et al., 2017; Hanslmayr et al., 2019; Wälti et al., 2020; Wang et al., 2018). It is assumed that changes in behavior are observed in these instances because rhythmic changes in visual stimulation give rise to SSVEPs via signal entrainment, implying interference with internal activity via outside signals (Thut, Schyns, et al., 2011). However, the validity of the assertion that visual stimulation inevitably leads to entrainment and interference has been debated in the past by questioning the source of the observable SSVEPs. Previous work has suggested that visual stimulation may cause a series of event-related potentials (ERPs) that superimpose over one another, mimicking the sinusoidal response that is the basis of SSVEPs (Capilla et al., 2011; Keitel et al., 2014). This would entail the assumption that SSVEPs and ongoing oscillations are independent, and altered behavior could not be considered evidence of a functional connection between oscillations and behavior. In an important attempt to investigate the source of SSVEPs in cases of visual stimulation, Notbohm and colleagues (2016; 2016) provided opposing evidence by systematically testing different combinations of timing, stimulation frequency, and intensity of rhythmic and arhythmic visual stimulation. In accordance with the Arnold tongue principle, the authors found pronounced phase coupling aligned with increasing stimulation intensity as well as decreasing distance of internal and external signals. Furthermore, intermittency of phase locking was observed in sequences of SSVEPs, which contradicts the argument of linear superposition, suggesting that visual stimulation likely leads to entrainment, interference, and the manipulation of ongoing oscillatory signals. The present findings lend support to the notion of interference via entrainment, as only participants receiving rhythmic stimulation exhibited any form of sustained SSVEPs that were otherwise absent in the arhythmic control condition. Taken together, it can be argued that the assertions regarding the functional relevance of pre-stimulus alpha oscillations in this work are grounded in established physiological principles, and that it further serves to illustrate the efficacy of sensory stimulation in elucidating the interplay between oscillation and memory formation.

1.6.4 Limitations and future directions

One could argue that a potential limitation of the present work lies in the structure of the SME paradigm itself. The widespread use of the paradigm presupposes that it constitutes a direct test of associative memory. Per definition, a significant portion of the underlying activity that can be measured with the SME task should correspond to the process of associative binding during encoding. However, it is important to acknowledge the involvement of several other neural processes in successful encoding, such as perception, attention, and even intentionality (Herweg et al., 2020; Schneider & Rose, 2016). Herweg and colleagues (2020) argued that the distinction between the corresponding neural correlates might be significantly less clear-cut than initially thought. Consequently, the neural patterns captured by the SME paradigm should be understood as the average of overlapping neural correlates from all processes potentially involved in realizing associative binding. Notably, the confound created by this overlap could be one of the many reasons for the variety in the results related to theta and alpha oscillations in the context of associative memory (Colgin, 2013; Herweg et al., 2020; Klimesch et al., 2006; Luo & Guan, 2018). Thus, it is necessary to consider the possibility that the findings regarding the role of theta oscillations presented here might be conflated or obscured by other neural mechanisms. For instance, it is conceivable that visual theta entrainment in Study 2 may have affected some cognitive process in the pre-stimulus period that ultimately was not involved in binding or preparation for binding, possibly explaining the present results. One way to circumvent this bias is to focus on contrasting different degrees of associative binding rather than contrasting encoding success with encoding failure directly (Guderian & Düzel, 2005; Herweg et al., 2020). For example, by using explicit metrics of association and comparing neural correlates of successful encoding with different degrees of association, correlates of perception or attention could be averaged out of the signal (Herweg et al., 2020; Solomon et al., 2019). I believe that future work would highly benefit from systematic investigations related to the experimental paradigms used to assess underlying mechanisms of associative memory. Ideally, studies could incorporate both types of contrasts within their SME designs, synthesize the results, and thus differentiate the contributing mechanisms more distinctly.

Another potential limitation could be indicated by the absence of theta stimulation effects in Study 2, despite the presence of measurable SMEs in the theta range found in Study 1. The memory system of the brain is a complex network of cortical areas and regions of the limbic system, such as the hippocampus whose oscillatory rhythms are essential for multisensory memory formation (Buzsáki & Moser, 2013; Herweg et al., 2020; Terada et al., 2017). Although there is some evidence to suggest that projections from the hippocampus can indeed drive theta oscillations in the neocortex (Ekstrom et al., 2005) and vice versa (Nyhus & Curran, 2010; Sirota et al., 2008), it is plausible that the assessment of functional effects in pre-stimulus theta activity may inherently require a more holistic approach that simultaneously considers both cortical and hippocampal mechanisms. In addition to the use of non-invasive stimulation techniques for investigating cortical functionality, focusing on where these insights intersect with findings from intracranial EEG studies (iEEG) may be the key to unlocking the full extent of theta functionality in multisensory memory formation (Becher et al., 2015; Herweg et al., 2020). Furthermore, the combination of excellent temporal resolution from EEG with good spatial resolution from fMRI measures may enable precise assessments regarding cortical as well as subcortical sources of theta rhythms (Bergström et al., 2013; Hanslmayr, Volberg, et al., 2011; Hermiller et al., 2019; Hoppstädter et al., 2015; Violante et al., 2017). However, given the challenges associated with this combination of imaging techniques, an alternative approach may be found in the advancement of statistical methodologies for source estimation, in conjunction with high-resolution physiological measures as provided by MEG (e.g. Albouy et al., 2017). While the present findings do not support functional relevance of pre-stimulus theta oscillations, this may be due to limitations of the used methodology to capture network effects and should be investigated in a more holistic framework in future work.

Although the present work should be categorized as basic rather than applied research, the insights gained may still contribute to future work in the clinical domain. If oscillatory activity is a neural correlate of cognitive processes, perturbations in the oscillatory patterns may thereby be considered as biomarkers in neuropsychiatric disorders (Başar & Güntekin, 2013; Hirano & Uhlhaas, 2021). For example, decreases in theta activity upon cognitive load have been observed in several types of pathologies, including Schizophrenia (Doege et al., 2010) or attention deficit hyperactivity disorder (ADHD; Groom et al., 2010). Moreover, similar patterns have been shown to occur in patients with memory-related disorders, such as Alzheimer's disease (AD; Caravaglios et al., 2010). The present finding that the process of encoding likely commences prior to the actual intake of sensory information, as well as the functional relevance of specific frequency bands, could prove useful in understanding how changes in oscillatory patterns within AD patients contribute to symptomology, and may inform new types of treatment (Caravaglios et al., 2010). For instance, some evidence suggests that neuromodulation through signal entrainment can modify abnormal circuitry, thereby restoring its function over time (Dostrovsky & Lozano, 2002). Based on this, recent work in the mouse model of AD has demonstrated a proof of concept for the potential of sensory stimulation to reduce the level of β-amyloid plaques in the brain to a degree that is comparable to effects of invasive stimulation based on optogenetics (Chan et al., 2021; Iaccarino et al., 2016; Singer et al., 2018). Although this has not been shown in human subjects before, instead, the use of deep brain stimulation in patients with moderate AD symptoms led to positive, moderate and long-term effects in neural activity and plasticity (Laxton et al., 2010; Lozano et al., 2016). Taken together, the literature suggests that neuromodulation through entrainment, even a variation that is non-invasive, such as sensory stimulation, could prove useful in treating symptoms of memory-related disorders. As anticipatory oscillations are likely inherently linked to successful encoding in healthy cohorts, future studies could investigate this further in clinical settings, especially in patients suffering from AD: Do pre-stimulus states show similar perturbations, and does its modulation have the potential to improve encoding, and subsequently quality of life? Future therapeutic solutions could benefit from these insights and inspire individualized modulation treatment without invasive procedures.

While speculative, the integration of insights on pre-stimulus oscillations and digital therapy tools for patients and elderly individuals may prove promising. For instance, researchers specializing in the underlying mechanisms of encoding and retrieval have developed an application aimed at improving episodic memory in everyday life scenarios (Martin et al., 2022). It has been proposed as a potential intervention to enhance memory encoding and consolidation, given the documented decline in the function of the hippocampus across the life span (Cabeza et al., 2018; Gorbach et al., 2017; Levine et al., 2002). Testing revealed that application use can lead to a significant increase in episodic memory retention (Martin et al., 2022). With ongoing advances in brain-computer interfaces (Gao et al., 2021; Zabcikova et al., 2022) and mobile solutions for recording EEG data becoming more accurate (Biondi et al., 2022), it is possible to envision similar applications utilizing real-time oscillatory data to identify the optimal time windows for encoding or consolidation, taking into account the relevance of ongoing brain states for memory. Approaches such as these may prove helpful in mitigating the decline in memory functionality that is associated with aging.

1.6.5 Conclusion

In this dissertation, I aimed to investigate how pre-stimulus oscillations shape the encoding of multisensory events. Study 1 demonstrated that pre-stimulus states in the alpha and theta range can be viewed as neural correlates of the subsequent success in encoding audiovisual associations. In Study 2, the causal manipulation of pre-stimulus activity via visual entrainment showed that pre-stimulus alpha states, in particular, functionally affect subsequent audiovisual integration. Furthermore, the order of sensory modalities was demonstrated to affect the manifestation of oscillatory states in Study 3, specifically before and during the completion of audiovisual associations. The presented evidence indicates a division of labor within the oscillatory landscape of encoding mechanisms, with alpha oscillations taking the role of a gatekeeper, regulating access to the knowledge system via inhibitory mechanisms that are contingent on task demands and the order in which sensory information is presented. Conversely, the results serve to reinforce the notion that theta oscillations are highly stimulus-dependent, but also suggest the necessity of further investigations into network dynamics between cortical and subcortical brain regions to further elucidate the potential involvement of anticipatory theta states for multisensory encoding. Thus, this dissertation demonstrates that the encoding of complex, multisensory stimuli into episodic memory likely begins before the information that needs to be memorized reaches the brain, suggesting that stimulus-evoked oscillations may interact with these anticipatory states in meaningful ways. Moreover, the present work underscores the value of iterative modifications of experimental paradigms, leading to cumulative insights. I believe that neurocognitive research has only scratched the surface in the potential use of non-invasive neuromodulation, as it became evident that future studies will need to divert attention to better understand the way it affects oscillatory activity in the brain. Despite its limitations, the present findings may contribute to our understanding of the underpinnings of episodic memory, and potentially to new ways of treating the decline of memory functionality in the future.

2 List of abbreviations

ACC	Anterior cingulate cortex
AD	Alzheimer’s disease
ADHD	attention deficit hyperactivity disorder
CA1	Cornu ammonis 1
CLS	Complementary Learning Systems
EC	Entorhinal cortex
EEG	Electroencephalography
ERP	Event-related potential
ICA	Independent Component Analysis
iEEG	intracranial Electroencephalography
LEC	Lateral entorhinal cortex
MEC	Medial entorhinal cortex
MEG	Magnetoencephalography
MTL	Medial temporal lobe
NE	No entrainment (fourth group in the between-subjects design of Study 2)
RT	Response time
SME	Subsequent Memory Effect
SSVEP	Steady-state visually evoked potential
TMS	Transcranial Magnetic Stimulation
wPLI	weighted Phase Lag Index

3 References

Addante, R. J., de Chastelaine, M., & Rugg, M. D. (2015). Pre-stimulus neural activity predicts successful encoding of inter-item associations. *NeuroImage*, *105*, 21–31. https://doi.org/10.1016/j.neuroimage.2014.10.046

Addante, R. J., Watrous, A. J., Yonelinas, A. P., Ekstrom, A. D., & Ranganath, C. (2011). Prestimulus theta activity predicts correct source memory retrieval. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(26), 10702–10707. https://doi.org/10.1073/pnas.1014528108

Albouy, P., Weiss, A., Baillet, S., & Zatorre, R. J. (2017). Selective Entrainment of Theta Oscillations in the Dorsal Stream Causally Enhances Auditory Working Memory Performance. *Neuron*, *94*(1), 193-206.e5. https://doi.org/10.1016/j.neuron.2017.03.015

Alvarez, P., & Squire, L. R. (1994). Memory consolidation and the medial temporal lobe: A simple network model. *Proceedings of the National Academy of Sciences*, *91*(15), 7041–7045. https://doi.org/10.1073/pnas.91.15.7041

Aminoff, E. M., Gronau, N., & Bar, M. (2007). The Parahippocampal Cortex Mediates Spatial and Nonspatial Associations. *Cerebral Cortex*, *17*(7), 1493–1503. https://doi.org/10.1093/cercor/bhl078

Aminoff, E. M., Kveraga, K., & Bar, M. (2013). The role of the parahippocampal cortex in cognition. *Trends in Cognitive Sciences*, *17*(8), 379–390. https://doi.org/10.1016/j.tics.2013.06.009

Andersen, P. (2007). *The Hippocampus Book*. Oxford University Press, USA.

Baddeley, A., Aggleton, J., & Conway, M. (Eds.). (2002). *Episodic Memory: New Directions in Research*. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198508809.001.0001

Başar, E., & Güntekin, B. (2013). Review of delta, theta, alpha, beta, and gamma response oscillations in neuropsychiatric disorders. In *Supplements to Clinical Neurophysiology* (Vol. 62, pp. 303–341). Elsevier. https://doi.org/10.1016/B978-0-7020-5307-8.00019-3

Battistoni, E., Stein, T., & Peelen, M. V. (2017). Preparatory attention in visual cortex. *Annals of the New York Academy of Sciences*, *1396*(1), 92–107. https://doi.org/10.1111/nyas.13320

Becher, A.-K., Höhne, M., Axmacher, N., Chaieb, L., Elger, C. E., & Fell, J. (2015). Intracranial electroencephalography power and phase synchronization changes during monaural and binaural beat stimulation. *European Journal of Neuroscience*, *41*(2), 254–263. https://doi.org/10.1111/ejn.12760

Beese, C., Meyer, L., Vassileiou, B., & Friederici, A. D. (2017). Temporally and spatially distinct theta oscillations dissociate a language-specific from a domain-general processing mechanism across the age trajectory. *Scientific Reports*, *7*(1), 11202. https://doi.org/10.1038/s41598-017-11632-z

Bellhouse-King, M. W., & Standing, L. G. (2007). Recognition Memory for Concrete, Regular Abstract, and Diverse Abstract Pictures. *Perceptual and Motor Skills*, *104*(3), 758–762. https://doi.org/10.2466/pms.104.3.758-762

Bengson, J. J., Kelley, T. A., Zhang, X., Wang, J. L., & Mangun, G. R. (2014). Spontaneous Neural Fluctuations Predict Decisions to Attend. *Journal of Cognitive Neuroscience*, *26*(11), 2578–2584. https://doi.org/10.1162/JOCN_A_00650

Bergström, Z. M., Henson, R. N., Taylor, J. R., & Simons, J. S. (2013). Multimodal imaging reveals the spatiotemporal dynamics of recollection. *NeuroImage*, *68*, 141–153. https://doi.org/10.1016/j.neuroimage.2012.11.030

Biondi, A., Santoro, V., Viana, P. F., Laiou, P., Pal, D. K., Bruno, E., & Richardson, M. P. (2022). Noninvasive mobile EEG as a tool for seizure monitoring and management: A systematic review. *Epilepsia*, *63*(5), 1041–1063. https://doi.org/10.1111/epi.17220

Bizley, J. K., & King, A. J. (2008). Visual–auditory spatial processing in auditory cortical neurons. *Brain Research*, *1242*, 24–36. https://doi.org/10.1016/j.brainres.2008.02.087

Bonnefond, M., & Jensen, O. (2013). The role of gamma and alpha oscillations for blocking out distraction. *Communicative and Integrative Biology*, *6*(1). https://doi.org/10.4161/cib.22702

Born, R. T., & Bradley, D. C. (2005). STRUCTURE AND FUNCTION OF VISUAL AREA MT. *Annual Review of Neuroscience*, *28*(Volume 28, 2005), 157–189. https://doi.org/10.1146/annurev.neuro.26.041002.131052

Brincat, S. L., Siegel, M., von Nicolai, C., & Miller, E. K. (2018). Gradual progression from sensory to task-related processing in cerebral cortex. *Proceedings of the National Academy of Sciences*, *115*(30), E7202–E7211. https://doi.org/10.1073/pnas.1717075115

Britz, J., & Michel, C. M. (2011). State-Dependent Visual Processing. *Frontiers in Psychology*, *2*. https://doi.org/10.3389/fpsyg.2011.00370

Buidze, T., Sommer, T., Zhao, K., Fu, X., & Gläscher, J. (2025). Expectation violations signal goals in novel human communication. *Nature Communications*, *16*(1), 1989. https://doi.org/10.1038/s41467-025-57025-z

Bussey, T. J., Saksida, L. M., & Murray, E. A. (2005). The Perceptual-Mnemonic/Feature Conjunction Model of Perirhinal Cortex Function. *The Quarterly Journal of Experimental Psychology Section B*, *58*(3–4b), 269–282. https://doi.org/10.1080/02724990544000004

Buzsáki, G. (2005). Theta rhythm of navigation: Link between path integration and landmark navigation, episodic and semantic memory. *Hippocampus*, *15*(7), 827–840. https://doi.org/10.1002/hipo.20113

Buzsaki, G. (2011). *Rhythms of the Brain*. Oxford University Press.

Buzsáki, G., & Moser, E. I. (2013). Memory, navigation and theta rhythm in the hippocampal-entorhinal system. *Nature Neuroscience 2013 16:2*, *16*(2), 130–138. https://doi.org/10.1038/nn.3304

Cabeza, R., Albert, M., Belleville, S., Craik, F. I. M., Duarte, A., Grady, C. L., Lindenberger, U., Nyberg, L., Park, D. C., Reuter-Lorenz, P. A., Rugg, M. D., Steffener, J., & Rajah, M. N. (2018). Maintenance, reserve and compensation: The cognitive neuroscience of healthy ageing. *Nature Reviews Neuroscience*, *19*(11), 701–710. https://doi.org/10.1038/s41583-018-0068-2

Cantero, J. L., Atienza, M., Stickgold, R., Kahana, M. J., Madsen, J. R., & Kocsis, B. (2003). Sleep-Dependent θ Oscillations in the Human Hippocampus and Neocortex. *Journal of Neuroscience*, *23*(34), 10897–10903. https://doi.org/10.1523/JNEUROSCI.23-34-10897.2003

Capilla, A., Pazo-Alvarez, P., Darriba, A., Campo, P., & Gross, J. (2011). Steady-State Visual Evoked Potentials Can Be Explained by Temporal Superposition of Transient Event-Related Responses. *PLOS ONE*, *6*(1), e14543. https://doi.org/10.1371/journal.pone.0014543

Caravaglios, G., Castro, G., Costanzo, E., Di Maria, G., Mancuso, D., & Muscoso, E. G. (2010). Theta power responses in mild Alzheimer's disease during an auditory oddball paradigm: Lack of theta enhancement during stimulus processing. *Journal of Neural Transmission*, *117*(10), 1195–1208. https://doi.org/10.1007/s00702-010-0488-2

Chan, D., Suk, H.-J., Jackson, B., Milman, N. P., Stark, D., Beach, S. D., & Tsai, L.-H. (2021). Induction of specific brain oscillations may restore neural circuits and be used for the treatment of Alzheimer's disease. *Journal of Internal Medicine*, *290*(5), 993–1009. https://doi.org/10.1111/joim.13329

Clouter, A., Shapiro, K. L., & Hanslmayr, S. (2017). Theta Phase Synchronization Is the Glue that Binds Human Associative Memory. *Current Biology*, *27*(20), 3143-3148.e6. https://doi.org/10.1016/j.cub.2017.09.001

Colgin, L. L. (2013). Mechanisms and Functions of Theta Rhythms. *Annual Review of Neuroscience*, *36*(Volume 36, 2013), 295–312. https://doi.org/10.1146/annurev-neuro-062012-170330

Cooper, R. A., & Ritchey, M. (2020). Progression from Feature-Specific Brain Activity to Hippocampal Binding during Episodic Encoding. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *40*(8), 1701–1709. https://doi.org/10.1523/JNEUROSCI.1971-19.2019

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*(3), 201–215. https://doi.org/10.1038/nrn755

Coste, C. P., Sadaghiani, S., Friston, K. J., & Kleinschmidt, A. (2011). Ongoing Brain Activity Fluctuations Directly Account for Intertrial and Indirectly for Intersubject Variability in Stroop Task Performance. *Cerebral Cortex*, *21*(11), 2612–2619. https://doi.org/10.1093/cercor/bhr050

da Silva, F. L. (1992). The Rhythmic Slow Activity (Theta) of the Limbic Cortex: An Oscillation in Search of a Function. In E. Başar & T. H. Bullock (Eds.), *Induced Rhythms in the Brain* (pp. 83–102). Birkhäuser. https://doi.org/10.1007/978-1-4757-1281-0_4

Danieli, K., Guyon, A., & Bethus, I. (2023). Episodic Memory formation: A review of complex Hippocampus input pathways. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, *126*, 110757. https://doi.org/10.1016/j.pnpbp.2023.110757

Deshmukh, S. S., Johnson, J. L., & Knierim, J. J. (2012). Perirhinal cortex represents nonspatial, but not spatial, information in rats foraging in the presence of objects: Comparison with lateral entorhinal cortex. *Hippocampus*, *22*(10), 2045–2058. https://doi.org/10.1002/hipo.22046

Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2007). Imaging recollection and familiarity in the medial temporal lobe: A three-component model. *Trends in Cognitive Sciences*, *11*(9), 379–386. https://doi.org/10.1016/j.tics.2007.08.001

Doege, K., Jansen, M., Mallikarjun, P., Liddle, E. B., & Liddle, P. F. (2010). How much does phase resetting contribute to event-related EEG abnormalities in schizophrenia? *Neuroscience Letters*, *481*(1), 1–5. https://doi.org/10.1016/j.neulet.2010.06.008

Dostrovsky, J. O., & Lozano, A. M. (2002). Mechanisms of deep brain stimulation. *Movement Disorders*, *17*(S3), S63–S68. https://doi.org/10.1002/mds.10143

Ebbinghaus, H. (1948). Concerning memory, 1885. In *Readings in the history of psychology* (pp. 304–313). Appleton-Century-Crofts. https://doi.org/10.1037/11304-034

Eichenbaum, H. (1997). How Does the Brain Organize Memories? *Science*, *277*(5324), 330–332. https://doi.org/10.1126/science.277.5324.330

Eichenbaum, H., Yonelinas, A. P., & Ranganath, C. (2007). The Medial Temporal Lobe and Recognition Memory. *Annual Review of Neuroscience*, *30*(Volume 30, 2007), 123–152. https://doi.org/10.1146/annurev.neuro.30.051606.094328

Ekstrom, A. D., Caplan, J. B., Ho, E., Shattuck, K., Fried, I., & Kahana, M. J. (2005). Human hippocampal theta activity during virtual navigation. *Hippocampus*, *15*(7), 881–889. https://doi.org/10.1002/HIPO.20109

Ergenoglu, T., Demiralp, T., Bayraktaroglu, Z., Ergen, M., Beydagi, H., & Uresin, Y. (2004). Alpha rhythm of the EEG modulates visual detection performance in humans. *Cognitive Brain Research*, *20*(3), 376–383. https://doi.org/10.1016/j.cogbrainres.2004.03.009

Fell, J., Ludowig, E., Staresina, B. P., Wagner, T., Kranz, T., Elger, C. E., & Axmacher, N. (2011). Medial temporal theta/alpha power enhancement precedes successful memory encoding: Evidence based on intracranial EEG. *Journal of Neuroscience*, *31*(14), 5392–5397. https://doi.org/10.1523/JNEUROSCI.3668-10.2011

Fellner, M.-C., Bäuml, K.-H. T., & Hanslmayr, S. (2013). Brain oscillatory subsequent memory effects differ in power and long-range synchronization between semantic and survival processing. *NeuroImage*, *79*, 361–370. https://doi.org/10.1016/j.neuroimage.2013.04.121

Feng, T., Silva, D., Foster, D. J., & Snyder, S. H. (2015). Dissociation between the Experience-Dependent Development of Hippocampal Theta Sequences and Single-Trial Phase Precession. *Journal of Neuroscience*, *35*(12), 4890–4902. https://doi.org/10.1523/JNEUROSCI.2614-14.2015

Fetz, E. E. (2013). Volitional Control of Cortical Oscillations and Synchrony. *Neuron*, *77*(2), 216–218. https://doi.org/10.1016/j.neuron.2013.01.003

Foxe, J. J., & Snyder, A. C. (2011). The Role of Alpha-Band Brain Oscillations as a Sensory Suppression Mechanism during Selective Attention. *Frontiers in Psychology*, *2*. https://doi.org/10.3389/fpsyg.2011.00154

Frackowiak, R. S. J. (2004). *Human brain function* (2nd ed). Elsevier Academic Press.

Friese, U., Daume, J., Göschl, F., König, P., Wang, P., & Engel, A. K. (2016). Oscillatory brain activity during multisensory attention reflects activation, disinhibition, and cognitive control. *Scientific Reports*, *6*(1), 32775. https://doi.org/10.1038/srep32775

Gao, X., Wang, Y., Chen, X., & Gao, S. (2021). Interface, interaction, and intelligence in generalized brain–computer interfaces. *Trends in Cognitive Sciences*, *25*(8), 671–684. https://doi.org/10.1016/j.tics.2021.04.003

Giocomo, L. M., Moser, M.-B., & Moser, E. I. (2011). Computational Models of Grid Cells. *Neuron*, *71*(4), 589–603. https://doi.org/10.1016/j.neuron.2011.07.023

Gorbach, T., Pudas, S., Lundquist, A., Orädd, G., Josefsson, M., Salami, A., de Luna, X., & Nyberg, L. (2017). Longitudinal association between hippocampus atrophy and episodic-memory decline. *Neurobiology of Aging*, *51*, 167–176. https://doi.org/10.1016/j.neurobiolaging.2016.12.002

Gregorio, F. D., Trajkovic, J., Roperti, C., Marcantoni, E., Luzio, P. D., Avenanti, A., Thut, G., & Romei, V. (2022). Tuning alpha rhythms to shape conscious visual perception. *Current Biology*, *32*(5), 988-998.e6. https://doi.org/10.1016/j.cub.2022.01.003

Griffiths, B. J., Martín-Buro, M. C., Staresina, B. P., & Hanslmayr, S. (2021). Disentangling neocortical alpha/beta and hippocampal theta/gamma oscillations in human episodic memory formation. *NeuroImage*, *242*, 118454. https://doi.org/10.1016/j.neuroimage.2021.118454

Griffiths, B. J., Martín-Buro, M. C., Staresina, B. P., Hanslmayr, S., & Staudigl, T. (2021). Alpha/beta power decreases during episodic memory formation predict the magnitude of alpha/beta power decreases during subsequent retrieval. *Neuropsychologia*, *153*, 107755. https://doi.org/10.1016/j.neuropsychologia.2021.107755

Groom, M. J., Cahill, J. D., Bates, A. T., Jackson, G. M., Calton, T. G., Liddle, P. F., & Hollis, C. (2010). Electrophysiological indices of abnormal error-processing in adolescents with attention deficit hyperactivity disorder (ADHD). *Journal of Child Psychology and Psychiatry*, *51*(1), 66–76. https://doi.org/10.1111/j.1469-7610.2009.02128.x

Gruber, M. J., & Otten, L. J. (2010). Voluntary control over prestimulus activity related to encoding. *Journal of Neuroscience*, *30*(29), 9793–9800. https://doi.org/10.1523/JNEUROSCI.0915-10.2010

Gruber, M. J., Watrous, A. J., Ekstrom, A. D., Ranganath, C., & Otten, L. J. (2013). Expected reward modulates encoding-related theta activity before an event. *NeuroImage*, *64*(1), 68–74. https://doi.org/10.1016/j.neuroimage.2012.07.064

Gruber, T., Keil, A., & Müller, M. M. (2001). Modulation of induced gamma band responses and phase synchrony in a paired associate learning task in the human EEG. *Neuroscience Letters*, *316*(1), 29–32. https://doi.org/10.1016/S0304-3940(01)02361-8

Guderian, S., & Düzel, E. (2005). Induced theta oscillations mediate large-scale synchrony with mediotemporal areas during recollection in humans. *Hippocampus*, *15*(7), 901–912. https://doi.org/10.1002/HIPO.20125

Guderian, S., Schott, B. H., Richardson-Klavehn, A., & Düzel, E. (2009). Medial temporal theta state before an event predicts episodic encoding success in humans. *Proceedings of the National Academy of Sciences*, *106*(13), 5365–5370. https://doi.org/10.1073/PNAS.0900289106

Haegens, S., Cousijn, H., Wallis, G., Harrison, P. J., & Nobre, A. C. (2014). Inter- and intra-individual variability in alpha peak frequency. *NeuroImage*, *92*, 46–55. https://doi.org/10.1016/j.neuroimage.2014.01.049

Hanslmayr, S., Aslan, A., Staudigl, T., Klimesch, W., Herrmann, C. S., & Bäuml, K.-H. (2007). Prestimulus oscillations predict visual perception performance between and within subjects. *NeuroImage*, *37*(4), 1465–1473. https://doi.org/10.1016/j.neuroimage.2007.07.011

Hanslmayr, S., Axmacher, N., & Inman, C. S. (2019). Modulating Human Memory via Entrainment of Brain Oscillations. *Trends in Neurosciences*, *42*(7), 485–499. https://doi.org/10.1016/j.tins.2019.04.004

Hanslmayr, S., Gross, J., Klimesch, W., & Shapiro, K. L. (2011). The role of alpha oscillations in temporal attention. *Brain Research Reviews*, *67*(1), 331–343. https://doi.org/10.1016/j.brainresrev.2011.04.002

Hanslmayr, S., Klimesch, W., Sauseng, P., Gruber, W., Doppelmayr, M., Freunberger, R., & Pecherstorfer, T. (2005). Visual discrimination performance is related to decreased alpha amplitude but increased phase locking. *Neuroscience Letters*, *375*(1), 64–68. https://doi.org/10.1016/j.neulet.2004.10.092

Hanslmayr, S., Spitzer, B., & Bäuml, K. H. (2009). Brain oscillations dissociate between semantic and nonsemantic encoding of episodic memories. *Cerebral Cortex*, *19*(7), 1631–1640. https://doi.org/10.1093/cercor/bhn197

Hanslmayr, S., Staresina, B. P., & Bowman, H. (2016). Oscillations and Episodic Memory: Addressing the Synchronization/Desynchronization Conundrum. *Trends in Neurosciences*, *39*(1), 16–25. https://doi.org/10.1016/j.tins.2015.11.004

Hanslmayr, S., & Staudigl, T. (2014). How brain oscillations form memories—A processing based perspective on oscillatory subsequent memory effects. *NeuroImage*, *85*, 648–655. https://doi.org/10.1016/j.neuroimage.2013.05.121

Hanslmayr, S., Staudigl, T., & Fellner, M. C. (2012). Oscillatory power decreases and long-term memory: The information via desynchronization hypothesis. *Frontiers in Human Neuroscience*, *6*, 1–20. https://doi.org/10.3389/fnhum.2012.00074

Hanslmayr, S., Volberg, G., Wimber, M., Raabe, M., Greenlee, M. W., & Bäuml, K. H. T. (2011). The relationship between brain oscillations and BOLD signal during memory formation: A combined EEG-fMRI study. *Journal of Neuroscience*, *31*(44), 15674–15680. https://doi.org/10.1523/JNEUROSCI.3140-11.2011

Haskins, A. L., Yonelinas, A. P., Quamme, J. R., & Ranganath, C. (2008). Perirhinal Cortex Supports Encoding and Familiarity-Based Recognition of Novel Associations. *Neuron*, *59*(4), 554–560. https://doi.org/10.1016/j.neuron.2008.07.035

Haslam, C., Jetten, J., Haslam, S. A., Pugliese, C., & Tonks, J. (2011). 'I remember therefore I am, and I am therefore I remember': Exploring the contributions of episodic and semantic self-knowledge to strength of identity. *British Journal of Psychology*, *102*(2), 184–203. https://doi.org/10.1348/000712610X508091

Hasselmo, M. E. (2012). *How we remember: Brain mechanisms of episodic memory*. MIT Press.

Hermiller, M. S., VanHaerents, S., Raij, T., & Voss, J. L. (2019). Frequency-specific noninvasive modulation of memory retrieval and its relationship with hippocampal network connectivity. *Hippocampus*, *29*(7), 595–609. https://doi.org/10.1002/HIPO.23054

Herrmann, C. S., Strüber, D., Helfrich, R. F., & Engel, A. K. (2016). EEG oscillations: From correlation to causality. *International Journal of Psychophysiology*, *103*, 12–21. https://doi.org/10.1016/j.ijpsycho.2015.02.003

Herweg, N. A., Apitz, T., Leicht, G., Mulert, C., Fuentemilla, L., & Bunzeck, N. (2016). Theta-alpha oscillations bind the hippocampus, prefrontal cortex, and striatum during recollection: Evidence from simultaneous EEG–fMRI. *Journal of Neuroscience*, *36*(12), 3579–3587. https://doi.org/10.1523/JNEUROSCI.3629-15.2016

Herweg, N. A., Solomon, E. A., & Kahana, M. J. (2020). Theta Oscillations in Human Memory. *Trends in Cognitive Sciences*, *24*(3), 208–227. https://doi.org/10.1016/j.tics.2019.12.006

Hirano, Y., & Uhlhaas, P. J. (2021). Current findings and perspectives on aberrant neural oscillations in schizophrenia. *Psychiatry and Clinical Neurosciences*, *75*(12), 358–368. https://doi.org/10.1111/pcn.13300

Holleman, E., & Battaglia, F. P. (2015). Memory Consolidation, Replay, and Cortico-Hippocampal Interactions. In M. Tatsuno (Ed.), *Analysis and Modeling of Coordinated Multi-neuronal Activity* (pp. 207–221). Springer. https://doi.org/10.1007/978-1-4939-1969-7_10

Hoppstädter, M., Baeuchl, C., Diener, C., Flor, H., & Meyer, P. (2015). Simultaneous EEG–fMRI reveals brain networks underlying recognition memory ERP old/new effects. *NeuroImage*, *116*, 112–122. https://doi.org/10.1016/j.neuroimage.2015.05.026

Hornstein, S. L., & Mulligan, N. W. (2001). Memory of Action Events: The Role of Objects in Memory of Self- and Other-Performed Tasks. *The American Journal of Psychology*, *114*(2), 199–217. https://doi.org/10.2307/1423515

Hsieh, L. T., & Ranganath, C. (2014). Frontal midline theta oscillations during working memory maintenance and episodic encoding and retrieval. *NeuroImage*, *85*, 721–729. https://doi.org/10.1016/j.neuroimage.2013.08.003

Hummel, F., Andres, F., Altenmüller, E., Dichgans, J., & Gerloff, C. (2002). Inhibitory control of acquired motor programmes in the human brain. *Brain*, *125*(2), 404–420. https://doi.org/10.1093/brain/awf030

Iaccarino, H. F., Singer, A. C., Martorell, A. J., Rudenko, A., Gao, F., Gillingham, T. Z., Mathys, H., Seo, J., Kritskiy, O., Abdurrob, F., Adaikkan, C., Canter, R. G., Rueda, R., Brown, E. N., Boyden, E. S., & Tsai, L.-H. (2016). Gamma frequency entrainment attenuates amyloid load and modifies microglia. *Nature*, *540*(7632), 230–235. https://doi.org/10.1038/nature20587

Irmiš, F., Lát, J., & Radil-Weiss, T. (1971). Individual differences in hippocampal EEG during rhombencephalic sleep and arousal. *Physiology & Behavior*, *7*(1), 117–119. https://doi.org/10.1016/0031-9384(71)90243-5

Janssens, S. E. W., Sack, A. T., Ten Oever, S., & de Graaf, T. A. (2022). Calibrating rhythmic stimulation parameters to individual electroencephalography markers: The consistency of individual alpha frequency in practical lab settings. *European Journal of Neuroscience*, *55*(11–12), 3418–3437. https://doi.org/10.1111/ejn.15418

Jaramillo, J., & Kempter, R. (2017). Phase precession: A neural code underlying episodic memory? *Current Opinion in Neurobiology*, *43*, 130–138. https://doi.org/10.1016/J.CONB.2017.02.006

Jensen, O., Gelfand, J., Kounios, J., & Lisman, J. E. (2002). Oscillations in the Alpha Band (9–12 Hz) Increase with Memory Load during Retention in a Short-term Memory Task. *Cerebral Cortex*, *12*(8), 877–882. https://doi.org/10.1093/cercor/12.8.877

Jensen, O., & Mazaheri, A. (2010). Shaping Functional Architecture by Oscillatory Alpha Activity: Gating by Inhibition. *Frontiers in Human Neuroscience*, *4*. https://doi.org/10.3389/fnhum.2010.00186

Jung, R., & Kornmüller, A. E. (1938). Eine Methodik der Ableitung lokalisierter Potentialschwankungen aus subcorticalen Hirngebieten. *Archiv für Psychiatrie und Nervenkrankheiten*, *109*(1), 1–30. https://doi.org/10.1007/BF02157817

Kadwe, P. P., Sklenar, A. M., Frankenstein, A. N., Levy, P. U., & Leshikar, E. D. (2022). The influence of memory on approach and avoidance decisions: Investigating the role of episodic memory in social decision making. *Cognition*, *225*, 105072. https://doi.org/10.1016/j.cognition.2022.105072

Kahana, M. J., Sekuler, R., Caplan, J. B., Kirschen, M., & Madsen, J. R. (1999). Human theta oscillations exhibit task dependence during virtual maze navigation. *Nature*, *399*(6738), 781–784. https://doi.org/10.1038/21645

Kaplan, R., Doeller, C. F., Barnes, G. R., Litvak, V., Düzel, E., Bandettini, P. A., & Burgess, N. (2012). Movement-Related Theta Rhythm in Humans: Coordinating Self-Directed Hippocampal Learning. *PLOS Biology*, *10*(2), e1001267. https://doi.org/10.1371/journal.pbio.1001267

Kawasaki, M., Yamada, Y., Ushiku, Y., Miyauchi, E., & Yamaguchi, Y. (2013). Inter-brain synchronization during coordination of speech rhythm in human-to-human social interaction. *Scientific Reports*, *3*(1), 1692. https://doi.org/10.1038/srep01692

Keitel, C., Quigley, C., & Ruhnau, P. (2014). Stimulus-Driven Brain Oscillations in the Alpha Range: Entrainment of Intrinsic Rhythms or Frequency-Following Response? *Journal of Neuroscience*, *34*(31), 10137–10140. https://doi.org/10.1523/JNEUROSCI.1904-14.2014

Khader, P. H., Jost, K., Ranganath, C., & Rösler, F. (2010). Theta and alpha oscillations during working-memory maintenance predict successful long-term memory encoding. *Neuroscience Letters*, *468*(3), 339–343. https://doi.org/10.1016/J.NEULET.2009.11.028

Kinreich, S., Djalovski, A., Kraus, L., Louzoun, Y., & Feldman, R. (2017). Brain-to-Brain Synchrony during Naturalistic Social Interactions. *Scientific Reports*, *7*(1), 17060. https://doi.org/10.1038/s41598-017-17339-5

Klein, C., Diaz Hernandez, L., Koenig, T., Kottlow, M., Elmer, S., & Jäncke, L. (2016). The Influence of Pre-stimulus EEG Activity on Reaction Time During a Verbal Sternberg Task is Related to Musical Expertise. *Brain Topography*, *29*(1), 67–81. https://doi.org/10.1007/s10548-015-0433-7

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Sciences*, *16*(12), 606–617. https://doi.org/10.1016/j.tics.2012.10.007

Klimesch, W., Doppelmayr, M., Schimke, H., & Ripper, B. (1997). Theta synchronization and alpha desynchronization in a memory task. *Psychophysiology*, *34*(2), 169–176. https://doi.org/10.1111/j.1469-8986.1997.tb02128.x

Klimesch, W., Fellinger, R., & Freunberger, R. (2011). Alpha oscillations and early stages of visual encoding. *Frontiers in Psychology*, *2*(118). https://doi.org/10.3389/fpsyg.2011.00118

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition–timing hypothesis. *Brain Research Reviews*, *53*(1), 63–88. https://doi.org/10.1016/j.brainresrev.2006.06.003

Klimesch, W., Schack, B., & Sauseng, P. (2006). The Functional Significance of Theta and Upper Alpha Oscillations. *Experimental Psychology*. https://econtent.hogrefe.com/doi/10.1027/1618-3169.52.2.99

Knudsen, E. I. (2018). Neural Circuits That Mediate Selective Attention: A Comparative Perspective. *Trends in Neurosciences*, *41*(11), 789–805. https://doi.org/10.1016/j.tins.2018.06.006

Knyazev, G. G. (2007). Motivation, emotion, and their inhibitory control mirrored in brain oscillations. *Neuroscience & Biobehavioral Reviews*, *31*(3), 377–395. https://doi.org/10.1016/j.neubiorev.2006.10.004

Köster, M., Martens, U., & Gruber, T. (2019). Memory entrainment by visually evoked theta-gamma coupling. *NeuroImage*, *188*, 181–187. https://doi.org/10.1016/j.neuroimage.2018.12.002

Kuhn, T. S. (1962). *Structure of Scientific Revolutions*. University of Chicago Press.

Lakatos, P., Gross, J., & Thut, G. (2019). A New Unifying Account of the Roles of Neuronal Entrainment. *Current Biology*, *29*(18), R890–R905. https://doi.org/10.1016/j.cub.2019.07.075

Laxton, A. W., Tang-Wai, D. F., McAndrews, M. P., Zumsteg, D., Wennberg, R., Keren, R., Wherrett, J., Naglie, G., Hamani, C., Smith, G. S., & Lozano, A. M. (2010). A phase I trial of deep brain stimulation of memory circuits in Alzheimer's disease. *Annals of Neurology*, *68*(4), 521–534. https://doi.org/10.1002/ana.22089

Lega, B., Burke, J., Jacobs, J., & Kahana, M. J. (2016). Slow-Theta-to-Gamma Phase–Amplitude Coupling in Human Hippocampus Supports the Formation of New Episodic Memories. *Cerebral Cortex*, *26*(1), 268–278. https://doi.org/10.1093/cercor/bhu232

Lega, B. C., Jacobs, J., & Kahana, M. (2012). Human hippocampal theta oscillations and the formation of episodic memories. *Hippocampus*, *22*(4), 748–761. https://doi.org/10.1002/hipo.20937

Levine, B., Svoboda, E., Hay, J. F., Winocur, G., & Moscovitch, M. (2002). Aging and autobiographical memory: Dissociating episodic from semantic retrieval. *Psychology and Aging*, *17*(4), 677–689. https://doi.org/10.1037/0882-7974.17.4.677

Lozano, A. M., Fosdick, L., Chakravarty, M. M., Leoutsakos, J.-M., Munro, C., Oh, E., Drake, K. E., Lyman, C. H., Rosenberg, P. B., Anderson, W. S., Tang-Wai, D. F., Pendergrass, J. C., Salloway, S., Asaad, W. F., Ponce, F. A., Burke, A., Sabbagh, M., Wolk, D. A., Baltuch, G., … Smith, G. S. (2016). A Phase II Study of Fornix Deep Brain Stimulation in Mild Alzheimer's Disease. *Journal of Alzheimer's Disease*, *54*(2), 777–787. https://doi.org/10.3233/JAD-160017

Luo, W., & Guan, J.-S. (2018). Do Brain Oscillations Orchestrate Memory? *Brain Science Advances*, *4*(1), 16–33. https://doi.org/10.26599/bsa.2018.9050008

Markowitsch, H. J., & Staniloiu, A. (2011). Memory, autonoetic consciousness, and the self. *Consciousness and Cognition*, *20*(1), 16–39. https://doi.org/10.1016/j.concog.2010.09.005

Marr, D. (1971). Simple memory: A theory for archicortex. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *262*(841), 23–81. https://doi.org/10.1098/rstb.1971.0078

Martin, C. B., Hong, B., Newsome, R. N., Savel, K., Meade, M. E., Xia, A., Honey, C. J., & Barense, M. D. (2022). A smartphone intervention that enhances real-world memory and promotes differentiation of hippocampal activity in older adults. *Proceedings of the National Academy of Sciences*, *119*(51), e2214285119. https://doi.org/10.1073/pnas.2214285119

Mathewson, K. E., Gratton, G., Fabiani, M., Beck, D. M., & Ro, T. (2009). To See or Not to See: Prestimulus α Phase Predicts Visual Awareness. *Journal of Neuroscience*, *29*(9), 2725–2732. https://doi.org/10.1523/JNEUROSCI.3963-08.2009

Mathewson, K. E., Prudhomme, C., Fabiani, M., Beck, D. M., Lleras, A., & Gratton, G. (2012). Making Waves in the Stream of Consciousness: Entraining Oscillations in EEG Alpha and Fluctuations in Visual Awareness with Rhythmic Visual Stimulation. *Journal of Cognitive Neuroscience*, *24*(12), 2321–2333. https://doi.org/10.1162/jocn_a_00288

McClelland, J., McNaughton, B., & O'Reilly, R. (1995). Why there are complementary learning systems in the hippocampus and neocortex: Insights from the successes and failures of connectionist models of learning and memory. *Psychological Review*, *102*(3), 419–457. https://doi.org/10.1037/0033-295X.102.3.419

McLain, N. J., Yani, M. S., & Kutch, J. J. (2022). Analytic consistency and neural correlates of peak alpha frequency in the study of pain. *Journal of Neuroscience Methods*, *368*, 109460. https://doi.org/10.1016/j.jneumeth.2021.109460

Meeuwissen, E. B., Takashima, A., Fernández, G., & Jensen, O. (2011). Increase in posterior alpha activity during rehearsal predicts successful long-term memory formation of word sequences. *Human Brain Mapping*, *32*(12), 2045–2053. https://doi.org/10.1002/hbm.21167

Merkow, M. B., Burke, J. F., Stein, J. M., & Kahana, M. J. (2014). Prestimulus theta in the human hippocampus predicts subsequent recognition but not recall. *Hippocampus*, *24*(12), 1562–1569. https://doi.org/10.1002/HIPO.22335

Michael, E., Covarrubias, L. S., Leong, V., & Kourtzi, Z. (2022). Learning at your brain's rhythm: Individualized entrainment boosts learning for perceptual decisions. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhac426

Miller, K. J., Sorensen, L. B., Ojemann, J. G., & Nijs, M. den. (2009). Power-Law Scaling in the Brain Surface Electric Potential. *PLOS Computational Biology*, *5*(12), e1000609. https://doi.org/10.1371/journal.pcbi.1000609

Minarik, T., Berger, B., & Sauseng, P. (2018). The involvement of alpha oscillations in voluntary attention directed towards encoding episodic memories. *NeuroImage*, *166*, 307–316. https://doi.org/10.1016/j.neuroimage.2017.10.064

Murdock, B. B. (1985). The contributions of Hermann Ebbinghaus. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *11*(3), 469–471. https://doi.org/10.1037/0278-7393.11.3.469

Nadel, L., & Moscovitch, M. (1997). Memory consolidation, retrograde amnesia and the hippocampal complex. *Current Opinion in Neurobiology*, *7*(2), 217–227. https://doi.org/10.1016/S0959-4388(97)80010-4

Nelli, S., Malpani, A., Boonjindasup, M., & Serences, J. T. (2021). Individual Alpha Frequency Determines the Impact of Bottom-Up Drive on Visual Processing. *Cerebral Cortex Communications*, *2*(2), tgab032. https://doi.org/10.1093/texcom/tgab032

Nichols, S. (2014). The Episodic Sense of Self. In J. D'Arms & D. Jacobson (Eds.), *Moral Psychology and Human Agency: Philosophical Essays on the Science of Ethics* (p. 0). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198717812.003.0007

Norman, K. A. (2010). How hippocampus and cortex contribute to recognition memory: Revisiting the complementary learning systems model. *Hippocampus*, *20*(11), 1217–1227. https://doi.org/10.1002/hipo.20855

Notbohm, A., & Herrmann, C. S. (2016). Flicker Regularity Is Crucial for Entrainment of Alpha Oscillations. *Frontiers in Human Neuroscience*, *10*. https://www.frontiersin.org/articles/10.3389/fnhum.2016.00503

Notbohm, A., Kurths, J., & Herrmann, C. S. (2016). Modification of Brain Oscillations via Rhythmic Light Stimulation Provides Evidence for Entrainment but Not for Superposition of Event-Related Responses. *Frontiers in Human Neuroscience*, *10*. https://www.frontiersin.org/articles/10.3389/fnhum.2016.00010

Nyhus, E., & Curran, T. (2010). Functional role of gamma and theta oscillations in episodic memory. *Neuroscience & Biobehavioral Reviews*, *34*(7), 1023–1035. https://doi.org/10.1016/J.NEUBIOREV.2009.12.014

Oberauer, K., & Bartsch, L. M. (2023). When Does Episodic Memory Contribute to Performance in Tests of Working Memory? *Journal of Cognition*, *6*(1). https://doi.org/10.5334/joc.311

O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Research*, *34*(1), 171–175. https://doi.org/10.1016/0006-8993(71)90358-1

O'Keefe, J., & Recce, M. L. (1993). Phase relationship between hippocampal place units and the EEG theta rhythm. *Hippocampus*, *3*(3), 317–330. https://doi.org/10.1002/HIPO.450030307

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. (2011). FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. *Computational Intelligence and Neuroscience*. https://doi.org/10.1155/2011/156869

O'Reilly, R. C., Bhattacharyya, R., Howard, M. D., & Ketz, N. (2014). Complementary Learning Systems. *Cognitive Science*, *38*(6), 1229–1248. https://doi.org/10.1111/j.1551-6709.2011.01214.x

Osipova, D., Takashima, A., Oostenveld, R., Fernández, G., Maris, E., & Jensen, O. (2006). Theta and gamma oscillations predict encoding and retrieval of declarative memory. *Journal of Neuroscience*, *26*(28), 7523–7531. https://doi.org/10.1523/JNEUROSCI.1948-06.2006

Otten, L. J., Quayle, A. H., Akram, S., Ditewig, T. A., & Rugg, M. D. (2006). Brain activity before an event predicts later recollection. *Nature Neuroscience*, *9*(4), 489–491. https://doi.org/10.1038/nn1663

Pariz, A., Fischer, I., Valizadeh, A., & Mirasso, C. (2021). Transmission delays and frequency detuning can regulate information flow between brain regions. *PLOS Computational Biology*, *17*(4), e1008129. https://doi.org/10.1371/journal.pcbi.1008129

Park, H., Lee, D. S., Kang, E., Kang, H., Hahm, J., Kim, J. S., Chung, C. K., & Jensen, O. (2014). Blocking of irrelevant memories by posterior alpha activity boosts memory encoding. *Human Brain Mapping*, *35*(8), 3972–3987. https://doi.org/10.1002/hbm.22452

Park, H., & Rugg, M. D. (2010). Prestimulus hippocampal activity predicts later recollection. *Hippocampus*, *20*(1), 24–28. https://doi.org/10.1002/hipo.20663

Pastore, R. E., & Scheirer, C. J. (1974). Signal detection theory: Considerations for general application. *Psychological Bulletin*, *81*(12), 945–958. https://doi.org/10.1037/h0037357

Payne, L., Guillory, S., & Sekuler, R. (2013). Attention-modulated alpha-band oscillations protect against intrusion of irrelevant information. *Journal of Cognitive Neuroscience*, *25*(9), 1463–1476. https://doi.org/10.1162/jocn_a_00395

Pikovsky, A., Rosenblum, M., & Kurths, J. (2003). Synchronization: A Universal Concept in Nonlinear Sciences. *Synchronization, by Arkady Pikovsky and Michael Rosenblum and Jürgen Kurths, Pp. 432. ISBN 052153352X. Cambridge, UK: Cambridge University Press, May 2003.*, *2*. https://doi.org/10.4249/scholarpedia.1459

Piolino, P., Desgranges, B., & Eustache, F. (2009). Episodic autobiographical memories over the course of time: Cognitive, neuropsychological and neuroimaging findings. *Neuropsychologia*, *47*(11), 2314–2329. https://doi.org/10.1016/j.neuropsychologia.2009.01.020

Pion-Tonachini, L., Kreutz-Delgado, K., & Makeig, S. (2019). ICLabel: An automated electroencephalographic independent component classifier, dataset, and website. *NeuroImage*, *198*, 181–197. https://doi.org/10.1016/j.neuroimage.2019.05.026

Preston, A. R., & Eichenbaum, H. (2013). Interplay of Hippocampus and Prefrontal Cortex in Memory. *Current Biology*, *23*(17), R764–R773. https://doi.org/10.1016/j.cub.2013.05.041

Ranganath, C., & Knight, R. T. (2002). Prefrontal cortex and episodic memory: Integrating findings from neuropsychology and functional brain imaging. In *The Cognitive Neuroscience of Memory* (1st ed.). Psychology Press.

Rauschecker, J. P. (2018). Where, When, and How: Are they all sensorimotor? Towards a unified view of the dorsal pathway in vision and audition. *Cortex*, *98*, 262–268. https://doi.org/10.1016/j.cortex.2017.10.020

Roberts, B. M., Clarke, A., Addante, R. J., & Ranganath, C. (2018). Entrainment enhances theta oscillations and improves episodic memory. *Cognitive Neuroscience*, *9*(3–4), 181–193. https://doi.org/10.1080/17588928.2018.1521386

Roberts, D. M., Fedota, J. R., Buzzell, G. A., Parasuraman, R., & McDonald, C. G. (2014). Prestimulus Oscillations in the Alpha Band of the EEG Are Modulated by the Difficulty of Feature Discrimination and Predict Activation of a Sensory Discrimination Process. *Journal of Cognitive Neuroscience*, *26*(8), 1615–1628. https://doi.org/10.1162/JOCN_A_00569

Robin, J. (2018). Spatial scaffold effects in event memory and imagination. *WIREs Cognitive Science*, *9*(4), e1462. https://doi.org/10.1002/wcs.1462

Romei, V., Bauer, M., Brooks, J. L., Economides, M., Penny, W., Thut, G., Driver, J., & Bestmann, S. (2016). Causal evidence that intrinsic beta-frequency is relevant for enhanced signal propagation in the motor system as shown through rhythmic TMS. *NeuroImage*, *126*, 120–130. https://doi.org/10.1016/j.neuroimage.2015.11.020

Rowland, D. C., Roudi, Y., Moser, M.-B., & Moser, E. I. (2016). Ten Years of Grid Cells. *Annual Review of Neuroscience*, *39*(Volume 39, 2016), 19–40. https://doi.org/10.1146/annurev-neuro-070815-013824

Rugg, M. D., Otten, L. J., & Henson, R. N. A. (2002). The neural basis of episodic memory: Evidence from functional neuroimaging. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *357*(1424), 1097–1110. https://doi.org/10.1098/rstb.2002.1102

Saalmann, Y. B., Pinsk, M. A., Wang, L., Li, X., & Kastner, S. (2012). The Pulvinar Regulates Information Transmission Between Cortical Areas Based on Attention Demands. *Science*. https://doi.org/10.1126/science.1223082

Sadaghiani, S., & Kleinschmidt, A. (2016). Brain Networks and α-Oscillations: Structural and Functional Foundations of Cognitive Control. *Trends in Cognitive Sciences*, *20*(11), 805–817. https://doi.org/10.1016/j.tics.2016.09.004

Salari, N., Büchel, C., & Rose, M. (2012). Functional Dissociation of Ongoing Oscillatory Brain States. *PLOS ONE*, *7*(5), e38090. https://doi.org/10.1371/JOURNAL.PONE.0038090

Salari, N., Büchel, C., & Rose, M. (2014). Neurofeedback training of gamma band oscillations improves perceptual processing. *Experimental Brain Research*, *232*(10), 3353–3361. https://doi.org/10.1007/s00221-014-4023-9

Sarnthein, J., Petsche, H., Rappelsberger, P., Shaw, G. L., & von Stein, A. (1998). Synchronization between prefrontal and posterior association cortex during human working memory. *Proceedings of the National Academy of Sciences*, *95*(12), 7092–7096. https://doi.org/10.1073/pnas.95.12.7092

Sato, N., & Yamaguchi, Y. (2007). Theta synchronization networks emerge during human object–place memory encoding. *NeuroReport*, *18*(5), 419. https://doi.org/10.1097/WNR.0b013e3280586760

Schlesiger, M. I., Cannova, C. C., Boublil, B. L., Hales, J. B., Mankin, E. A., Brandon, M. P., Leutgeb, J. K., Leibold, C., & Leutgeb, S. (2015). The medial entorhinal cortex is necessary for temporal organization of hippocampal neuronal activity. *Nature Neuroscience*, *18*(8), 1123–1132. https://doi.org/10.1038/nn.4056

Schneider, S. L., & Rose, M. (2016). Intention to encode boosts memory-related pre-stimulus EEG beta power. *NeuroImage*, *125*, 978–987. https://doi.org/10.1016/J.NEUROIMAGE.2015.11.024

Schneidman, E., Puchalla, J. L., Segev, R., Harris, R. A., Bialek, W., & Berry, M. J. (2011). Synergy from Silence in a Combinatorial Neural Code. *Journal of Neuroscience*, *31*(44), 15732–15741. https://doi.org/10.1523/JNEUROSCI.0301-09.2011

Scholz, S., Schneider, S. L., & Rose, M. (2017). Differential effects of ongoing EEG beta and theta power on memory formation. *PLOS ONE*, *12*(2), e0171913. https://doi.org/10.1371/journal.pone.0171913

Schulz, E., Tiemann, L., Schuster, T., Gross, J., & Ploner, M. (2011). Neurophysiological Coding of Traits and States in the Perception of Pain. *Cerebral Cortex*, *21*(10), 2408–2414. https://doi.org/10.1093/cercor/bhr027

Shamma, S. (2001). On the role of space and time in auditory processing. *Trends in Cognitive Sciences*, *5*(8), 340–348. https://doi.org/10.1016/S1364-6613(00)01704-6

Shannon, C. E., & Weaver, W. (1949). *The mathematical theory of communicaiton*. University of Illinois Press.

Singer, A. C., Martorell, A. J., Douglas, J. M., Abdurrob, F., Attokaren, M. K., Tipton, J., Mathys, H., Adaikkan, C., & Tsai, L. H. (2018). Noninvasive 40-Hz light flicker to recruit microglia and reduce amyloid beta load. *Nature Protocols*, *13*(8), 1850–1868. https://doi.org/10.1038/s41596-018-0021-x

Sirota, A., Montgomery, S., Fujisawa, S., Isomura, Y., Zugaro, M., & Buzsáki, G. (2008). Entrainment of Neocortical Neurons and Gamma Oscillations by the Hippocampal Theta Rhythm. *Neuron*, *60*(4), 683–697. https://doi.org/10.1016/j.neuron.2008.09.014

Skelin, I., Kilianski, S., & McNaughton, B. L. (2019). Hippocampal coupling with cortical and subcortical structures in the context of memory consolidation. *Neurobiology of Learning and Memory*, *160*, 21–31. https://doi.org/10.1016/j.nlm.2018.04.004

Solomon, E. A., Stein, J. M., Das, S., Gorniak, R., Sperling, M. R., Worrell, G., Inman, C. S., Tan, R. J., Jobst, B. C., Rizzuto, D. S., & Kahana, M. J. (2019). Dynamic Theta Networks in the Human Medial Temporal Lobe Support Episodic Memory. *Current Biology*, *29*(7), 1100-1111.e4. https://doi.org/10.1016/j.cub.2019.02.020

Spaak, E., Lange, F. P. de, & Jensen, O. (2014). Local Entrainment of Alpha Oscillations by Visual Stimuli Causes Cyclic Modulation of Perception. *Journal of Neuroscience*, *34*(10), 3536–3544. https://doi.org/10.1523/JNEUROSCI.4385-13.2014

Squire, L. R. (1992). Memory and the hippocampus: A synthesis from findings with rats, monkeys, and humans. *Psychological Review*, *99*(2), 195–231. https://doi.org/10.1037/0033-295x.99.2.195

Squire, L. R., Genzel, L., Wixted, J. T., & Morris, R. G. (2015). Memory Consolidation. *Cold Spring Harbor Perspectives in Biology*, *7*(8), a021766. https://doi.org/10.1101/cshperspect.a021766

Squire, L. R., & Zola-Morgan, S. (1991). The Medial Temporal Lobe Memory System. *Science*, *253*(5026), 1380–1386. https://doi.org/10.1126/science.1896849

Stanislaw, H., & Todorov, N. (1999). Calculation of signal detection theory measures. *Behavior Research Methods, Instruments, and Computers*, *31*(1), 137–149. https://doi.org/10.3758/BF03207704

Staudigl, T., & Hanslmayr, S. (2013). Theta Oscillations at Encoding Mediate the Context-Dependent Nature of Human Episodic Memory. *Current Biology*, *23*(12), 1101–1106. https://doi.org/10.1016/j.cub.2013.04.074

Staudigl, T., Vollmar, C., Noachtar, S., & Hanslmayr, S. (2015). Temporal-pattern similarity analysis reveals the beneficial and detrimental effects of context reinstatement on human memory.

Journal of Neuroscience, *35*(13), 5373–5384. https://doi.org/10.1523/JNEUROSCI.4198-14.2015

Strunk, J., & Duarte, A. (2019). Prestimulus and poststimulus oscillatory activity predicts successful episodic encoding for both young and older adults. *Neurobiology of Aging*, *77*, 1–12. https://doi.org/10.1016/j.neurobiolaging.2019.01.005

Summerfield, C., & Mangels, J. A. (2005). Coherent theta-band EEG activity predicts item-context binding during encoding. *NeuroImage*, *24*(3), 692–703. https://doi.org/10.1016/j.neuroimage.2004.09.012

Tarasi, L., & Romei, V. (2024). Individual Alpha Frequency Contributes to the Precision of Human Visual Processing. *Journal of Cognitive Neuroscience*, *36*(4), 602–613. https://doi.org/10.1162/jocn_a_02026

Tass, P., Rosenblum, M. G., Weule, J., Kurths, J., Pikovsky, A., Volkmann, J., Schnitzler, A., & Freund, H.-J. (1998). Detection of N:m Phase Locking from Noisy Data: Application to Magnetoencephalography. *Physical Review Letters*, *81*(15), 3291–3294. https://doi.org/10.1103/PhysRevLett.81.3291

Terada, S., Sakurai, Y., Nakahara, H., & Fujisawa, S. (2017). Temporal and Rate Coding for Discrete Event Sequences in the Hippocampus. *Neuron*, *94*(6), 1248-1262.e4. https://doi.org/10.1016/J.NEURON.2017.05.024

Thut, G., Schyns, P., & Gross, J. (2011). Entrainment of Perceptually Relevant Brain Oscillations by Non-Invasive Rhythmic Stimulation of the Human Brain. *Frontiers in Psychology*, *2*. https://doi.org/10.3389/fpsyg.2011.00170

Thut, G., Veniero, D., Romei, V., Miniussi, C., Schyns, P., & Gross, J. (2011). Rhythmic TMS Causes Local Entrainment of Natural Oscillatory Signatures. *Current Biology*, *21*(14), 1176–1185. https://doi.org/10.1016/j.cub.2011.05.049

Toba, M. N., Malkinson, T. S., Howells, H., Mackie, M.-A., & Spagna, A. (2024). Same, Same but Different? A Multi-Method Review of the Processes Underlying Executive Control. *Neuropsychology Review*, *34*(2), 418–454. https://doi.org/10.1007/s11065-023-09577-4

Tort, A. B. L., Komorowski, R. W., Manns, J. R., Kopell, N. J., & Eichenbaum, H. (2009). Theta–gamma coupling increases during the learning of item–context associations. *Proceedings of the National Academy of Sciences*, *106*(49), 20942–20947. https://doi.org/10.1073/pnas.0911331106

Tse, D., Langston, R. F., Kakeyama, M., Bethus, I., Spooner, P. A., Wood, E. R., Witter, M. P., & Morris, R. G. M. (2007). Schemas and Memory Consolidation. *Science*, *316*(5821), 76–82. https://doi.org/10.1126/science.1135935

Tulving, E. (1972). Episodic and semantic memory. In *Organization of Memory* (pp. 382–402). Academic Press, Inc.

Tulving, E. (1985). How many memory systems are there? *American Psychologist*, *40*(4), 385–398. https://doi.org/10.1037/0003-066X.40.4.385

Tulving, E., & Markowitsch, H. J. (1998). Episodic and declarative memory: Role of the hippocampus. *Hippocampus*, *8*(3), 198–204. https://doi.org/10.1002/(SICI)1098-1063(1998)8:3%253C198::AID-HIPO2%253E3.0.CO;2-G

Uncapher, M. R., Hutchinson, J. B., & Wagner, A. D. (2011). Dissociable Effects of Top-Down and Bottom-Up Attention during Episodic Encoding. *Journal of Neuroscience*, *31*(35), 12613–12628. https://doi.org/10.1523/JNEUROSCI.0152-11.2011

Van Dijk, H., Schoffelen, J. M., Oostenveld, R., & Jensen, O. (2008). Prestimulus Oscillatory Activity in the Alpha Band Predicts Visual Discrimination Ability. *Journal of Neuroscience*, *28*(8), 1816–1823. https://doi.org/10.1523/JNEUROSCI.1853-07.2008

van Strien, N. M., Cappaert, N. L. M., & Witter, M. P. (2009). The anatomy of memory: An interactive overview of the parahippocampal–hippocampal network. *Nature Reviews Neuroscience*, *10*(4), 272–282. https://doi.org/10.1038/nrn2614

Vandekerckhove, M. M. P. (2009). Memory, autonoetic consciousness and the self: Consciousness as a continuum of stages. *Self and Identity*, *8*(1), 4–23. https://doi.org/10.1080/15298860801961927

Vanderwolf, C. H. (1969). Hippocampal electrical activity and voluntary movement in the rat. *Electroencephalography and Clinical Neurophysiology*, *26*(4), 407–418. https://doi.org/10.1016/0013-4694(69)90092-3

Vinck, M., Oostenveld, R., Van Wingerden, M., Battaglia, F., & Pennartz, C. M. A. (2011). An improved index of phase-synchronization for electrophysiological data in the presence of volume-conduction, noise and sample-size bias. *NeuroImage*, *55*(4), 1548–1565. https://doi.org/10.1016/j.neuroimage.2011.01.055

Violante, I. R., Li, L. M., Carmichael, D. W., Lorenz, R., Leech, R., Hampshire, A., Rothwell, J. C., & Sharp, D. J. (2017). Externally induced frontoparietal synchronization modulates network dynamics and enhances working memory performance. *eLife*, *6*. https://doi.org/10.7554/eLife.22001

Wälti, M. J., Woolley, D. G., & Wenderoth, N. (2020). Assessing Rhythmic Visual Entrainment and Reinstatement of Brain Oscillations to Modulate Memory Performance. *Frontiers in Behavioral Neuroscience*, *14*. https://doi.org/10.3389/fnbeh.2020.00118

Wamsley, E. J. (2013). Dreaming, waking conscious experience, and the resting brain: Report of subjective experience as a tool in the cognitive neurosciences. *Frontiers in Psychology*, *4*. https://doi.org/10.3389/fpsyg.2013.00637

Wang, D., Clouter, A., Chen, Q., Shapiro, K. L., & Hanslmayr, S. (2018). Single-trial phase entrainment of theta oscillations in sensory regions predicts human associative memory performance. *Journal of Neuroscience*, *38*(28), 6299–6309. https://doi.org/10.1523/JNEUROSCI.0349-18.2018

Wang, D., Marcantoni, E., Clouter, A., Shapiro, K. L., & Hanslmayr, S. (2024). Rhythmic sensory stimulation as a noninvasive tool to study plasticity mechanisms in human episodic memory. *Current Opinion in Behavioral Sciences*, *58*, 101412. https://doi.org/10.1016/j.cobeha.2024.101412

Watrous, A. J., Miller, J., Qasim, S. E., Fried, I., & Jacobs, J. (2018). Phase-tuned neuronal firing encodes human contextual representations for navigational goals. *eLife*, *7*, e32554. https://doi.org/10.7554/eLife.32554

Weible, A. P., Rowland, D. C., Monaghan, C. K., Wolfgang, N. T., & Kentros, C. G. (2012). Neural Correlates of Long-Term Object Memory in the Mouse Anterior Cingulate Cortex. *Journal of Neuroscience*, *32*(16), 5598–5608. https://doi.org/10.1523/JNEUROSCI.5265-11.2012

Weible, A. P., Rowland, D. C., Pang, R., & Kentros, C. (2009). Neural Correlates of Novel Object and Novel Location Recognition Behavior in the Mouse Anterior Cingulate Cortex. *Journal of Neurophysiology*, *102*(4), 2055–2068. https://doi.org/10.1152/jn.00214.2009

Williams, J. H. (2001). Frequency-specific effects of flicker on recognition memory. *Neuroscience*, *104*(2), 283–286. https://doi.org/10.1016/S0306-4522(00)00579-0

Wilson, D. I. G., Watanabe, S., Milner, H., & Ainge, J. A. (2013). Lateral entorhinal cortex is necessary for associative but not nonassociative recognition memory. *Hippocampus*, *23*(12), 1280–1290. https://doi.org/10.1002/hipo.22165

Winterling, S. L., Shields, S. M., & Rose, M. (2019). Reduced memory-related ongoing oscillatory activity in healthy older adults. *Neurobiology of Aging*, *79*, 1–10. https://doi.org/10.1016/j.neurobiolaging.2019.03.012

Yamaguchi, Y. (2003). A theory of hippocampal memory based on theta phase precession. *Biological Cybernetics*, *89*(1), 1–9. https://doi.org/10.1007/s00422-003-0415-9

Zabcikova, M., Koudelkova, Z., Jasek, R., & Lorenzo Navarro, J. J. (2022). Recent advances and current trends in brain-computer interface research and their applications. *International Journal of Developmental Neuroscience*, *82*(2), 107–123. https://doi.org/10.1002/jdn.10166

4 Summary (German)

Die Fähigkeit, sich Erfahrungen multisensorisch einzuprägen, ist eng mit verschiedenen Formen elektrophysiologischer Aktivität in verschiedenen Hirnarealen verknüpft. In diesem Kontext spielen Theta- (3–7 Hz) und Alpha-Oszillationen (8–12 Hz) eine zentrale Rolle bei der Informationsspeicherung für die spätere Gedächtniskodierung sowie bei der Optimierung kognitiver Prozesse durch die Hemmung von konkurrierenden Informationen. Gleichzeitig ist das Gehirn permanent aktiv und zeigt anhaltende oszillatorische Muster, selbst in Abwesenheit externer Reize.

Ziel der vorliegenden Arbeit war die Untersuchung der Auswirkungen dieser kontinuierlichen, prä-stimulusbezogenen Gehirnzustände auf die Bildung multisensorischer Assoziationen im Rahmen des Gedächtnisses. Zu diesem Zweck wurden drei empirische Studien durchgeführt. In der ersten Studie erlernten die ProbandInnen semantisch nicht miteinander verbundene Bild-Ton-Assoziationen im Rahmen eines Subsequent-Memory-Effect-Paradigmas. Die Ergebnisse zeigen, dass später erinnerte Assoziationen bereits vor Stimuluspräsentation erhöhte Theta- und Alpha-Aktivität aufwiesen. Dies weist darauf hin, dass niederfrequente, prä-stimulusbezogene Oszillationen ein wichtiges Korrelat erfolgreicher Gedächtnisbildung sind. Aufbauend auf diesen Befunden wurde in der zweiten Studie eine modifizierte Version des Paradigmas verwendet, die visuelle sensorische Stimulation einsetzte, um Theta- und Alpha-Aktivität vor der Kodierung der Gedächtnisinhalte gezielt zu modulieren. Die Ergebnisse der Studie legen nahe, dass die visuelle Stimulation im Alpha-Band die Gedächtnisleistung signifikant im Vergleich zu Kontrollbedingungen steigern kann. Dies deutet darauf hin, dass prä-stimulusbezogene Alpha-Aktivität eine potenziell kausale Rolle bei der Kodierung multisensorischer Assoziationen spielt. In der dritten Studie wurden die audiovisuellen Stimuluspaare sequentiell statt simultan präsentiert, um zu prüfen, ob die Reihenfolge der Modalitäten die spätere Gedächtnisbildung beeinflusst und ob sie als kontextuelles Merkmal in der Gedächtnisspur repräsentiert wird. Die Ergebnisse weisen auf eine modalitätsabhängige Beziehung zwischen niederfrequenten Oszillationen vor und während der Kodierung und der späteren Gedächtnisleistung hin. Dies legt nahe, dass die zeitliche Reihenfolge sensorischer Information den laufenden sowie den stimulusinduzierten Gehirnzustand beeinflussen kann.

Die vorliegenden Beobachtungen legen eine funktionale Arbeitsteilung zwischen Theta- und Alpha-Oszillationen nahe und erweitern die bestehenden Annahmen bezüglich Bindungs- und Inhibitionsmechanismen auf den Bereich laufender, prä-stimulusbezogener Gehirnzustände. Die vorliegenden Befunde stützen die Hypothese, dass die Fähigkeit, Erfahrungen zu speichern, nicht erst mit dem Auftreten eines Reizes beginnt, sondern bereits mit dem Zustand des Gehirns unmittelbar davor. Obwohl diese Erkenntnisse gewisse Einschränkungen aufweisen, leisten sie doch einen Beitrag zum Verständnis davon, wie Gedächtnis entsteht, und könnten zukünftige Forschung in klinischen wie nicht-klinischen Bereichen bereichern.

5 Summary (English)

The ability to form memories of multisensory experiences is strongly tied to different types of electrophysiological activity exhibited by different areas of the brain. Among those, theta (3-7 Hz) and alpha (8-12 Hz) oscillations have been shown to be heavily involved in processes of binding information for subsequent memory encoding, as well as inhibiting interfering information in favor of process optimization. However, the brain is always active, exhibiting ongoing oscillatory activity even in the absence of stimulation.

The goal of this dissertation was to investigate how these ongoing, pre-stimulus brain states affect the formation of multisensory associations in service to memory. Three empirical studies were conducted in an attempt to shed light on this question. In the first study, participants were required to memorize individual associations between semantically unrelated images and sounds in the context of a Subsequent Memory Effects paradigm. The findings show that later remembered associations exhibited significant increases in theta as well as alpha activity before the stimulus was even presented, suggesting that pre-stimulus low-frequency oscillations are an important correlate of memory success. Based on these results, a modified version of the SME paradigm was used in the second study, in which visual sensory stimulation was utilized to actively modulate theta and alpha activity before encoding happened. The study demonstrated that visual stimulation in the alpha band can significantly increase memory performance as compared to controls, suggesting that pre-stimulus alpha activity may be functionally relevant to the process of encoding multisensory associations. In the third study, the same audiovisual stimulus pairs were presented sequentially rather than simultaneously to assess whether modality order affects subsequent encoding, and whether it can be treated as a contextual feature in the memory trace. The findings suggest a modality-dependent correlation of low-frequency oscillation before and during encoding with subsequent memory performance, suggesting that the order in which sensory information arrives in the brain can affect ongoing and stimulus-evoked brain states.

Taken together, these observations point towards a division of labor between theta and alpha oscillations, expanding the notion of binding and inhibition to the domain of ongoing pre-stimulus oscillatory states. The evidence supports the idea that the ability to memorize experiences does not start with having something to experience, but with the state the brain is in before the experience and its encoding begins. Although not without limitations, these insights contribute to our understanding of how the phenomenon of memory comes to be, and may further contribute to future work in clinical and non-clinical settings.

6 Tools

ChatGPT version 5, OpenAI (https://chatgpt.com/)

- Grammar and spelling checks
- Improving readability and flow

DeepL Write, DeepL SE (https://www.deepl.com/de/write)

- Grammar and spelling checks
- Improving readability and flow for academic writing style

7 Author contribution

Ostrowski, J., & Rose, M. (2024). Increases in pre-stimulus theta and alpha oscillations precede successful encoding of crossmodal associations. Scientific Reports, 14(1), 7895. https://doi.org/10.1038/s41598-024-58227-z

Jan Ostrowski: Software, Validation, Formal Analysis, Investigation, Data Curation, Writing—Original Draft, Writing—Review and Editing, Visualization.

Ostrowski, J.*, Maack, M.C.*, & Rose, M. (accepted). Disentangling the Functional Roles of Pre-Stimulus Oscillations in Crossmodal Associative Memory Formation via Sensory Entrainment. bioRxiv 2025.06.24.661289. https://doi.org/10.1101/2025.06.24.661289

Note: By the time of submission of this thesis, this article has been accepted for publication by Scientific Reports. An edited version of this article has not been available yet, so the most recent version of the manuscript was attached to this thesis.

Jan Ostrowski: Study design, Pre-registraton, Data acquisition and curation, Software, Validation, Formal analysis, Writing – Original draft, Writing – Review and Editing, Visualization, all in cooperation with Marike C. Maack.

Maack, M. C., Ostrowski, J., & Rose, M. (2025). The order of multisensory associative sequences is reinstated as context feature during successful recognition. Scientific Reports, 15(1), 18120. https://doi.org/10.1038/s41598-025-02553-3

Jan Ostrowski: Software, Validation, Formal analysis, Writing – Review and Editing, Visualization.

---

* Shared first authorship

8 Acknowledgements

This thesis is the culmination of four years of hard work that, while being nerve-wracking on occasion, proved quite rewarding. At the beginning of this manuscript, I cited Thomas Kuhn's *Structures of Scientific Revolutions* because I firmly believe that science is inherently collaborative, and that every piece of new insight, no matter how large or small, advances the collective quest for understanding. And because science is a collaborative endeavor, I would like to take this opportunity to thank the people who accompanied me on my own quest and helped make this dissertation possible.

First and foremost, I would like to thank Prof. Dr. Michael Rose for his patience and trust, and academic guidance through every stage of this project. Thank you for the lively discussions and for always welcoming questions, whether simple or complicated. I am also grateful to Prof. Dr. Helen Blank and Dr. Patrick Bruns for serving on my thesis committee and providing invaluable feedback and fresh perspectives over the course of my work. Furthermore, I extend my thanks to Prof. Dr. Andreas Engel and Dr. Patrick Bruns for taking the time and evaluating my work as part of the examination committee.

A heartfelt thank you goes to everyone at the Institute of Systems Neuroscience – especially my fellow lab members Marike, Carina, Maren, Christoph, Leonie, and Sebastian. Thank you for all the support, emotional and otherwise, for the fun and laughter, and for every shared lunch break. You were the best lab mates one could wish for! Caspar, your warmth and wisdom are one of a kind – thank you for being there and always finding the right things to say. I would also like to thank Annika, Fabi, Maria, and Cari for the fun, the games, and the open doors. All of you are a major reason why my time at the institute was so enjoyable, and I am grateful to now call many of you friends.

I would also like to thank those who contributed to my decision to start this PhD journey. My gratitude goes to Dr. Rebecca Förster for guiding me through my first real experimental study as a B.Sc. student in Bielefeld. Likewise, I am thankful to Dr. Philipp Schröder for his great supervision, his support in publishing my first scientific article, and his encouragement to continue along the academic path.

Most importantly, my deepest thanks go to Yvonne – my partner in crime. Thank you for your patience, your love, and for reminding me that it is all right to be proud of what you achieve. I could not have done this without your support.

Finally, to my parents: thank you so much for giving me the time and freedom to find my own path, and for your unwavering patience and support, even when that path involved a few detours.

9 Curriculum Vitae

Jan Ostrowski, born February 14th, 1991, in Lwow, Ukraine

Education

Jul 2021 – present	Graduate Studies in Cognitive Neuroscience (Dr. rer. biol. hom.) University Medical Center Hamburg-Eppendorf
Oct 2018 – May 2021	M.Sc. in Cognitive Science University of Tübingen
Oct 2015 – Sep 2018	B.Sc. in Psychology University of Bielefeld
Oct 2010 – Sep 2015	B.A. in Philosophy University of Düsseldorf

Work experience

Jul 2021 – Jun 2025	Research associate Institute for System Neuroscience, University Medical Center Hamburg-Eppendorf
Feb 2020 – Apr 2021	Research assistant Department of Psychology, University of Tübingen
Dec 2018 – Apr 2021	Research assistant Leibniz Institute for Knowledge Media, Tübingen
Oct 2016 – Sep 2018	Research assistant Department of Neurocognitive Psychology, University of Bielefeld

10 Reprints

10.1 Study 1: Increases in pre-stimulus theta and alpha oscillations precede successful encoding of crossmodal associations

Ostrowski, J., & Rose, M. (2024). Increases in pre-stimulus theta and alpha oscillations precede successful encoding of crossmodal associations. Scientific Reports, 14(1), 7895. https://doi.org/10.1038/s41598-024-58227-z

www.nature.com/scientificreports

scientific reports

OPEN

Increases in pre-stimulus theta and alpha oscillations precede successful encoding of crossmodal associations

Jan Ostrowski & Michael Rose

A central aspect of episodic memory is the formation of associations between stimuli from different modalities. Current theoretical approaches assume a functional role of ongoing oscillatory power and phase in the theta band (3–7 Hz) for the encoding of crossmodal associations. Furthermore, ongoing activity in the theta range as well as alpha (8–12 Hz) and low beta activity (13–20 Hz) before the presentation of a stimulus is thought to modulate subsequent cognitive processing, including processes that are related to memory. In this study, we tested the hypothesis that pre-stimulus characteristics of low frequency activity are relevant for the successful formation of crossmodal memory. The experimental design that was used specifically allowed for the investigation of associative memory independent from individual item memory. Participants ($n = 51$) were required to memorize associations between audiovisual stimulus pairs and distinguish them from newly arranged ones consisting of the same single stimuli in the subsequent recognition task. Our results show significant differences in the state of pre-stimulus theta and alpha power between remembered and not remembered crossmodal associations, clearly relating increased power to successful recognition. These differences were positively correlated with memory performance, suggesting functional relevance for behavioral measures of associative memory. Further analysis revealed similar effects in the low beta frequency ranges, indicating the involvement of different pre-stimulus-related cognitive processes. Phase-based connectivity measures in the theta band did not differ between remembered and not remembered stimulus pairs. The findings support the assumed functional relevance of theta band oscillations for the formation of associative memory and demonstrate that an increase of theta as well as alpha band oscillations in the pre-stimulus period is beneficial for the establishment of crossmodal memory.

Keywords EEG, Theta oscillations, Alpha oscillations, Pre-stimulus interval, Crossmodal associations, Episodic memory, Phase-based connectivity

Patterns of ongoing brain activity can modulate how subsequent stimuli are perceived and processed[1–4]. This pre-stimulus activity has been shown to also affect how information is encoded to long-term memory, subsequently affecting memory performance itself[5–8]. Furthermore, previous research suggests that oscillatory activity across a wide range of frequency bands might be involved in the process, including low-frequency oscillations[9,10], as well as oscillations as high as 55–70 Hz[11]. In terms of episodic memory, particularly spatial information is represented in the hippocampus through the firing of event or place cells, which is embedded in an ongoing theta rhythm of 3–7 Hz[12,13]. The information can be coded by the firing rate through the mechanism of specific receptive fields on the one hand, but also in the temporal domain by shifting the firing sequences along the phase of the overarching theta cycle (phase precession). However, these mechanisms are not only applicable to spatial information, but might also explain how associative information is encoded to long-term memory. As most of the content of episodic memory involves information integrated from different sensory modalities, it is all the more relevant that recent work extended the explanatory scope of rate and temporal coding, claiming that the same mechanism is used to form associations between discrete stimuli from different modalities and form relational networks between them, which ultimately serves episodic memory[14]. The authors suggest that event cells in the

Department of Systems Neuroscience, University Medical Center Hamburg-Eppendorf, Hamburg, Germany. email: j.ostrowski@uke.de

hippocampus coding for discrete events fire according to transient theta phase precession and subsequently lock onto the early theta phase. It can be assumed that the phase of theta oscillations may represent windows of short-term synaptic plasticity, and coordinate inputs from different sources. Thus, oscillatory pre-stimulus activity in the theta frequency band might be crucial for the formation of crossmodal associations in humans.

Specifically, evidence from non-invasive electroencephalography (EEG) studies suggests that increases in theta power before stimulus onset might be related to enhanced performance in tasks measuring episodic or long-term memory[10]. While some studies suggested that theta oscillations might be involved in item memory[15,16], increased theta has also been associated specifically with better recollection of contextual information, where the association of stimuli to one of few contexts needed to be memorized[6,17]. Moreover, there is evidence suggesting that theta oscillations may play a role not only in the binding of stimuli to contexts but also in the encoding of individual associations between two stimuli[18]. In that study, participants were required to memorize individual word pairs, and were later cued by one of the words and instructed to verbalize the other half of the pair. The authors report significant increases in theta power, specifically in the pre-stimulus interval. This line of evidence gains additional support by studies utilizing intracranial EEG (iEEG), showing that the hippocampus displays increased theta oscillations associated with better memory performance[19]. However, it is still unclear whether pre-stimulus theta power is involved in modulating the encoding of individual associations between stimuli from different sensory modalities.

In this context, insights from research using animal models might provide a framework to investigate the role of theta amplitude and phase characteristics in the encoding of crossmodal associations. Supporting evidence was reported by Terada and colleagues[14], who trained rats to perform a cue-combination task that required the integration and subsequent association of sequentially presented sound and odor stimuli. The results suggest that the firing of hippocampal neurons might represent associations between multimodal stimuli, with phase information from the theta band serving as a marker for the temporal order of discrete events. However, evidence in humans has been scarce. In one recent study, Clouter and colleagues presented participants with a multimodal memory task, in which they were required to memorize the association between a movie clip and a sound[20]. Both stimuli were presented simultaneously during encoding, but the authors manipulated the synchrony between them by fluctuating the luminance of the video and the amplitude of the sound according to a 4 Hz sine wave, while also varying their phase offset. The results show that memory performance was best when no phase offset was introduced, and that the effect was specific to the theta band. Another study followed up on these results and showed that even the single-trial phase synchrony between visual and auditory cortices, whose activity was entrained by 4 Hz fluctuations of the stimuli, could predict success in the formation of associations between different sensory information for long-term memory[21]. Thus, in addition to studies that showed a relevance of theta band amplitude modulation, the latter studies revealed an important role of phase coupling for the encoding of material from different modalities. The presented evidence further suggests that successful encoding of crossmodal associations may rely on elevated functional connectivity between the corresponding sensory areas, and that the connectivity might be centered on rhythmic components within the range of theta oscillations.

While theta oscillations seem to play a crucial role before and during the encoding of complex information to memory, there is also evidence on the involvement of oscillations in the alpha (8–12 Hz) and beta frequency bands (13–30 Hz). Alpha oscillations have been theorized to play a crucial role in selective attention[22], which was suggested to aid encoding by inhibiting distracting information[9,23]. Investigations using iEEG measurements support this idea as increases in medial temporal pre-stimulus alpha power were reported to be associated with better memory performance[19]. Similarly, beta band activity has been observed to benefit memory encoding via inhibitory processes[24]. In the context of crossmodal associations, Scholz and colleagues reported that pre-stimulus beta oscillations in the lower bands (13–17 Hz) were indicative of successful encoding of audiovisual source memory[6]. However, it remains unclear how ongoing alpha and beta oscillations might contribute to the formation of individual crossmodal associations.

In the present study, we aimed to directly assess the relevance of pre-stimulus amplitude and phase characteristics for the formation of individual crossmodal associations between visual and auditory stimuli. In particular, pre-stimulus theta, alpha and low beta band activity, i.e. activity *before* the encoding of multimodal stimuli, might play a functional role in subsequent memory performance. We additionally examined oscillatory effects regarding post-stimulus processing as well as effects during memory retrieval. In terms of phase characteristics, phase coupling in the theta band can be hypothesized to be important during the processing of the stimuli for binding crossmodal information. Thus, if phase-based connectivity contributes to the encoding of audiovisual associative information, differences should be observed in the connectivity between visual and auditory areas. Specifically, successful memory formation would be accompanied by increased phase-based connectivity between auditory and visual areas, as compared to unsuccessful memory formation during the processing of the stimuli. Thus, we analyzed the phase-based connectivity between occipital electrodes (image-related activity)[25] and frontocentral electrodes (sound-related activity)[26,27].

We employed a Subsequent Memory Effects (SME) task, which is an established experimental design to investigate mechanisms related to the encoding of information to (episodic) memory. This paradigm has been used in a variety of modalities, including EEG[5,6,28,29], magnetoencephalogram (MEG)[10,30], and functional imaging[31,32]. The majority of the studies investigating SMEs, however, focused on the encoding of individual associations within one single sensory modality[5,17,33–35]. We modified the unimodal design to allow for individual crossmodal associations to be encoded. Participants were required to memorize associations between images and sounds while brain activity was recorded via EEG. One experimental run consisted of an encoding phase, a short distraction task, and a subsequent testing phase in the form of cued recognition. During encoding, semantically unrelated real-life images and sounds were presented simultaneously after a cue. Participants were instructed to indicate whether both individual stimuli were animal-related while making an effort to memorize the stimulus pair as a whole. After the distraction task, which required the participants to count backwards for several minutes, they were presented with the same stimulus pairs as during encoding, as well as the same number of new pairs consisting of the same individual images and sounds but randomly shuffled for new combinations. Participants needed to indicate whether they remembered the pair from the previous encoding phase or not. The stimulus pairs always consisted of individual stimuli that were presented during encoding and only the pairing was identical or different. Therefore, this task design enabled us to specifically target memory performance in terms of associations rather than individual stimuli.

Methods

Participants

In total, 55 healthy participants were recruited for this study. We had to exclude the data from four participants because of too many missing trials (1), low data quality (1), and hardware problems during data acquisition (2). This resulted in a final sample of $N = 51$ participants (64.71% female) that could be used for analysis, with a mean age of 24.41 years (SD = 3.82), ranging from 18 to 34 years. Participants had normal or corrected-to-normal vision and hearing ability. All participants gave their informed consent and received financial reimbursement for taking part in the study. This investigation was approved by the ethics committee of the Hamburg Medical Council (PV5893). We confirm that all experiments were performed in accordance with relevant guidelines and regulations.

Task and procedure

For this study, we implemented a Subsequent Memory Effects (SME) task consisting of three experimental runs. Each run consisted of an encoding phase, a short intermission, and a subsequent recognition phase (see Fig. 1 for a schematic overview of one experimental run). As we wanted to measure crossmodal memory, pairs consisting of one image and one sound were randomly selected from an internal stimulus database. The images were shown with a resolution of 640 × 480 pixels, a 24-bit color depth, and depicted photographs of natural or man-made scenes. A white fixation cross was layered over every image. The sounds were real-life recordings of either sounds and noises from nature (e.g. animal calls) or from a man-made environment (e.g. a honk from a car). All sounds were cropped to a duration of 2 s, and featured a bit rate of 1411 kBit/s. The pairs were pulled in a manner so that the stimulus material was unique in each run and did not repeat between runs. Specifically, each pair and individual stimulus occurred only once across the three encoding phases from the three experimental runs. Furthermore, images were paired with sounds so that congruency effects within pairs were avoided[36]. For example, while the image of a wolf could not have been paired with the sound of a wolf howl, it could have been paired with the sound of bird call or a honking car, as this would not constitute semantic congruence.

The encoding phase of each run consisted of 47 trials in which the audiovisual pairs were presented simultaneously for 2 s. The stimulus pairs were preceded by a red fixation cross with a duration of 2 s. After stimulus offset, the white fixation cross remained for a fixed duration of 1 s, which was followed by a variable inter-trial interval of 2 to 4 s. For every encoding trial, the participants were instructed to memorize the stimulus pairs, and to indicate with a button press whether both image and sound represented an animal (right mouse button) or not (left mouse button). Button presses were registered as a response during the 2 s of stimulus presentation and subsequent 1 s (Fig. 1) but were otherwise counted as a missed response. The encoding phase was followed

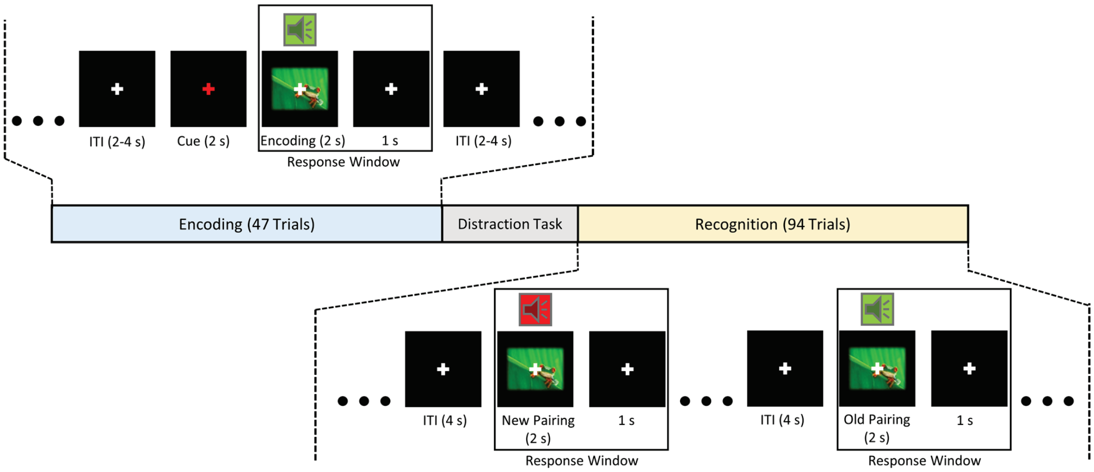


Figure 1. Schematic overview of one experimental run of the SME task. The run consists of an encoding phase, in which image-sound pairs needed to be memorized. This was followed by a short distraction task, where participants were required to count down in steps of 7/9/13 from 100/115/125. Subsequently, old and new pairs consisting of the same individual stimuli presented during encoding were shown, and participants indicated whether they remembered the particular pairing or not.

by a brief intermission of approximately 3 min, in which the participants were asked to count down aloud from 100 (115 and 125 in the second and third run, respectively) in steps of 7 (9 and 13 in the second and third run, respectively).

In the subsequent recognition phase, the 47 audiovisual pairings from the preceding encoding phase were presented again. In addition, 47 new pairings were shown that were created from the individual images and sounds from previously learned pairs. In the instruction, participants were explicitly informed about the nature of new pairings and were further told that no new images and sounds would be introduced. All stimulus pairs were presented for 2 s, with a white fixation cross in the middle of the screen during stimulus presentation and for a fixed duration of 1 s directly after. During these 3s, association recognition was tested, as the participants were asked to indicate via button-press whether the current pair had already been presented in the preceding encoding phase (left mouse button) or not (right mouse button). The participants were encouraged to give a positive response only when confident, and to give a negative response when in doubt, to reduce the risk of false positive responses. The subsequent inter-trial interval was set to 4 s, during which a white fixation cross was visible. Across three experimental runs, participants were presented with 141 unique encoding trials and 282 recognition trials in total.

Analysis of behavioral data

The behavioral performance of the categorization task during encoding was assessed by computing the average percentage of trials in which participants correctly identified whether both the visual and auditory stimulus represented an animal. In the recognition phase, we extracted the percentages of correctly remembered old pairings (hit), not remembered old pairings (misses), correctly rejected new pairings (correct rejections), and seemingly remembered new pairings (false alarm). As a measure of sensitivity and memory performance, *d'* was computed by calculating the difference between the z-transformed hit and false alarm rates. Then, the subject-specific *d'* values were submitted to a one-sample *t*-test to investigate the likelihood of memories of stimulus pairs being formed across the sample. Furthermore, a two-factorial repeated-measures ANOVA was used to analyze reaction times during the recognition task, with the first factor *type of pairing* (old vs. new) and the second factor *type of response* (correct vs. incorrect).

Analysis of EEG data

Data acquisition

After giving informed consent and filling out a short demographic questionnaire, participants were seated in an electrically shielded and sound-attenuated chamber. We used a 60-channel electrode setup (ActiCap, BrainProducts, Gilching, Germany) to record EEG, whereas four additional electrodes were placed on the left and right temple, as well as above and below the left eye, to record vertical and horizontal EOG. The signal was referenced online to *FCz* and re-referenced offline to a common average. The ground electrode was placed on the neck below *Oz*, and electrode impedances were kept below 15 kΩ. The signal was amplified with a low cut-off frequency of 0.53 (0.3 s time constant) and recorded at a sampling rate of 500 Hz. EEG activity was recorded during all encoding and recognition phases, but not during intermissions.

Preprocessing and time–frequency decomposition for power analysis

The offline preprocessing of the acquired EEG data was done using the Fieldtrip toolbox[37] for MATLAB (Release 2021a, The MathWorks Inc., Natick, Massachusetts, USA). For every trial, epochs were extracted from -1.5 s up until 2.5 s relative to stimulus onset. We used a high-pass filter at 0.5 Hz as implemented in Fieldtrip to filter out extreme low-frequency fluctuations. The data was then visually inspected and trials containing artifacts, such as high-frequency noise indicating muscular activity or spikes reminiscent of bad electrode connection, were removed. Independent Component Analysis (ICA) was used to identify components corresponding to eye blinks and lateral eye movements, which were then removed from the data. Per participant, 3.73 (SD = 1.8) components were removed on average, with most of them corresponding to muscle-related (M = 2.06, SD = 1.7) and blink artifacts (M = 1.02, SD = 0.32). Then, the data was again visually inspected, and trials that were still containing artifacts were removed. Finally, trials were separated into REM and NOTREM groups based on the responses from the corresponding recognition phase. A trial was considered as a REM trial if two conditions were met: First, the stimulus needed to be an "old" pair from the encoding phase, and the participant should have indicated that they remembered this pair. Second, the participant should have correctly identified a shuffled pair as new that contained the image shown in the original old pair. Conversely, a trial was considered a NOTREM trial if an old pair was not recognized. On average, 7.91% (SD = 7.61%) and 7.96% (SD = 7.96%) of trials were removed from the encoding data in the REM and NOTREM condition, respectively, resulting in an average of 59.29 (SD = 18.74) REM and 53.53 (SD = 18.07) NOTREM trials per participant after accounting for trials with missing responses. Bad channels were identified in the initial visual inspection, removed from the data, and interpolated using the weighted average from the neighboring channels after the ICA. Only one channel from one individual data set was interpolated in the course of the analysis.

Data from the recognition phase was preprocessed in the same manner as the encoding data. On average, 5.65 (SD = 3.14) independent components were removed from the data, the majority of which relating to blinks (M = 1.02, SD = 0.24) and muscular artifacts (M = 3.39, SD = 2.74). Here, a trial was categorized as REM if an "old" pair was presented and the participant recognized it correctly. If an "old" pair was presented and the participant did not remember it, it was categorized as a NOTREM trial. During preprocessing, 6.34% of trials with a correctly remembered stimulus pair were removed, while 6.27% of trials with not remembered stimuli were removed. This resulted in an average of 70 and 54 trials per participant, respectively.

Time–frequency decomposition was conducted in the frequency range of 1 to 40 Hz, with frequency bins of 1 Hz, and for the time interval of − 1 s to 2 s relative to stimulus onset. We chose the *mtmconvol* method for convolution as implemented in Fieldtrip[37] with a sliding Hanning window of a fixed length of 500 ms and a step size of 100 ms. This method is a computationally more efficient version of a convolution with a complex wavelet, where the wavelet itself is constructed by convoluting the real and imaginary sine component at each frequency with the tapering function. The data and the tapered wavelet are then Fourier-transformed and element-wise multiplied in the frequency domain. At the end, the inverse Fourier transform of the result is computed. The additional 500 ms of data before and after the time interval of interest extracted during preprocessing served as padding to avoid edge artifacts from the time–frequency decomposition. For both conditions (REM, NOTREM), the resulting power values were averaged across trials for each participant. No baseline correction was applied since we were primarily interested in within-subjects differences of oscillatory power between the REM and NOTREM conditions. Furthermore, the experimental design did not allow for a suitable baseline period, as encoding-related processes could not be ruled out during the inter-trial interval. The same procedure was applied for encoding as well as recognition data.

Phase-based connectivity

As the theta band is thought to be involved in the process of binding incoming information[20], we investigated whether memory performance with crossmodal stimuli could be differentiated by measures of phase-based functional connectivity. Thus, cross-spectral density data from all electrode combination pairs were extracted for the theta frequency range (3–7 Hz) in bins of 1 Hz and − 1 s to 0.5 s relative to stimulus onset in steps of 100 ms for single trials from all subjects. Next, functional connectivity was estimated using the weighted Phase Lag Index (wPLI[38]), which utilizes the imaginary part of cross-spectral densities to compute the measure and is a non-directional marker of phase-based connectivity. To avoid positive bias, we used a squared estimated of wPLI as implemented in Fieldtrip[37].

Statistical analysis of EEG data

In this study, we focused on the analysis of the time–frequency EEG data acquired during the encoding phase of the experiment. Based on previous research, the main analysis focused on potential SMEs for the pre-stimulus time interval in the theta, alpha, and beta frequency band (3–30 Hz). For that purpose, we used a non-parametric permutation testing approach with cluster-based correction for multiple comparisons as implemented in Fieldtrip[37] to statistically compare time–frequency data corresponding to REM trials to data from NOTREM trials from the encoding phase. To compare the specificity of the assumed relevance of theta band activity, the statistical analysis was calculated for the frequency spectrum of 1 to 40 Hz and a time window of − 1 to 2 s relative to stimulus onset. In this approach, paired-samples *t*-tests were conducted for every channel-time–frequency data point across participants between the REM and NOTREM condition. Adjacent data points showing significant differences between conditions ($p < 0.05$) were clustered in sets based on temporal, spatial, and spectral criteria. The sum of statistical values within each cluster was taken as cluster-level statistic, and the maximum of cluster-level values was chosen as the main test statistic for the comparison of conditions. Next, the Monte Carlo method was used to create a distribution of *t*-values by creating a single data set containing all trials from both conditions and randomly partitioned it into two groups. Statistical comparisons between these artificially created conditions were again conducted on the level of individual data points, and a cluster-level main statistic was computed. The drawing procedure was repeated 2000 times. On every iteration, the maximum cluster-level statistics for positive and negative clusters were extracted to create the cluster-level null-hypothesis distribution. The final *p*-value for the comparison of conditions was computed by assessing the proportion of random partitions with a larger test statistic than the one from the observed data. This procedure was repeated for all clusters found in the data, generating a *p*-value for the condition comparison for every cluster.

Building on the results from the main analysis, a correlational analysis was performed to investigate whether the magnitude of differences in oscillatory power between REM and NOTREM trials scaled with memory performance. For each channel-time–frequency data point in the range of 1 to 40 Hz and − 1 s to 2 s relative to stimulus onset, the difference in oscillatory power between REM and NOTREM trials was calculated. We then correlated the difference values with the performance measure *d'* across participants using Pearson's correlation coefficient. To correct for multiple comparisons, the same cluster-based correction was applied to the data as described in the previous paragraph. Furthermore, we investigated the relationship between pre- and post-stimulus activity. For this purpose, we selected those data points in the theta band from the pre-stimulus (− 1 s to − 0.1 s before stimulus onset) and the post-stimulus interval (0.1 s to 2 s after stimulus onset) that showed a significant difference between the REM and NOTREM condition as suggested by the results of their statistical comparison. The same analysis was conducted for the alpha band separately. After calculating the mean difference values for the pre-stimulus and post-stimulus intervals of each participant, we used the Pearson correlation coefficient to correlate the resulting means. This process was repeated for all channels that displayed significant data points in the respective frequency bands during both pre-stimulus as well as post-stimulus intervals, resulting in correlation coefficients for each channel. The Bonferroni method was utilized to correct for multiple correlations and adjust the resulting *p*-values accordingly.

To test whether connectivity between visual and auditory areas is increased for REM trials as compared to NOTREM trials, we chose *O1, O2, Oz, PO7, PO3, POz, PO4,* and *PO8* as seed channels. For every seed channel, the connectivity data corresponding to frontocentral channels was extracted and submitted to cluster-based permutation testing, using paired-samples *t*-tests on the sample level. Frontocentral electrodes were chosen as follows: *F1, F2, Fz, FC3, FC1, FC2, FC4, C3, C1, Cz, C2, C4.*

Results

Behavioral results

In the categorization task during encoding, participants performed with an average accuracy of 92.48% (SD = 9.89%), indicating a sufficiently high compliance with the task. Reaction times from trials with later remembered and later not remembered stimulus pairs did not differ significantly, $t(50) = 1.7711$, $p = 0.0826$, although participants responded slightly faster on NOTREM trials (M = 1415.9 ms, SD = 311 ms) than on REM trials (M = 1449.9 ms, SD = 332.5 ms). See Fig. 2 for a visualization of the behavioral results.

During the recognition phase, participants had to indicate whether the presented stimulus pair had already been shown during encoding or whether it was a new pair. The hit rate was defined as the percentage of trials in which old pairs were correctly identified as known, whereas the false-positive rate was defined as the percentage of trials in which new pairs were incorrectly identified as old. On average, the participants achieved a hit rate of 52.98% (SD = 13.63%) and a false-positive rate of 14.27% (SD = 8.66%). Responses were not recorded on an average of 5.08% of trials. We calculated d' as a sensitivity measure for recognition performance, yielding a mean value of $d' = 1.2456$ across the sample. The results from a one-sided *t*-test revealed that the mean d' value was significantly different from 0, $t(50) = 15.057$, $p < 0.001$, indicating that the recognition performance was above chance across participants.

We analyzed the reaction times from the recognition phase using a repeated-measures ANOVA with the factors *type of pairing* (old vs. new) and *type of response* (REM/correct rejection vs NOTREM/false alarm). Main effects of *type of pairing*, $F(1,50) = 10.9464$, $p < 0.01$, as well as *type of response* were found, $F(1,50) = 108.0863$, $p < 0.001$. Furthermore, the interaction between these factors was also found to be significant, $F(1,50) = 9.2168$, $p < 0.01$. Thus, the correct recall of previously shown stimulus pairs and the correct identification of new stimulus pairs as new was accompanied by faster reaction times. In contrast, participants tended to respond slower in trials where old pairs were not remembered, as well as in trials where new pairs were falsely categorized as old. However, the difference in reaction times between levels of *type of response* (REM/correct rejection vs NOTREM/false alarm) was larger for new pairs (1604.4 ms vs. 1872.1 ms, $p < 0.001$) than for old ones (1621.2 ms vs. 1769.6 ms, $p < 0.01$; see Fig. 2c).

Oscillatory results

Oscillatory power before and during encoding

To assess whether oscillations before and during encoding differentiate between successful and unsuccessful memory formation, we analyzed the differences in power between REM and NOTREM trials for the corresponding time interval. The statistical comparison was conducted for the time interval of − 1 s to 2 s relative to stimulus onset, and for a frequency range of 1 Hz to 40 Hz. The analysis revealed a significant difference in oscillatory power between REM and NOTREM trials before and during the encoding of crossmodal associations ($p < 0.05$). Using a cluster-based permutation approach, a significant cluster was found in the pre-stimulus interval ranging from 1 to 18 Hz, suggesting higher oscillatory power for REM trials as compared to NOTREM trials (see Fig. 3). Similarly, increased power during REM trials was also observed during early encoding up to 0.9 s relative to stimulus onset in a frequency range of 1 to 27 Hz. Moreover, the analysis revealed an inverted effect in the late post-stimulus between 1 and 2 s after stimulus onset, spanning from 9 to 34 Hz, showing a negative cluster that did not extend into the theta band.

In the pre-stimulus theta range (3–7 Hz), the differences resulted to be most pronounced over the parietal as well as central areas of the right hemisphere, as well as over frontal-midline areas. The strongest effect was found

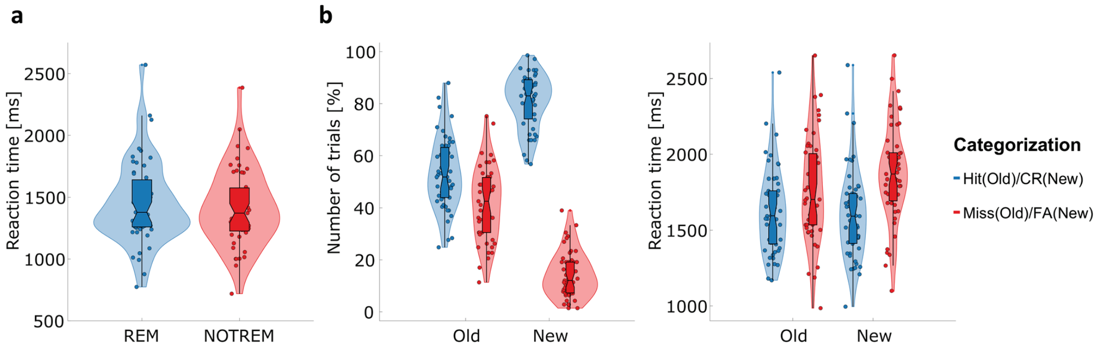


Figure 2. Behavioral results from the SME task. (**a**) Distribution of reaction times for the categorization task during encoding for REM and NOTREM trials across the whole experiment. (**b**) Distribution of relative number of trials (*left*) as well as reaction times (*right*) for each response category of the recognition task. For the violin plots, areas are normalized to equal within each figure. Point markers represent mean values for each participant. The horizontal line within the boxplots marks the median of the respective subset, while the notch around the median represents its 95% confidence interval. The upper and lower edge of the boxplot mark the third and first quartile of the data, respectively. The legend only refers to (**b**). *CR* correct rejection, *FA* false alarm.

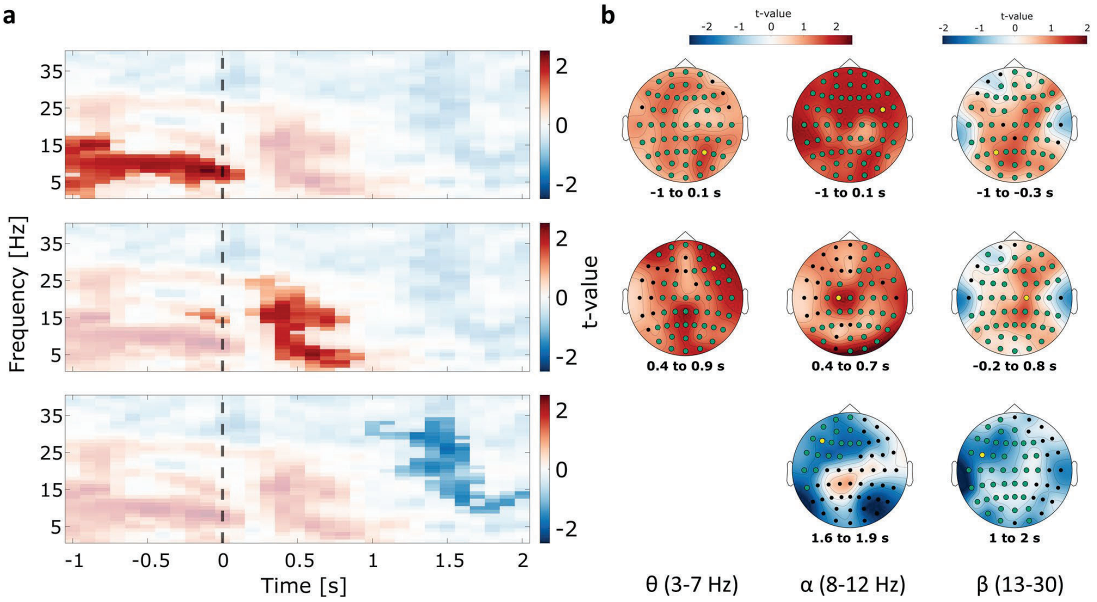


Figure 3. Subsequent memory effects on time–frequency power before and during encoding. Each row corresponds to one of the three distinct clusters observed in the data. (**a**) Time–frequency plots showing the results of the statistical comparison of REM – NOTREM. The vertical dashed line marks the stimulus onset. Positive *t*-values signify greater power for REM trials than NOTREM trials. Opaque data points show a significant difference at $p < 0.5$. Each plot shows one of the three distinct clusters, with *t*-values averaged over the respective electrodes that are part of the cluster: Cluster 1 (*top*) averaged over all electrodes; Cluster 2 (*middle*) averaged over all electrodes except *F7, FT7,* and *T7*; Cluster 3 (*bottom*) averaged over all electrodes except *AF4, AF8, C6, CP4, CP6, F6, F8, FC6, FT8, Fp2, Oz, P4, P6, P8, PO8, T8, TP8*. (**b**) Topographical distributions of t-values within each cluster. The columns display the distributions for the respective frequency band. Channels that are part of the respective cluster are marked in green, while yellow markers show the electrodes with maximum effect.

at electrode *P4*, showing the highest number of data points in the theta range with a statistically significant difference between REM and NOREM trials (Fig. 4). These results indicate that theta power before stimulus onset might be beneficial for the successful encoding of crossmodal associative information. For alpha band oscillations (8–12 Hz), the effect appeared to be most pronounced right before stimulus onset within the lower frequencies of the frequency band. Here, the effects are centered on left temporal as well as right frontal cortical areas, with the maximum effect at location *FC6*. In terms of effects in the beta band (13–30 Hz), the pre-stimulus cluster incorporated only the lower frequencies between 13 and 18 Hz. In this frequency range, the largest effect was observed over left parietal and right frontal areas, most notably at electrode *P3*.

The analysis further revealed a positive cluster in the early post-stimulus interval during encoding. The differences in theta power were most pronounced in central parietal regions as well as frontal areas in the right hemisphere. The strongest effect was observed at electrode *F6* (see Fig. 4). The results indicate that higher theta power during encoding might be positively related to the formation of crossmodal associations. Similar to the pre-stimulus interval, the early post-stimulus cluster spans also the alpha as well as the beta range up to 27 Hz. The maximum effect in the alpha range for this time interval was found at electrode *C1*, while electrode *C2* showed largest effect in the beta band. In the late post-stimulus cluster, however, where REM trials displayed significantly lower oscillatory power as compared to NOTREM trials, differences in beta band activity comprised most of the cluster. Here, the effect was most notable at location *FC5*.

In a next step, we investigated whether memory performance measured by the sensitivity index *d'* scales with the differences in oscillatory power between REM and NOTREM trials. Memory performance was correlated with the power differences for the same time–frequency range (1–40 Hz, − 1 s to 2 s relative to stimulus onset) and corrected for multiple comparisons. The analysis revealed a positive cluster spanning a frequency range of 4–15 Hz and a time interval of − 1 s to 1 s relative to stimulus onset ($p < 0.05$), indicating that greater differences between oscillatory power from REM and NOTREM trials tend to be accompanied by increased memory performance (Fig. 5a,b). For the pre-stimulus interval, the maximum correlation was observed in left parietal and right anterior frontal areas for both the alpha (8–12 Hz) and the theta band (5–7 Hz). Conversely, frontal midline areas showed the highest correlation in the theta band after stimulus onset, while for the alpha band the effect was centered around left anterior frontal and central locations. Furthermore, we were interested in the relationship between REM – NOTREM power differences before and after stimulus onset in the encoding phase for the theta band. A correlational analysis was conducted to estimate the association of power differences in the theta band

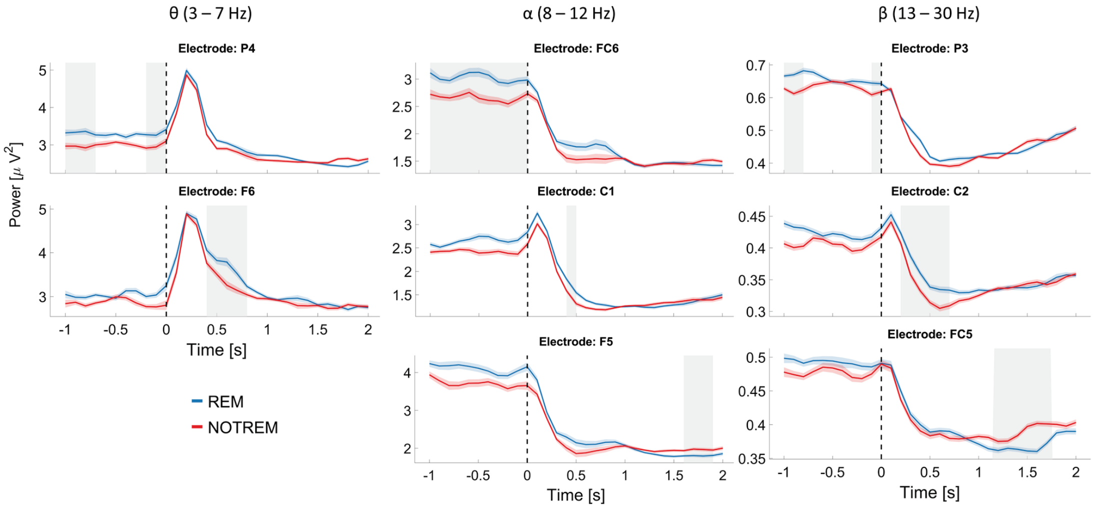


Figure 4. Power time courses for channels with maximum effects. The plot depicts power time courses for single electrodes averaged over the respective frequency bands. Columns denote the frequency range across which oscillatory power was averaged, whereas rows correspond to the three distinct clusters found in the statistical comparison of REM and NOTREM trials (row 1: pre-stimulus cluster; row 2: early post-stimulus cluster; row 3: late pre-stimulus cluster). The shadings around the lines mark the corrected standard error of means across participants[39]. Grey areas mark the time interval for which the difference between REM and NOTREM trials was significant in the respective cluster. The vertical dashed line marks the onset of the audiovisual stimulus pairs.

between pre-stimulus and post-stimulus time intervals. After correcting for multiple comparisons, we observed a significant positive correlation at location *FC6*, $r(49) = 0.48$, $p < 0.05$ (Fig. 5c), indicating that greater pre-stimulus REM-NOTREM power differences coincided with greater post-stimulus differences. When conducting the same analysis in the alpha band, a significant correlation was found at electrode *FC2*, $r(49) = 0.48$, $p < 0.05$.

A possible confound in the analysis of pre-stimulus oscillations could arise from encoding-related activity spilling over across the inter-trial interval and influencing subsequent pre-stimulus activity. To control for that, we investigated whether the duration of the inter-trial interval could reliably predict pre-stimulus theta power on a single-trial basis by using a linear regression approach. Average pre-stimulus theta power was extracted for every REM and NOTREM trial for every participant and was used as the response variable for the model. Only data points that showed significant differences in oscillatory power between REM and NOTREM in cluster-based permutation testing were selected for averaging. Inter-trial duration was submitted as a continuous predictor, while the subsequent memory performance (REM or NOTREM) was used as a binomial predictor. The model differed significantly from a constant model, $F(5664) = 12.4$, $p < 0.001$, but the effect was exclusively driven by the predictor for memory performance, $t = -4.68$, $p < 0.001$. In contrast, inter-trial interval duration did not predict pre-stimulus theta-power on a single-trial basis, $t = -1.62$, $p = 0.104$, indicating that a confound based on oscillatory activity from preceding trials is unlikely.

Phase-based functional connectivity before and during encoding

Cluster-based permutation testing was used to conduct a statistical comparison of phase-based connectivity measures between REM and NOTREM trials to investigate whether visual and auditory areas display increased connectivity in REM trials as compared to NOTREM trials. Statistical estimates were obtained for every time–frequency datapoint from the combinations of seed electrodes to frontocentral electrodes. For all seed electrodes, no significant clusters were found in the data, suggesting that phase-based connectivity between frontocentral and occipital areas did not differ between REM and NOTREM trials. However, on a descriptive level, increased connectivity between occipital and frontocentral sites could be observed for trials with remembered stimuli.

Oscillatory power during memory retrieval

Next, we investigated whether the effects found in the time interval before encoding could also be found before memory retrieval. We used cluster-based permutation analysis to compare oscillatory power between trials where old stimuli were correctly remembered and trials where old stimuli were categorized as not known. No statistically significant difference in the theta band was found in the pre-stimulus interval. Furthermore, we report no difference in alpha or beta power for the pre-stimulus interval in that analysis. However, results show one large negative cluster in the post-stimulus interval, stretching from 0.3 s to 2 s after stimulus onset, and ranging from 1 to 34 Hz across all channels (Fig. 6). This indicates that old stimuli which were correctly remembered were associated with lower theta as well as alpha and beta power during memory retrieval as compared to old stimuli that were not remembered. The effect in the theta band is mainly driven by activity in fronto-temporal

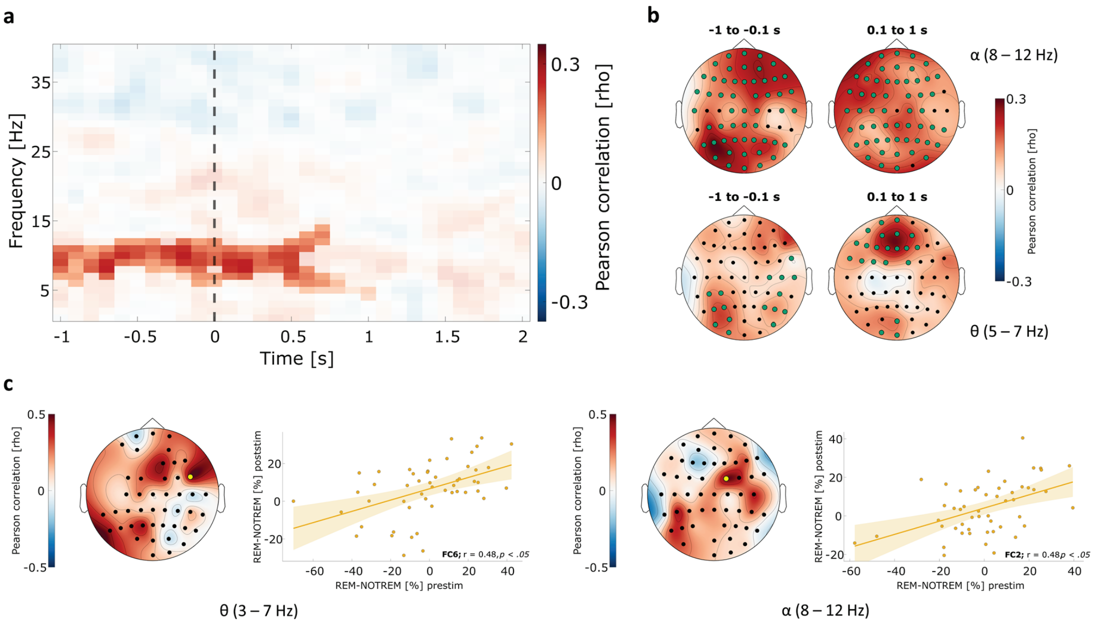


Figure 5. Correlation of pre-stimulus SME magnitude with memory performance and post-stimulus SME. (**a**) Time–frequency plot depicting the results of point-wise correlation of SME magnitude and memory performance measured as *d'*. Data points show individual correlation coefficients, while the opaque data points mark the significant cluster ($p < 0.05$). Positive values signify a positive correlation. The stimulus onset is marked by a vertical dashed line. (**b**) Topographical distribution of correlation coefficients averaged over the pre-stimulus (*left*) and post-stimulus interval (*right*) for the alpha (*top*) and theta band (*bottom*). Channels that are part of the cluster in this time–frequency range are marked in green. (**c**) Relationship between pre-stimulus and post-stimulus SME magnitude for theta and alpha oscillations. For each frequency band, the topographical distribution of correlation coefficients is shown (*left*). The channels with a statistically significant correlation after correcting for multiple comparisons are marked in yellow. Scatter plots show the detailed correlation for the channels with the largest effect.

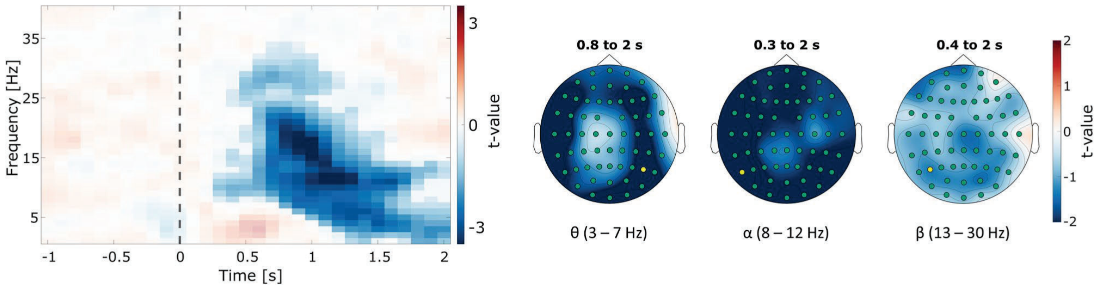


Figure 6. Memory effects on time–frequency power before and during recognition. Depicted are the results of statistically comparing oscillatory power between hit trials (old pairs correctly remembered) and miss trials (old pairs not remembered) from the recognition phase. The time–frequency plot (*left*) shows the *t*-values for every time–frequency data point, averaged over all electrodes. Opaque data points mark the extent of the negative cluster ($p < 0.05$). The stimulus onset is marked by the vertical dashed line. The topographies (*right*) show the topographical distribution of *t*-values averaged over the respective time intervals and frequency bands. Channels that are part of the cluster in this range are marked in green. The yellow circle marks the electrode with largest effect in the statistical comparison.

and lateral-central areas measured 1.2 s to 2 s after stimulus onset, as well as lateral parietal regions. Notably, the maximum effect was observed at electrode *P6*. For the alpha band, the effect peaked at electrode *P7*, while *P5* showed the maximum difference in the beta band. However, the onsets of the alpha and beta band effects were found to be at 0.3 s and 0.5 s after stimulus onset, respectively.

Discussion

The present study investigated the involvement of pre-stimulus oscillatory activity and coupling in the formation of crossmodal associative memory by employing a multimodal Subsequent Memory Effects (SME) paradigm. Participants were required to memorize the association between simultaneously presented images and sounds, and the success of encoding was tested in a subsequent recognition test. We examined the differences in oscillatory power as well as phase-based functional connectivity in the pre-stimulus time interval. Notably, our analyses revealed significant differences in pre-stimulus power in the theta frequency range (3–7 Hz): trials with later remembered stimulus pairs (REM) were accompanied by increased theta as compared to trials with later not remembered stimuli (NOTREM) in the time period directly preceding the stimulus presentation. Similar differences were observed in the alpha (8–12 Hz) as well as the low beta range (13–18 Hz). Interestingly, the magnitude of SMEs in the theta and alpha band positively scaled with memory performance, suggesting a linear relationship between pre-stimulus increases in theta-alpha power and the ability to encode multimodal associations. However, our findings could not support our hypothesis regarding functional connectivity, as the modulation of phase-related connectivity in the theta band did not show a pronounced difference between remembered and not-remembered stimulus pairs. Thus, the present results point towards a memory-related function of theta band power but not phase-based connectivity. Additionally, oscillatory power before and during recognition was compared between REM and NOTREM trials, revealing decreased theta power for REM trials as compared to NOTREM trials. These effects were also found for the alpha and beta bands.

The present findings are in line with previous evidence of increases in theta power before stimulus presentation that were found to be related to more successful encoding of associative content[6,7,10,17]. Increases in theta power during encoding have been associated with better memory performance in experiments using SMEs before, especially when oscillatory data was gathered using non-invasive scalp EEG or MEG[10]. This line of evidence is supported by similar results posited by studies that did not use conventional SME contrasts but compared successful and unsuccessful memory formation based on secondary measures of episodic association, such as confidence ratings[5,40]. Interestingly, intracranial studies rarely reported exclusively positive relationships between theta power and memory performance, but instead rather both positive and negative associations[10,41,42]. In one study, however, Fell and colleagues found increases in hippocampal as well as rhinal cortex theta power in the pre-stimulus interval for later remembered words[19]. Taken together, the evidence seems to support the hypothesis of a positive association of theta power and memory performance in general, with the present results expanding the effect on audiovisual stimulus pairs and the encoding of their associations. This argument is supported by the positive relationship of SME magnitude and *d'* as a measure of memory performance found in this study. Similar results have been presented before in healthy adults[7], supporting the assumption that fluctuations in pre-stimulus theta power might be considered behaviorally relevant. As the maximum effect in the present study was found in right lateral parietal regions, one could speculate about the effect's origin in multisensory processing areas. The angular gyrus, for example, has been strongly associated with the processing of multimodal information, especially combining pieces of sensory information[43]. However, this assumption should be treated with caution due to the spatial limitations of EEG measurements.

In addition to the pre-stimulus difference in theta power, a similar effect was found in the post-stimulus time interval during encoding. Theta power decreased further in NOTREM trials than in REM trials between 500 ms and 900 ms after stimulus onset. This finding is in line with previous reports on higher theta power during encoding being associated with better memory performance[44–47]. Furthermore, visual source memory was found to be accompanied by increased post-stimulus theta power[17]. The present findings show that the encoding of associations of information from different modalities can be similarly modulated by theta activity. However, judging from the topographic distributions of both pre-stimulus and post-stimulus activity, one could assume that mechanisms by which fluctuations in theta power are involved might differ. While differences in pre-stimulus theta power are centered on right parietal and anterior frontal regions, post-stimulus effects peak at central and prefrontal locations. Despite the differing topographies, REM-NOTREM differences in pre- and post-stimlus theta power were found to positively correlate. Interestingly, there was no significant correlation in right parietal locations, but in right frontal areas instead. These results indicate the possibility of differential roles of pre- and post-stimulus theta activity for the formation of crossmodal associations, while still suggesting functional connectedness. Although one cannot conclude any form of causal effect from the present results, one could speculate that pre-stimulus oscillations might affect the memorization of audiovisual associations indirectly by modifying oscillations during the encoding. Further studies are needed to investigate a potentially causal relationship and the mechanisms that might be involved.

Apart from the effects observed in the theta band, our analyses revealed similar differences between REM and NOTREM trials for alpha and low beta activity, showing higher pre-stimulus power for REM trials in both frequency bands. Consequently, the present evidence suggests that associative memory performance may also benefit from increased alpha and beta activity before the encoding of the stimulus is required. This concept aligns with previous research that has explored the links between memory and alpha or beta activity, albeit in terms of preparatory mechanisms and attention. The involvement of alpha activity, for instance, has been thought of as inhibiting task-irrelevant processes to facilitate the encoding of items[9,23,48–50]. Specifically, positive alpha SMEs in the pre- and post-stimulus intervals as observed in the present work might indicate that already encoded information is being suppressed in favor of the upcoming and then current stimulus pair, respectively[30,51,52]. As participants were presented with a multitude of audiovisual pairs that required memorization in each experimental run, it seems plausible that the encoding of a pair would benefit from the suppression of other stimuli that were shown during the encoding phase. These considerations are supported by the positive correlation of REM-NOTREM differences in alpha power and memory performance in the present work, suggesting a role of alpha oscillations and subsequently top-down processes that might be at least as relevant as the proposed theta-based mechanism of binding information.

Similarly, beta activity has been suggested to indicate cognitive preparation processes, as increased oscillatory power was measured for intentional encoding as compared to incidental[11]. These preparation processes were also proposed to be independent of the modality of the stimuli, suggesting the involvement of attentional processes[6]. It seems reasonable to assume that the successful encoding of crossmodal associations recorded in the present study would benefit from preparatory attentional processes as well, as participants were also explicitly instructed to memorize these associations. In contrast, we observed a strong negative effect in the late post-stimulus interval primarily in the beta band. Decreases in the beta band have been theorized to reflect semantic processing of to-be-encoded items[30,47], and are assumed to originate in the left prefrontal cortex[53]. Although one must account for spatial inaccuracies when interpreting EEG results, the present findings point in a similar direction, as the maximum effect for this SME was observed in left frontal areas. One could speculate that oscillations in the beta range serve multiple purposes depending on whether or not actual stimulus material needs to be processed or not. Positive SMEs before stimulus onset might reflect stimulus-independent preparatory processes, while negative SMEs during stimulus presentation could be interpreted as a marker of semantic processing. Furthermore, as the effect is mostly centered around left frontal areas instead of visual or auditory locations, one could argue that the semantic processing takes place independent of sensory modality, but on the level of associations.

The topographies of pre-stimulus SMEs further support the notion that theta as well as alpha and beta oscillations might contribute to successful memory formation in different ways. While power differences in the theta range were most pronounced in right parietal areas, the effects in the alpha range were centered on left temporal and frontal locations. Effects in the beta range were found to be strongest around left parietal and right frontal areas. Frontal midline theta oscillations have long since been associated with episodic memory formation and retrieval[54], while sections of the parietal lobe are usually associated with multisensory association processes[55,56]. The different topographical distributions of power differences for the pre-stimulus interval could thus be interpreted as the involvement of different cognitive processes. Considering the results from pre- and post-stimulus activity, we suggest increased pre-stimulus theta power to represent non-general preparatory processes specifically for binding, while being a marker for the actual binding of information during encoding. One could assume that these binding-specific processes are modulated by processes of task-specific inhibition in the alpha, as well as preparatory and semantic processing in the beta range. However, as evidence for spatial patterns is limited in EEG, future studies will need to test the contribution of different brain areas to the reported effects by investigating differences in BOLD signal using fMRI measurements, as well as address the question of which frequency band might be the primary driver of subsequent memory effects in the encoding of crossmodal associations.

No differences were found between REM and NOTREM trials in terms of phase-based connectivity in the pre-stimulus and post-stimulus intervals. Thus, the evidence could not support our second hypothesis, suggesting that functional connectivity between visual and auditory areas might not be beneficial for the encoding of crossmodal associations. These results are not in line with several previous studies that were able to establish a phase-based relation between auditory and visual areas by oscillating audiovisual stimulus pairs in a theta frequency for differing degrees of synchrony[20,21]. Memory performance was found to be best when stimuli were not shown at a phase offset and oscillated at a frequency of 4 Hz. Under the assumption that the phase synchrony at stimulus onset was involved in the effect that the authors found, the present results might point in the same direction, although the effect is ostensibly weaker. In another study, pre-stimulus theta connectivity within the default mode network showed the lowest prediction accuracy when predicting associative memory performance as compared to other frequency bands[33]. Interestingly, the authors reported generally higher prediction accuracies based on connectivity measures calculated for the post-stimulus interval. Notably, other lines of evidence suggest that pre-stimulus theta phase may only be connected to successful, but not to the unsuccessful encoding of associative pairings, while not observing any significant effects for pre-stimulus theta power[34]. However, the present results could also be interpreted in a way such that cortical connectivity might only play an ancillary role in binding crossmodal information for long-term memory. Instead, it could be speculated that sensory areas are phase-locked to cells in the hippocampus individually but are not functionally connected to each other for the binding process. Indeed, hippocampal projections have been suggested to drive theta oscillations in neocortical areas[57]. Furthermore, theta oscillations have been reported to reflect the dynamic integration of information from multiple sources[58], as well as present a mechanism to functionally align the hippocampus to prefrontal cortices during recollection[40]. Additional evidence from animal studies points towards the importance of hippocampal CA1 cells for the integration of not only spatial but different kinds of sensory information from stimuli whose presentation overlapped in the time domain[14]. The authors argued that the hippocampus organizes relational networks for episodic memory, integrating phase-locked information coming in from sensory modalities. However, further research into phase-based connectivity between the hippocampus and sensory areas in the neocortex is needed, as the present results cannot account for oscillatory activity in deeper layers of the brain.

Finally, we also investigated oscillatory activity before and during retrieval. The analysis revealed that power significantly decreased in the post-stimulus interval for trials in which already-shown stimuli were remembered. This effect was found not only in the theta band but also in alpha and beta oscillations. As most studies investigating oscillatory mechanisms in episodic memory focus on effects during or before encoding, evidence on desynchronization during retrieval in the theta band has been rarely presented before. Some studies presented evidence on a positive relationship between theta power during retrieval and successful episodic memory[5], whereas work in the context of interference and interference resolution reported positive as well as negative effects[59,60]. In one study, Pastötter and Bäuml found decreases in power that were associated with better memory performance only in high theta frequencies, while lower frequencies showed increases instead[60]. The present results are only partially in line with the previous evidence, as decreases in theta power associated with better memory performance were also found in the lower frequency of the theta band. One possible explanation could be that the power in REM trials decreased further due to longer processing time of the auditory stimuli of the pairs[61]. This decrease could then be interpreted as a positive effect for behavior. On another note, decreases in alpha power during the retrieval of associative information have been shown before. When participants were required to remember associations between words, Martín-Buro and colleagues found post-stimulus decreases between 10 and 12 Hz as early as 0.5 s after stimulus onset, predominantly in left parietal areas[62]. By comparing different degrees of successful encoding the authors suggested that decreases in alpha power during retrieval might reflect the accumulation of mnemonic evidence. Although, in the present study, successful trials were compared to trials with unsuccessful encoding, one could argue that the results might reflect a similar gradient of mnemonic evidence accumulation even for associations between different modalities, given that the peak effects were also found in left parietal areas. However, interpreting these results should be done with caution, as no hypotheses were formulated regarding the effects of oscillatory activity before and during retrieval. We recommend further research focusing explicitly on oscillatory activity during retrieval to expand understanding in that matter.

Conclusion

This study investigated subsequent memory effects for oscillatory activity in the theta, alpha and low beta frequency range. Specifically, differences in oscillatory power and naturally occurring phase-based connectivity between later remembered and not remembered audiovisual stimulus pairs were analyzed. Importantly, theta power was found to differentiate between successful and unsuccessful encoding already prior to the stimulus presentation, i.e. in the pre-stimulus interval. The magnitude of this effect was found to be directly related to memory performance. Similar effects were observed in the alpha band and, to a lesser degree, in the beta band. In contrast, only weak evidence was observed for the assumed role of phase-based connectivity between visual and auditory brain areas for memory performance. The present findings reinforce the notion that theta band activity might be relevant in binding information from different modalities for episodic memory, and, more generally, highlight the impact of brain states before stimulus presentation on their subsequent processing. We argue that the theta-based binding mechanism might work in conjunction with inhibitory, as well as preparatory and semantic processes represented by alpha and beta oscillations, respectively, that benefit the encoding of crossmodal associations. Further research is needed to elucidate the interactions between oscillations of different frequencies, as well as the involvement of hippocampal theta oscillations in cortical processes for crossmodal associative memory.

Data availability

All data and code can be made available upon request through a data sharing agreement with the authors.

Received: 1 December 2023; Accepted: 26 March 2024

References

1. Salari, N., Büchel, C. & Rose, M. Functional dissociation of ongoing oscillatory brain states. *PLoS ONE* **7**(5), e38090. https://doi.org/10.1371/JOURNAL.PONE.0038090 (2012).
2. Roberts, D. M., Fedota, J. R., Buzzell, G. A., Parasuraman, R. & McDonald, C. G. Prestimulus oscillations in the alpha band of the EEG are modulated by the difficulty of feature discrimination and predict activation of a sensory discrimination process. *J. Cogn. Neurosci.* **26**(8), 1615–1628. https://doi.org/10.1162/JOCN_A_00569 (2014).
3. Van Dijk, H., Schoffelen, J. M., Oostenveld, R. & Jensen, O. Prestimulus oscillatory activity in the alpha band predicts visual discrimination ability. *J. Neurosci.* **28**(8), 1816–1823. https://doi.org/10.1523/JNEUROSCI.1853-07.2008 (2008).
4. Bengson, J. J., Kelley, T. A., Zhang, X., Wang, J. L. & Mangun, G. R. Spontaneous neural fluctuations predict decisions to attend. *J. Cogn. Neurosci.* **26**(11), 2578–2584. https://doi.org/10.1162/JOCN_A_00650 (2014).
5. Addante, R. J., Watrous, A. J., Yonelinas, A. P., Ekstrom, A. D. & Ranganath, C. Prestimulus theta activity predicts correct source memory retrieval. *Proc. Natl. Acad. Sci. U. S. A.* **108**(26), 10702–10707. https://doi.org/10.1073/pnas.1014528108 (2011).
6. Scholz, S., Schneider, S. L. & Rose, M. Differential effects of ongoing EEG beta and theta power on memory formation. *PLoS One* **12**(2), e0171913. https://doi.org/10.1371/journal.pone.0171913 (2017).
7. Winterling, S. L., Shields, S. M. & Rose, M. Reduced memory-related ongoing oscillatory activity in healthy older adults. *Neurobiol. Aging* **79**, 1–10. https://doi.org/10.1016/j.neurobiolaging.2019.03.012 (2019).
8. Salari, N. & Rose, M. Dissociation of the functional relevance of different pre-stimulus oscillatory activity for memory formation. *Neuroimage* **125**, 1013–1021. https://doi.org/10.1016/j.neuroimage.2015.10.037 (2016).
9. Klimesch, W., Fellinger, R. & Freunberger, R. Alpha oscillations and early stages of visual encoding. *Front. Psychol.* https://doi.org/10.3389/fpsyg.2011.00118 (2011).
10. Herweg, N. A., Solomon, E. A. & Kahana, M. J. Theta oscillations in human memory. *Trends Cogn. Sci.* **24**(3), 208–227. https://doi.org/10.1016/j.tics.2019.12.006 (2020).
11. Schneider, S. L. & Rose, M. Intention to encode boosts memory-related pre-stimulus EEG beta power. *Neuroimage* **125**, 978–987. https://doi.org/10.1016/j.neuroimage.2015.11.024 (2016).
12. Buzsáki, G. & Moser, E. I. Memory, navigation and theta rhythm in the hippocampal-entorhinal system. *Nat. Neurosci.* **16**(2), 130–138. https://doi.org/10.1038/nn.3304 (2013).
13. Huxter, J., Burgess, N. & O'Keefe, J. Independent rate and temporal coding in hippocampal pyramidal cells. *Nature* **425**(6960), 828–832. https://doi.org/10.1038/nature02058 (2003).
14. Terada, S., Sakurai, Y., Nakahara, H. & Fujisawa, S. Temporal and rate coding for discrete event sequences in the hippocampus. *Neuron* **94**(6), 1248-1262.e4. https://doi.org/10.1016/J.NEURON.2017.05.024 (2017).
15. Gruber, M. J., Watrous, A. J., Ekstrom, A. D., Ranganath, C. & Otten, L. J. Expected reward modulates encoding-related theta activity before an event. *Neuroimage* **64**(1), 68–74. https://doi.org/10.1016/j.neuroimage.2012.07.064 (2013).

16. Merkow, M. B., Burke, J. F., Stein, J. M. & Kahana, M. J. Prestimulus theta in the human hippocampus predicts subsequent recognition but not recall. *Hippocampus* **24**(12), 1562–1569. https://doi.org/10.1002/HIPO.22335 (2014).
17. Staudigl, T. & Hanslmayr, S. Theta oscillations at encoding mediate the context-dependent nature of human episodic memory. *Curr. Biol.* **23**(12), 1101–1106. https://doi.org/10.1016/j.cub.2013.04.074 (2013).
18. Haque, R. U., Wittig, J. H., Damera, S. R., Inati, S. K. & Zaghloul, K. A. Cortical low-frequency power and progressive phase synchrony precede successful memory encoding. *J. Neurosci.* **35**(40), 13577–13586. https://doi.org/10.1523/JNEUROSCI.0687-15.2015 (2015).
19. Fell, J. *et al.* Medial temporal theta/alpha power enhancement precedes successful memory encoding: Evidence based on intracranial EEG. *J. Neurosci.* **31**(14), 5392–5397. https://doi.org/10.1523/JNEUROSCI.3668-10.2011 (2011).
20. Clouter, A., Shapiro, K. L. & Hanslmayr, S. Theta phase synchronization is the glue that binds human associative memory. *Curr. Biol.* **27**(20), 3143-3148.e6. https://doi.org/10.1016/j.cub.2017.09.001 (2017).
21. Wang, D., Clouter, A., Chen, Q., Shapiro, K. L. & Hanslmayr, S. Single-trial phase entrainment of theta oscillations in sensory regions predicts human associative memory performance. *J. Neurosci.* **38**(28), 6299–6309. https://doi.org/10.1523/JNEUROSCI.0349-18.2018 (2018).
22. Klimesch, W. Alpha-band oscillations, attention, and controlled access to stored information. *Trends Cogn. Sci.* **16**(12), 606–617. https://doi.org/10.1016/j.tics.2012.10.007 (2012).
23. Strunk, J. & Duarte, A. Prestimulus and poststimulus oscillatory activity predicts successful episodic encoding for both young and older adults. *Neurobiol. Aging* **77**, 1–12. https://doi.org/10.1016/j.neurobiolaging.2019.01.005 (2019).
24. Waldhauser, G. T., Johansson, M. & Hanslmayr, S. Alpha/beta oscillations indicate inhibition of interfering visual memories. *J. Neurosci.* **32**(6), 1953–1961. https://doi.org/10.1523/JNEUROSCI.4201-11.2012 (2012).
25. Sokol, S. Visually evoked potentials: Theory, techniques and clinical applications. *Surv. Ophthalmol.* **21**(1), 18–44. https://doi.org/10.1016/0039-6257(76)90046-1 (1976).
26. Mulert, C. *et al.* Auditory cortex and anterior cingulate cortex sources of the early evoked gamma-band response: Relationship to task difficulty and mental effort. *Neuropsychologia* **45**(10), 2294–2306. https://doi.org/10.1016/j.neuropsychologia.2007.02.020 (2007).
27. Leicht, G. *et al.* Reduced early auditory evoked gamma-band response in patients with schizophrenia. *Biol. Psychiatry* **67**(3), 224–231. https://doi.org/10.1016/j.biopsych.2009.07.033 (2010).
28. Otten, L. J., Quayle, A. H., Akram, S., Ditewig, T. A. & Rugg, M. D. Brain activity before an event predicts later recollection. *Nat. Neurosci.* **9**(4), 489–491. https://doi.org/10.1038/nn1663 (2006).
29. Gruber, M. J. & Otten, L. J. Voluntary control over prestimulus activity related to encoding. *J. Neurosci.* **30**(29), 9793–9800. https://doi.org/10.1523/JNEUROSCI.0915-10.2010 (2010).
30. Hanslmayr, S., Staudigl, T. & Fellner, M. C. Oscillatory power decreases and long-term memory: The information via desynchronization hypothesis. *Front. Hum. Neurosci.* **6**, 1–20. https://doi.org/10.3389/fnhum.2012.00074 (2012).
31. Park, H. & Rugg, M. D. Prestimulus hippocampal activity predicts later recollection. *Hippocampus* **20**(1), 24–28. https://doi.org/10.1002/hipo.20663 (2010).
32. Addante, R. J., de Chastelaine, M. & Rugg, M. D. Pre-stimulus neural activity predicts successful encoding of inter-item associations. *Neuroimage* **105**, 21–31. https://doi.org/10.1016/j.neuroimage.2014.10.046 (2015).
33. Kim, D., Jeong, W., Kim, J. S. & Chung, C. K. Single-trial EEG connectivity of default mode network before and during encoding predicts subsequent memory outcome. *Front. Syst. Neurosci.* https://doi.org/10.3389/fnsys.2020.591675 (2020).
34. Cruzat, J. *et al.* The phase of Theta oscillations modulates successful memory formation at encoding. *Neuropsychologia* **154**, 107775. https://doi.org/10.1016/j.neuropsychologia.2021.107775 (2021).
35. Staudigl, T., Vollmar, C., Noachtar, S. & Hanslmayr, S. Temporal-pattern similarity analysis reveals the beneficial and detrimental effects of context reinstatement on human memory. *J. Neurosci.* **35**(13), 5373–5384. https://doi.org/10.1523/JNEUROSCI.4198-14.2015 (2015).
36. Parise, C. V. & Spence, C. Audiovisual crossmodal correspondences and sound symbolism: A study using the implicit association test. *Exp. Brain Res.* **220**(3–4), 319–333. https://doi.org/10.1007/s00221-012-3140-6 (2012).
37. Oostenveld, R., Fries, P., Maris, E. & Schoffelen, J. FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput. Intell. Neurosci.* https://doi.org/10.1155/2011/156869 (2011).
38. Vinck, M., Oostenveld, R., Van Wingerden, M., Battaglia, F. & Pennartz, C. M. A. An improved index of phase-synchronization for electrophysiological data in the presence of volume-conduction, noise and sample-size bias. *Neuroimage* **55**(4), 1548–1565. https://doi.org/10.1016/j.neuroimage.2011.01.055 (2011).
39. Morey, R. D. Confidence intervals from normalized data: A correction to Cousineau (2005). *Tutor. Quant. Methods Psychol.* **4**(2), 61–64. https://doi.org/10.20982/tqmp.04.2.p061 (2008).
40. Herweg, N. A. *et al.* Theta-alpha oscillations bind the hippocampus, prefrontal cortex, and striatum during recollection: Evidence from simultaneous EEG–fMRI. *J. Neurosci.* **36**(12), 3579–3587. https://doi.org/10.1523/JNEUROSCI.3629-15.2016 (2016).
41. Greenberg, J. A., Burke, J. F., Haque, R., Kahana, M. J. & Zaghloul, K. A. Decreases in theta and increases in high frequency activity underlie associative memory encoding. *Neuroimage* **114**, 257–263. https://doi.org/10.1016/J.NEUROIMAGE.2015.03.077 (2015).
42. Weidemann, C. T. *et al.* Neural activity reveals interactions between episodic and semantic memory systems during retrieval. *J. Exp. Psychol. Gen.* **148**(1), 1–12. https://doi.org/10.1037/XGE0000480 (2019).
43. Seghier, M. L. The angular gyrus: Multiple functions and multiple subdivisions. *Neuroscience* **19**(1), 43–61. https://doi.org/10.1177/1073858412440596 (2013).
44. Khader, P. H., Jost, K., Ranganath, C. & Rösler, F. Theta and alpha oscillations during working-memory maintenance predict successful long-term memory encoding. *Neurosci. Lett.* **468**(3), 339–343. https://doi.org/10.1016/J.NEULET.2009.11.028 (2010).
45. Hanslmayr, S. *et al.* The relationship between brain oscillations and BOLD signal during memory formation: A combined EEG-fMRI study. *J. Neurosci.* **31**(44), 15674–15680. https://doi.org/10.1523/JNEUROSCI.3140-11.2011 (2011).
46. Osipova, D. *et al.* Theta and gamma oscillations predict encoding and retrieval of declarative memory. *J. Neurosci.* **26**(28), 7523–7531. https://doi.org/10.1523/JNEUROSCI.1948-06.2006 (2006).
47. Hanslmayr, S., Spitzer, B. & Bäuml, K. H. Brain oscillations dissociate between semantic and nonsemantic encoding of episodic memories. *Cereb. Cortex* **19**(7), 1631–1640. https://doi.org/10.1093/cercor/bhn197 (2009).
48. Bonnefond, M. & Jensen, O. The role of gamma and alpha oscillations for blocking out distraction. *Commun. Integr. Biol.* **6**(1), e22702. https://doi.org/10.4161/cib.22702 (2013).
49. Minarik, T., Berger, B. & Sauseng, P. The involvement of alpha oscillations in voluntary attention directed towards encoding episodic memories. *Neuroimage* **166**, 307–316. https://doi.org/10.1016/j.neuroimage.2017.10.064 (2018).
50. Payne, L., Guillory, S. & Sekuler, R. Attention-modulated alpha-band oscillations protect against intrusion of irrelevant information. *J. Cogn. Neurosci.* **25**(9), 1463–1476. https://doi.org/10.1162/jocn_a_00395 (2013).
51. Jensen, O., Gelfand, J., Kounios, J. & Lisman, J. E. Oscillations in the alpha band (9–12 Hz) increase with memory load during retention in a short-term memory task. *Cereb. Cortex* **12**(8), 877–882. https://doi.org/10.1093/cercor/12.8.877 (2002).
52. Meeuwissen, E. B., Takashima, A., Fernández, G. & Jensen, O. Increase in posterior alpha activity during rehearsal predicts successful long-term memory formation of word sequences. *Hum. Brain Mapp.* **32**(12), 2045–2053. https://doi.org/10.1002/hbm.21167 (2011).

53. Meeuwissen, E. B., Takashima, A., Fernández, G. & Jensen, O. Evidence for human fronto-central gamma activity during long-term memory encoding of word sequences. *PLoS One* **6**(6), e21356. https://doi.org/10.1371/journal.pone.0021356 (2011).
54. Hsieh, L. T. & Ranganath, C. Frontal midline theta oscillations during working memory maintenance and episodic encoding and retrieval. *Neuroimage* **85**, 721–729. https://doi.org/10.1016/j.neuroimage.2013.08.003 (2014).
55. Sereno, M. I. & Huang, R. S. Multisensory maps in parietal cortex. *Curr. Opin. Neurobiol.* **24**(1), 39–46. https://doi.org/10.1016/j.conb.2013.08.014 (2014).
56. Rohe, T. & Noppeney, U. Distinct computational principles govern multisensory integration in primary sensory and association cortices. *Curr. Biol.* **26**(4), 509–514. https://doi.org/10.1016/j.cub.2015.12.056 (2016).
57. Ekstrom, A. D. *et al.* Human hippocampal theta activity during virtual navigation. *Hippocampus* **15**(7), 881–889. https://doi.org/10.1002/HIPO.20109 (2005).
58. Feng, T., Silva, D., Foster, D. J. & Snyder, S. H. Dissociation between the experience-dependent development of hippocampal theta sequences and single-trial phase precession. *J. Neurosci.* **35**(12), 4890–4902. https://doi.org/10.1523/JNEUROSCI.2614-14.2015 (2015).
59. Khader, P. H. & Rösler, F. EEG power changes reflect distinct mechanisms during long-term memory retrieval. *Psychophysiology* **48**(3), 362–369. https://doi.org/10.1111/j.1469-8986.2010.01063.x (2011).
60. Pastötter, B. & Bäuml, K.-H.T. Distinct slow and fast cortical theta dynamics in episodic memory retrieval. *Neuroimage* **94**, 155–161. https://doi.org/10.1016/j.neuroimage.2014.03.002 (2014).
61. Robinson, C. W., Chadwick, K. R., Parker, J. L. & Sinnett, S. Listen to your heart: Examining modality dominance using cross-modal oddball tasks. *Front. Psychol.* https://doi.org/10.3389/FPSYG.2020.01643 (2020).
62. Martín-Buro, M. C., Wimber, M., Henson, R. N. & Staresina, B. P. Alpha rhythms reveal when and where item and associative memories are retrieved. *J. Neurosci.* **40**(12), 2510–2518. https://doi.org/10.1523/JNEUROSCI.1982-19.2020 (2020).

Acknowledgements

The present research was supported by the German Research Foundation (DFG; SFB/Transregio 169, Project B3, and DFG RO 2653/9-1). We thank Marike Maack for the lively discussion and helpful comments on the manuscript, as well as Carla Mourkojannis and Donna Löding for their help in data acquisition.

Author contributions

Jan Ostrowski: Software, Validation, Formal Analysis, Investigation, Data Curation, Writing—Original Draft, Writing—Review and Editing, Visualization. Michael Rose: Conceptualization, Methodology, Software, Validation, Resources, Writing—Review and Editing, Supervision, Project administration, Funding acquisition.

Funding

Open Access funding enabled and organized by Projekt DEAL.

Competing interests

The authors declare no competing interests.

Additional information

Correspondence and requests for materials should be addressed to J.O.

10.2 Study 2: Disentangling the Functional Roles of Pre-Stimulus Oscillations in Crossmodal Associative Memory Formation via Sensory Entrainment

Ostrowski, J.*, Maack, M.C.*, & Rose, M. (accepted). Disentangling the Functional Roles of Pre-Stimulus Oscillations in Crossmodal Associative Memory Formation via Sensory Entrainment. bioRxiv 2025.06.24.661289. https://doi.org/10.1101/2025.06.24.661289

Note: By the time of submission of this thesis, this article has been accepted for publication by Scientific Reports. An edited version of this article has not been available yet, so the most recent version of the manuscript was attached to this thesis.

Disentangling the Functional Roles of Pre-Stimulus Oscillations in Crossmodal Associative Memory Formation via Sensory Entrainment

Jan Ostrowski[1†], Marike C. Maack[1†], Michael Rose[1*]

1 *Department of Systems Neuroscience, University Medical Center Hamburg-Eppendorf, Hamburg, Germany;* j.ostrowski@uke.de, m.maack@uke.de, rose@uke.de

† Equal contributions

** Correspondence:* rose@uke.de

16-digit ORCID:

JO: 0000-0001-9928-272X

MM: 0000-0002-6960-4465

MR: 0000-0002-9789-7066

Impact Statement

By using sensory entrainment of pre-stimulus oscillations we could show that alpha-band stimulation in particular enhanced crossmodal memory. These findings reveal a frequency-specific functional dissociation and highlight the potential of targeting preparatory brain rhythms to improve crossmodal memory formation.

Abstract

The state of neural dynamics prior to the presentation of an external stimulus significantly influences its subsequent processing. This neural preparatory mechanism might be of particular importance for crossmodal memory formation. The integration of stimuli across different sensory modalities is a fundamental mechanism underlying the formation of episodic memories. However, the causal role of pre-stimulus neural activity in this process remains largely unclear. In this preregistered study, we investigate the direct relationship between transient brain states induced by sensory entrainment and crossmodal memory encoding. Participants (*n* = 105) received rhythmic visual stimuli at theta (5 Hz) or alpha (9 Hz) frequencies to evoke specific brain states. EEG recordings confirmed successful entrainment, with sustained increases in neural activity within the stimulated frequency bands persisting until stimulus onset. Notably, induced alpha oscillatory activity enhanced recognition memory performance reflected by increased sensitivity, and suggesting that alpha oscillations prepare the brain for optimal multisensory integration. These findings highlight the functional significance of distinct oscillatory brain states in facilitating memory encoding by increasing cortical excitability before stimulus presentation. Overall, our results emphasize the importance of pre-stimulus brain states in shaping the efficiency of memory formation across sensory modalities and shed light on how dynamic neural preparations support learning.

Keywords

Pre-Stimulus Entrainment, Visual Sensory Stimulation, Crossmodal Learning, Associative Memory Formation, Theta Oscillations, Alpha Oscillations

Introduction

Multisensory learning is fundamental for human cognition, enabling the encoding and retrieval of complex environmental information. In daily life, individuals continuously integrate sensory information from multiple modalities, such as visual and auditory stimuli, to enhance memory performance. This ability to form crossmodal associations supports essential cognitive functions, especially episodic memory formation[1,2]. Given the relevance of multisensory learning, understanding the underlying neural mechanisms has become a key objective in cognitive neuroscience. Brain oscillations play a critical role in coordinating neural activity during multisensory learning. Theta oscillations (3–7 Hz) have been widely implicated in the formation of episodic memory, particularly in binding disparate elements of experience into coherent memories[3–5]. Research suggests that theta rhythms support the temporal organization of information, facilitating associative encoding across modalities[6–8]. Additionally, alpha oscillations (8–12 Hz) have been associated with attentional selection, serving as a gating mechanism to suppress irrelevant sensory input and enhance task-relevant processing[9–11]. However, the precise role of pre-stimulus theta and alpha dynamics of memory formation during multisensory learning remains unclear.

A growing body of evidence highlights the importance of pre-stimulus neural activity in shaping subsequent cognitive processing[12–17]. Pre-stimulus theta and alpha power fluctuations have been linked to successful memory formation[18–22], suggesting that oscillatory states before stimulus presentation may serve a preparatory function[23–25]. In particular, we were able to support this notion in a previous investigation, where participants were required to memorize audiovisual pairs in a Subsequent Memory Effects task (SME)[26]. We could demonstrate that theta and alpha oscillations have a significant impact on memory encoding during the pre-stimulus phase, as increases in theta (3–7 Hz) and alpha power (8–12 Hz) observed before stimulus presentation were associated with enhanced memory performance. Specifically, higher pre-stimulus theta and alpha activity has been linked to better recognition of crossmodal associations between stimuli, such as visual and auditory inputs.

These findings propose that pre-stimulus oscillations might optimize encoding conditions[14,27], aligning neural activity with upcoming information[19,22,28,29]. However, a causal link between pre-stimulus oscillatory activity and successful learning has not yet been demonstrated. One promising approach is the modulation of pre-stimulus frequencies through entrainment. These methods, such as transcranial alternating current stimulation (tACS) and rhythmic sensory stimulation, provide the means to modulate oscillatory activity in a non-invasive manner[30–33]. The application of external rhythmic stimulation can synchronize endogenous neural rhythms at targeted frequencies[34–37], thereby affecting cognitive processes, and subsequently behavior[30,38,39]. In sensory entrainment, neural oscillations are modified by an external visual or auditory stimulus during encoding. Depending on the sensory domain, either luminance or amplitude oscillate in a specific frequency, leading to increases in oscillatory power. As the brain synchronizes with these external rhythms, it may become more aligned at integrating sensory details into structured memories[40–43]. Given the evidence that pre-stimulus oscillatory activity can affect memory performance, investigating whether externally applied rhythmic stimulation can modulate these oscillatory states to enhance learning is crucial to reveal a direct functional role of this neural mechanism. Furthermore, this might allow researchers to determine in a causal framework whether the potential enhancement of multisensory memory formation stems from improved temporal binding (theta) or more effective suppression of irrelevant information (alpha). However, studies investigating sensory entrainment in the context of multisensory learning have yielded mixed results so far[43–45].

This pre-registered study aims to examine a direct link between pre-stimulus states of theta and alpha oscillations and multisensory memory formation by using visual sensory entrainment, while also addressing existing challenges in sensory entrainment through an optimized experimental paradigm. Using a between-subjects design, participants were required to memorize and later recognize pairs of visual and auditory stimuli. Visual sensory entrainment was presented immediately before each stimulus from the encoding task at either 5 Hz (theta group) or 9 Hz (alpha group). The choice of entrainment frequencies was based on observed effects from prior research where the same SME paradigm was use[26]. Arrhythmic stimulation was used as a control condition in which the entrainment oscillations were derived randomly from frequencies between 13 and 24 Hz. This approach extends previous work through a refined experimental design, allowing us to test whether pre-stimulus sensory entrainment might influence neural oscillations and memory performance. We used visual stimulation to entrain theta and alpha rhythms in the occipital cortex, as evidence suggests that oscillatory entrainment in sensory regions can influence memory-related networks[44]. While frontal-midline theta oscillations are a known correlate of memory, especially during stimulus presentation[46], our approach examines how preparatory visual-cortical oscillations might propagate their effects to these memory networks during pre-stimulus crossmodal encoding.

Building upon prior research, the current study aims to replicate and extend previous findings through a refined experimental design that systematically manipulates brain oscillations before stimulus onset. First, we first expected that using an oscillating image as a stimulus for sensory entrainment will be successful in modifying oscillatory activity and hypothesized that it will lead to increased oscillatory power within the entrained frequency ranges (H1). Importantly, we hypothesized that both theta (H2a) and alpha (H2b) entrainment would enhance memory performance as compared to controls. Moreover, we hypothesized that theta and alpha entrainment might affect memory performance to a different degree, resulting in potential differences between the two conditions (H2c). Additionally, we expected that both theta and alpha entrainment might lead to improved memory performance as compared to no entrainment, which we assessed through a statistical comparison with the dataset from the previous study (H3).

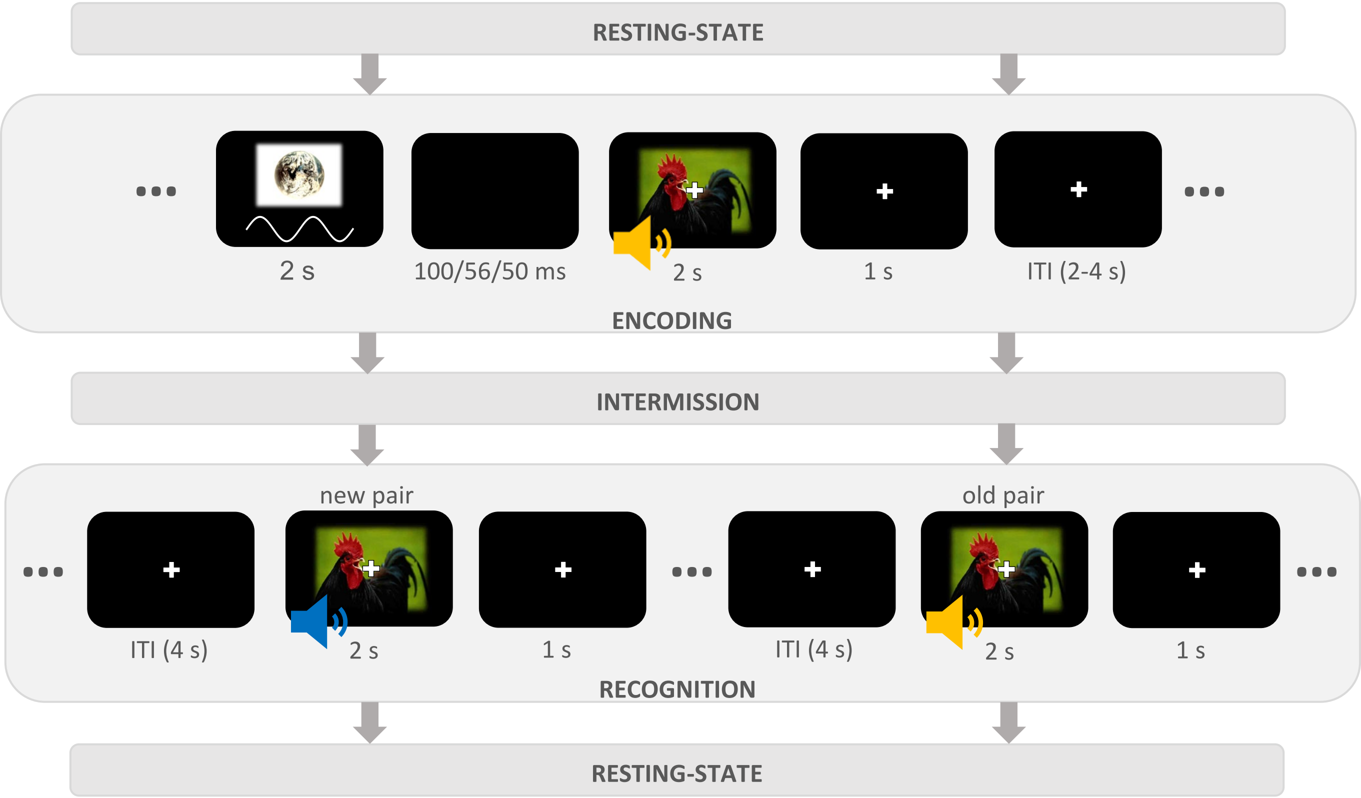


Figure 1. Schematic overview of one experimental run of the SME task. Each encoding trial began with a frequency-specific visual entrainment stimulus that lasted 2 s, followed by a black screen whose presentation duration differed depending on the group (theta: 100 ms; alpha: 56 ms; control: 50 ms). During entrainment, the luminance varied in a sinusoidal manner, resulting in a rhythmic oscillation of 5 Hz in the theta group and 9 Hz in the alpha group. Then, an image–sound pair was presented for 2 s, followed by a fixation cross for 1 s. Taken together, this comprised the possible window for responses. Participants judged whether both stimuli represented animals and were instructed to memorize each audiovisual combination. A fixation cross remained visible on the screen during the subsequent inter-trial interval of 2 to 4 s. In the recognition task, participants were presented with previously shown (old) and recombined (new) audiovisual pairs and indicated whether they remembered the particular combination of image and sound or not. Stimuli were shown for 2 s, and responses were recorded up to 3 s after stimulus onset. The inter-trial interval was fixed at 4 s, during which a fixation cross was shown. In the intermission between each encoding and recognition task, participants were presented with a short distraction task.

Results

In this study, participants (n = 105) performed in a sequential memory encoding and recognition task across three experimental runs, each containing audiovisual pairings that the participants were instructed to memorize (**Figure 1**). Prior to each pairing in the encoding phase, participants were exposed to rhythmic visual stimulation at either theta (5 Hz) or alpha (9 Hz) frequencies, or exposed to arrhythmic stimulation (control) for two seconds. Each encoding run was followed by a short distractor task and a recognition phase, in which previously seen pairs were randomly intermixed with recombined lures. Participants indicated whether each pair was old or new via button press. We implemented an open-ended sequential design for gathering evidence, taking advantage of the Bayesian statistical framework. The data collection concluded either when at least moderate evidence had been gathered to accept or reject the null hypothesis for the respective contrast or when group size reached $k = 35$ for each group.

Successful pre-stimulus visual stimulation enhanced power in targeted frequency

The focus of this study was to test whether visual sensory entrainment before the presentation of a stimulus would affect its subsequent encoding and thus result in changes in memory performance. As a prerequisite, we needed to make sure that the entrainment procedure would increase oscillatory power in the frequency bands corresponding to the entrainment frequencies (H1). To that end, oscillatory power in the late entrainment period (-1.1 s to -0.1 s relative to stimulus onset) from the theta and alpha entrainment groups was contrasted with the recorded activity from the control group. Two-tailed independent-samples *t*-tests were used on sample level, with a cluster-based permutation approach to account for multiple comparisons. The analysis was conducted for a frequency range of 1 to 40 Hz across the entire channel space. Comparing activity from the theta group with the control group, our analysis revealed a positive cluster ranging from 3 to 7 Hz and spanning the entire late entrainment period ($p < .025$, corrected, **Supplementary Figure S1a**), demonstrating the successful entrainment of pre-stimulus theta activity. The continuous sinusoidal visual stimulation produced continuous oscillatory EEG activity, as evidenced by spectral peaks at the stimulation frequencies and enduring power elevations throughout the entrainment period (**Figure 2a**). Simultaneously, a negative cluster was observed that ranged from 13 Hz to 40 Hz ($p < .025$, corrected), covering most of the beta as well as lower gamma bands. In the comparison between the alpha group and control group, a positive cluster was found in the range of 6 to 10 Hz that spanned the whole analysis window ($p < .025$, corrected), also showing the specific entrainment of alpha band oscillations before the onset of the stimulus pair. Furthermore, the analysis revealed a negative cluster in the high beta/low gamma band ranging from 29 to 34 Hz, spanning the whole analysis window as well ($p < .025$, corrected). Generally, the topographical distributions suggest that the entrainment seemed to be centered around occipital and parieto-occipital electrodes, which was the case for both the theta and the alpha group (Figure 2b and 2c). Moreover, the effects in all entrainment groups were restricted to the pre-stimulus period (Figure 2), since our analysis revealed that oscillatory activity after stimulus onset did not differ between the theta, alpha, and control groups ($p = .069$; **Supplementary Figure S2**) In addition, comparing pre-stimulus power from both entrainment groups with oscillatory activity from the NE group using identical analysis parameters revealed similar patterns. Specifically, we found a significant positive cluster in the theta frequency range (theta vs NE; $p < .025$, corrected) as well as in the alpha band (alpha vs NE; $p < .025$, corrected). The common effects found in the control as well as in the NE contrast are shown in **Figure 2b** and **2c**, demonstrating the specificity of the different entrainment protocols (for visualizations of individual contrasts, see **Supplementary S2).** In the control condition, no effects were observed in neither the theta nor alpha band, underscoring that the periodic structure of stimulation is necessary for neural entrainment[36]**.** These results suggest that the entrainment of 5 Hz in the theta group and 9 Hz in the alpha group successfully modified oscillatory activity in the pre-stimulus window and the targeted frequency selectively and consistently. As no alpha modification was observed in the theta group, and no theta modification in the alpha group, the observations support our hypothesis that sensory visual entrainment can selectively modify ongoing oscillations (H1).

In some studies, the entrainment frequency is individually tailored to match participants' endogenous rhythms[34,47]. This approach is particularly common in alpha entrainment research, where resting-state EEG is used to identify the individual alpha frequency (IAF) as a target for stimulation[48–51]. To explore whether the match between stimulation frequency and endogenous alpha rhythms modulated entrainment strength in the present study, we computed the absolute difference between each participant's IAF and the stimulation frequency in the alpha group (9 Hz). The IAF was extracted from resting-state EEG recorded prior to the main experiment by calculating power spectra using a multitaper fast Fourier transform (1–40 Hz). It was defined as the frequency showing the maximum power within the 8–12 Hz range, averaged across posterior electrodes (Pz, POz, Oz, O1, O2). Thus, we correlated this IAF distance with the maximal relative change in alpha power during the entrainment window in the encoding phase, as an index of entrainment strength. This analysis was restricted to participants in the alpha entrainment condition. The correlation was not statistically significant, *r*(43) = –0.034, *p* = .849, indicating that the individual distance from the stimulation frequency was likely not linearly associated with the strength of neural entrainment as indexed by maximal alpha power modulation. Surprisingly, the same analysis for theta revealed a significant negative correlation between the individual theta frequency (ITF) distance and the maximal relative change in theta power during the encoding phase, *r*(55) = –0.296, *p* = 0.028. This suggests that a smaller difference between the individual theta frequency and the entrainment frequency might be associated with greater increases in theta power.

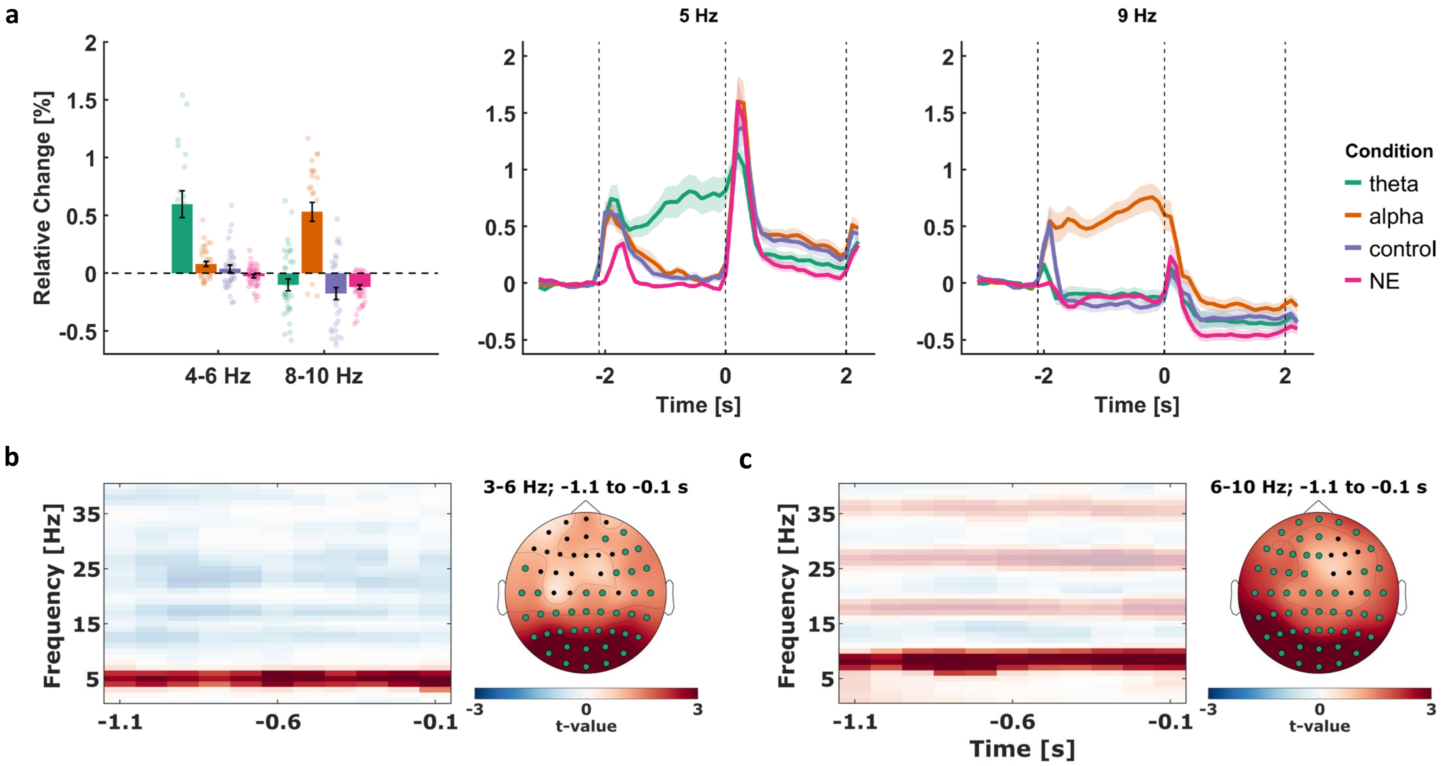


Fig. 2. Effects of visual sensory entrainment on recorded EEG activity. (a) Left shows the average relative change of oscillatory power in reference to the baseline period for every group. Specifically, the average change is displayed for the mean activity from the 5 Hz and 9 Hz envelopes (± 1 Hz). Each data point shows the respective mean value for one participant, and the black error bars represent the standard error of means. Right shows the average time courses of relative change in power for the 5 Hz and 9 Hz narrow bands across the whole trial period for every group. The shadings around the lines represent the standard error of means across participants. All three figures depict relative change derived from the mean of the occipital electrodes O1, O2, and Oz. The first dashed vertical line marks the onset of the entrainment stimulus, while the other two mark the stimulus presentation window.

(b) Visualization of the common effects of visual entrainment that were found in the contrast of the theta group with the control group, as well as in the contrast with the NE group. The time-frequency plot (left) shows the dimension of the common cluster along the time and frequency dimensions, depicting the average t-values across all contributing electrodes. Positive t-values signify greater relative change in the theta group, while opaque data points mark a significant difference at $p < .025$ (corrected). On the right, the topographical distribution of the common effects is shown, with electrodes contributing to the cluster marked in green. **(c)** Same as in (b) but for the alpha entrainment group.

Alpha but not theta entrainment enhances memory performance

In this study, we aimed to determine whether changes in oscillatory activity during the pre-stimulus interval could causally influence an individual's ability to encode audiovisual associations. First, the analysis of performance in the categorization task during encoding yielded moderate evidence in support of the null hypothesis, $BF_{10} = 0.381$, suggesting no significant differences in accuracy across conditions. These findings suggest that participants consistently adhered to task demands throughout the experiment, supporting the validity of subsequent analyses on oscillatory activity and memory performance (see **Supplementary 3** for further details). Notably, memory performance in the recognition task as measured by the sensitivity index *d'* was significantly enhanced in the alpha entrainment group ($M = 1.46$, $SD = 0.60$) as compared to the control group ($M = 1.18$, $SD = 0.50$; **Figure 3a**). An independent-samples *t*-test yielded a Bayes factor of $BF_{10} = 3.29$, providing moderate evidence for the alternative hypothesis and suggesting that increased alpha-band activity induced by visual entrainment may facilitate the formation of audiovisual associations (H2b). Further analysis revealed that this effect was primarily driven by a measurable increase in hit rate in the alpha group (M = 61.498%, SD = 14.443%) as compared to the control group (M = 49.792%, SD = 15.029%), $BF_{10} = 22.5742$. Simultaneously, no differences were observed in the false positive rate between the groups (alpha: M = 13.9%, SD = 6.67%; control: M = 13%, SD = 5.73%), $BF_{10} = 0.2852$ (**Figure 3b**). This suggests that participants in the alpha group were more likely to correctly recognize an old stimulus pair compared to those in the control condition. In contrast, the comparison of sensitivity between the theta group ($M = 1.28$, $SD = 0.55$) and the control group yielded a Bayes factor of $BF_{10} = 0.49$, indicating weak evidence for the null-hypothesis. Similarly, the direct comparison between the theta and alpha groups resulted in a Bayes factor of $BF_{10} = 0.53$, further suggesting weak support for the null hypothesis. The corresponding posterior distributions are shown in **Figure 3d**. Although these results do not support our hypotheses H2a and H2c, they provide evidence that any effect of theta entrainment on encoding performance may be smaller or more variable than anticipated. Together, these findings point to a potentially specific role of alpha oscillations in enhancing audiovisual memory encoding, highlighting the importance of frequency-specific mechanisms in pre-stimulus neural dynamics.

To address our preregistered hypothesis (H3), we compared memory performance in the entrainment groups to that of participants from a previous study who were not exposed to any rhythmic stimulation during the pre-stimulus interval but instead viewed a static fixation cross (NE group; M = 1.27, SD = 0.53). The results of the Bayesian *t*-test showed that neither the theta group nor the control group differed significantly from the NE group, $BF_{10} = 0.26$ and $BF_{10} = 0.16$, respectively, indicating moderate-to-strong evidence for the absence of an effect. The comparison between the alpha group and the NE group yielded a Bayes factor of $BF_{10} = 1.03$, indicating that the data did not provide conclusive evidence for either hypothesis. However, we found moderate evidence suggesting that the hit rate measured in the alpha group still differed from the hit rate in the NE group (M = 52.662%, SD = 13.724%), BF_{10} = 3.8563. Again, we also found moderate evidence that the false positive rate from the NE group (M = 12.8%, SD = 6.1%) was likely not statistically different from the false positive rate in the alpha group. This indicates that participants receiving alpha band stimulation correctly remembered old stimuli more often than participants who were not stimulated at all. In addition, we investigated whether sensory entrainment might have affected how memory performance changed across the experiment. While we found that memory performance generally increased over the course of the experiment, this effect was not modulated by the pre-stimulus condition, BF = 0.0343, indicating that the improvement was consistent across entrainment conditions (see **Supplementary 4** for further details).

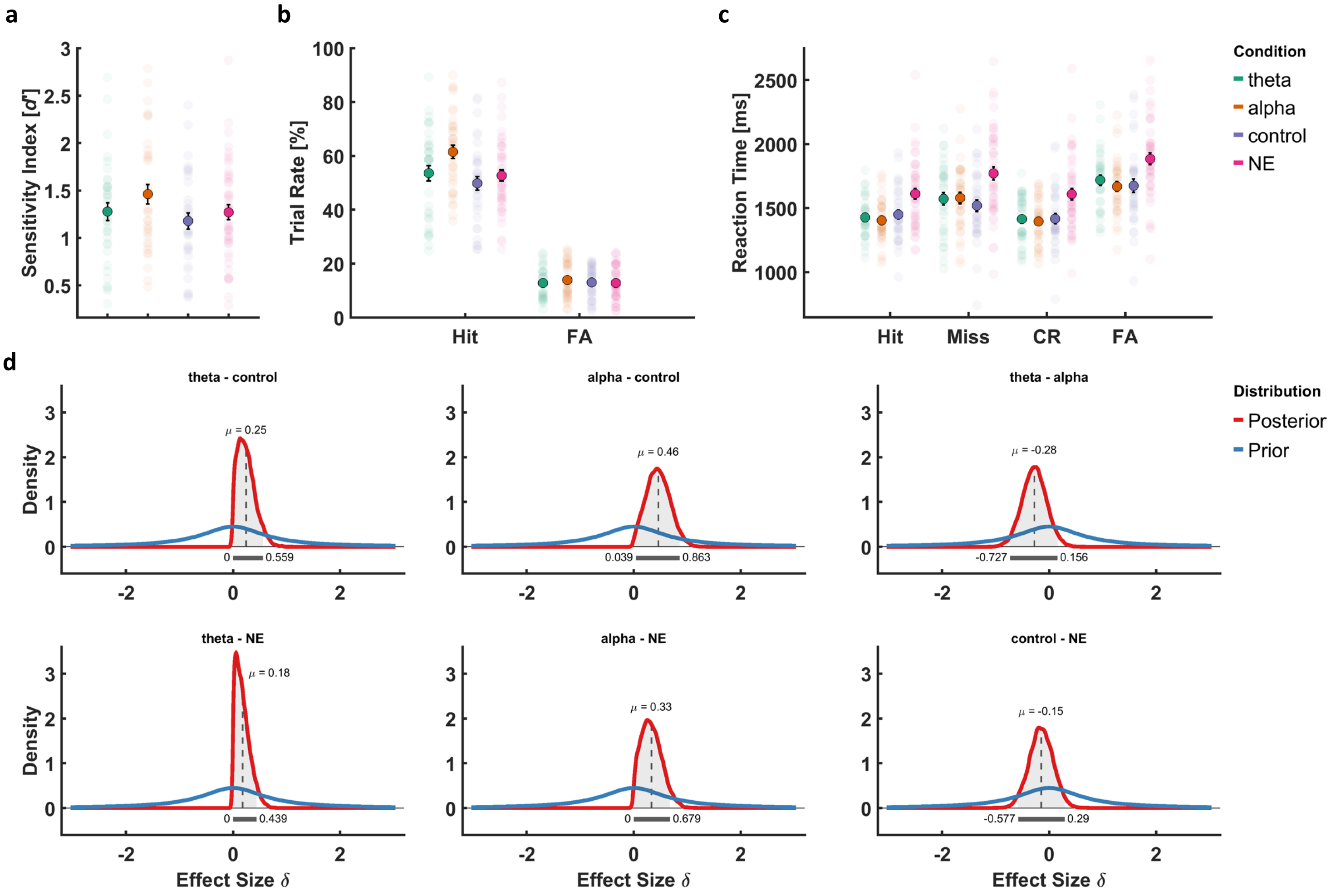


Figure 3. Effects of neural entrainment on recognition memory performance. (a) Mean sensitivity index (d’) with standard errors of the mean (SEM) across the three entrainment conditions **(b)** Average trial rates depicting the proportion of remembered old pairs (Hit) and new pairs erroneously categorized as old (false alarms; FA) across individuals for each group. Black error bars mark the SEM. **(c)** Group means of reaction times (RTs) for all response categories from the recognition task illustrating differences in processing speed between the groups. In addition to Hits and FAs, the figure includes RTs for not recognized old pairs (Miss) and correctly rejected new pairs (CR). Individual group means are reported in Supplementary 5. **(d)** Prior and posterior distributions for the individual group contrasts for sensitivity indices. The Highest Density Interval (HDI) is marked by the grey bar and the light grey shaded area under the curve of the posterior distribution. The mean effect size μ is marked by the dashed line.

Visual stimulation accelerates response times

Next, we explored the effect of visual entrainment on response times. First, we compared group means of reaction times from the categorization task during encoding using the Bayesian version of a one-way ANOVA with the factor *pre-stimulus condition* (theta, alpha, control, NE). The analysis revealed moderate evidence in favor of the alternative hypothesis, $BF_{10} = 5.0737$, suggesting relevant differences in response times between the groups during encoding. Further analysis revealed that participants in the NE group responded significantly slower as compared to the stimulation groups (see **Supplementary 3** for details). Next, differences in reaction times from the recognition task were assessed using the same statistical approach but conducted separately for all four response categories (hits, misses, correct rejections, false alarms). Importantly, we found strong evidence that response times differed significantly between conditions for every response category (hit: $BF_{10} = 78.0847$; miss: $BF_{10} = 8.0419$; correct rejections: $BF_{10} = 49.3906$; false alarms: $BF_{10} = 18.2397$). Subsequent analyses revealed that the stimulation groups did not differ in response times, regardless of which response category was tested. The NE group, however, displayed consistently slower reaction times than the other groups for every response category (**Figure 3c;** see **Supplementary 5** for more information on the individual group contrasts). The results suggest that participants who received visual stimulation during the encoding phase responded faster in the recognition phase than participants who were not stimulated. In addition, we investigated whether the entrainment condition would affect the discrepancy in response times between recognition trials with correct and incorrect responses. To that end, response times from all response categories were grouped according to the correctness of the corresponding trial and submitted to a Bayesian mixed-design ANOVA. The analysis yielded strong evidence in favor of the null hypothesis, $BF_{10} = 0.1161$, indicating that the difference in response times between correct and incorrect trials was not modulated by the stimulation condition.

No lasting effect of entrainment condition on resting state activity and salience reports

To complement our pre-registered analysis, we conducted exploratory investigations examining resting-state EEG data before and after the experiment, as well as differences between groups in subjective salience reports. Comparing the difference in resting-state activity from before and after the experiment across the theta, alpha and control groups revealed no notable differences ($p = .2972$, corrected). This suggests that any changes in baseline activity due to the experiment were not dependent on the entrainment condition and appeared to be a general effect instead (see also **Supplementary 6**). To control for the subjective experience of the visual entrainment, participants rated its pleasantness and salience as well as their own perceived attention and fatigue at the end of every encoding task. Although we observed noticeable decreases in perceived attention as well as increases in perceived fatigue over the course of the experiment, $BF_{attention} = 1.855 \times 10^{9}$, $BF_{fatigue} = 0.3415 \times 10^{15}$, these effects did not interact with the entrainment condition, $BF_{attention} = 0.195$, $BF_{fatigue} = 0.0552$ (**Supplementary 7**). Overall, these results suggest that subjective perceptions and task engagement were comparable across groups, reducing the likelihood of confounds influencing the behavioral outcomes.

Discussion

This study aimed to investigate the causal role of pre-stimulus oscillations in the encoding of crossmodal associations. Using visual sensory entrainment targeted at theta (5 Hz) and alpha (9 Hz) frequencies, we aimed to modulate neural rhythmic activity prior to stimulus presentation and assess its impact on memory performance. Our main findings demonstrated successful frequency-specific entrainment of pre-stimulus oscillations. Notably, alpha-band entrainment before stimulus presentation resulted in significantly improved recognition memory, as evidenced by increased sensitivity driven by higher hit rates. In contrast, pre-stimulus theta entrainment did not produce measurable behavioral effects. These results support a functional dissociation of pre-stimulus alpha and theta oscillations in relation to memory encoding, with alpha activity playing a more prominent role in facilitating successful associative memory formation. Importantly, these effects were driven solely by transient pre-stimulus modulation, with no evidence for lasting entrainment effects during stimulus presentation or changes in post-experiment resting-state activity, enabling the differentiation of their respective functional contributions.

Previous research has demonstrated that pre-stimulus brain activity significantly influences episodic memory formation[14,18–22]. Oscillatory activity, particularly within the theta (3–7 Hz) and alpha (8–12 Hz) bands, has been frequently associated with successful encoding processes[23,26]. Elevated pre-stimulus theta power has been linked to enhanced binding of contextual information and more accurate source memory, suggesting a preparatory role for subsequent memory performance[18]. Similarly, increases in alpha oscillations prior to stimulus onset are thought to reflect a state of attentional preparation, facilitating the encoding of complex audiovisual associations[24]. Importantly, attentional engagement modulates these oscillatory patterns, indicating that intentional focus can create neural conditions beneficial for memory formation[19,52].

Our findings build upon this established framework, demonstrating that externally induced pre-stimulus alpha entrainment boosts audiovisual associative encoding. The observed increase in alpha power in our experimental condition aligns with theories that posit alpha oscillations as essential for sensory anticipation and attentional gating[9,53–55]. This externally driven alpha synchronization likely enhanced preparatory attentional states, enabling more efficient inhibition of irrelevant information and promoting engagement of memory-related neural networks such as parietal and hippocampal regions[3,56–59]. Behaviorally, this facilitation translated into higher recognition sensitivity, driven primarily by increased hit rates, while false alarm rates remained unaffected. These findings support the hypothesis that alpha oscillations modulate sensory preparation and attentional gating during encoding via bottom-up processes, and thereby improve associative memory performance. While visual stimulation activated occipital alpha generators, the subsequent memory benefits may involve a broader network. Parietal regions, which prior work has implicated in alpha-mediated attention and memory[11], could be recruited via cortico-cortical connections. Thus, entraining occipital alpha oscillations might lead to preparatory states in the visual cortex. Parietal or temporal regions could then benefit from that oscillatory state to facilitate associative encoding.

It may seem counterintuitive that boosting alpha oscillations – which are commonly associated with increased cortical inhibition – would improve memory encoding, as higher alpha power is typically linked to inhibitory gating of cortical processing[10,16,60–63]. However, this finding aligns with the view of alpha as an active information gating mechanism[9,10]. By entraining alpha oscillations prior to stimulus onset, we likely enhanced the brain's ability to suppress irrelevant activity and sharpen attentional focus on the expected crossmodal input. In predictive processing terms, the alpha rhythm may carry top-down predictions that prepare visual and association cortices for the incoming stimuli[64]. Thus, rather than simply inhibiting processing, pre-stimulus alpha oscillations might facilitate encoding by gating inputs to ensure that the relevant visual and auditory information is integrated with minimal interference.

In contrast, pre-stimulus theta entrainment did not produce significant behavioral benefits, despite successfully increasing theta power. This suggests that power enhancement alone may be not sufficient to influence memory performance within this paradigm. A key factor could be the temporal specificity of theta's role in encoding. While theta oscillations were shown to be critical for episodic memory and associative binding[6–8], their effectiveness appears to depend heavily on activity during stimulus processing[46,65]. Prior studies demonstrating memory improvements with theta entrainment typically targeted the period during stimulus presentation, likely optimizing engagement of memory networks[7,44,66]. These findings indicate that the contribution of theta activity to memory encoding may be more dynamic, occurring during active processing rather than as a preparatory state alone. Our targeting of pre-stimulus activity likely aimed to set a preparatory neural state that may not have directly engaged the neural mechanisms necessary for effective multisensory binding, although oscillatory power was modulated. Furthermore, the role of theta oscillations in memory encoding often involves activity across widespread and synchronized networks such as hippocampal-cortical circuits[65,67,68], which may not have been fully engaged through unimodal occipital stimulation alone. While the stimulation successfully increased theta power, the lack of phase coherence or cross-regional synchronization may have limited its influence on encoding. These findings emphasize that the contribution of theta activity to memory may be more context-dependent and particularly crucial during active processing phases, rather than solely during pre-stimulus intervals. This aligns with prior studies emphasizing the importance of timing and phase alignment in theta-mediated memory processes.

In addition to the effects of entrainment on primary performance measures we observed a secondary effect on response times. Specifically, participants that received visual stimulation before the encoding of audiovisual pairs responded consistently faster during encoding and, most importantly, during the subsequent recognition task as compared to participants who did not undergo entrainment, while no differences were observed between the three entrainment groups. Given this pattern of results, it is plausible to assume that the faster response times from the entrainment groups could be interpreted as an effect of increased alertness during the encoding period due to general visual stimulation before stimulus onset. Visual stimulation also appeared to accelerate response times during both encoding and recognition. This speeding was observed for any rhythmic pre-stimulus (both theta and alpha), suggesting a general alerting or arousal-related effect rather than a frequency-tuned cognitive modulation. Brief rhythmic visual stimulation likely acted as an alerting cue, heightening participants' readiness to respond—consistent with prior work showing that visual flashes increase arousal and shorten reaction times[69–71]**.** Visual stimulation in general has been associated with an increase of alertness before[69,70,72], while alertness, in turn, has been shown to decrease RTs in tasks recruiting executive control systems[71,73]. One could argue that visual information processing might benefit from an improved inhibition of peripheral information[74]. This indicates that visual stimulation might have enhanced a preparatory mechanism that is independent from the specific cognitive demand of encoding information but might rather point towards an increased ability to remain vigilant and maintain attention throughout the task despite increasing subjective feelings of fatigue. Future studies might elucidate hidden patterns in this effect by investigating how sensory entrainment affects response times on a trial-by-trial basis, and whether entrainment magnitude may predict attention maintenance.

Although the entrainment procedure applied in this study led to a reliable modification of pre-stimulus theta and alpha activity, our analyses revealed that both the theta and alpha group exhibited significantly lower beta band power as compared to controls. While we cannot rule out completely that the behavioral effects presented here could also be attributed to modifications of beta band oscillations, it's plausible to assume that the observed difference was caused by increases in beta activity in the control group rather than decreases in the theta and alpha groups. This is supported by the fact that we found no negative clusters in the beta band when comparing activity from the theta and alpha groups with the NE group, and that the effects common to both the control and NE group contrasts are centered around the respective entrainment frequencies. Instead, the arhythmic stimulation in the control group might have modified pre-stimulus beta-oscillations due to potential additive effects of single-frequency cycles randomly chained together. As individual arhythmic luminance functions were computed for every participant in the control group, individual cycles of the same frequency that ended up at the same time point could have had an amplifying effect during averaging procedures, resulting in what seemed as beta power enhancement. However, this does not invalidate the usefulness of arythmic stimulation, as it plays a complementary role in validating and specifying the precision of entrainment procedures. With this, the present work is in line with previous studies using arhythmic stimulation as an additional control mechanism to ensure that oscillatory responses to the entrainment actually arise from the rhythmicity of a specific frequency[36–38,75].

A key challenge in interpreting the effects of rhythmic stimulation concerns whether the observed frequency-specific activity reflects true entrainment of endogenous oscillations or merely a linear summation of evoked responses. True entrainment entails phase alignment of intrinsic neural oscillators to an external rhythm, producing sustained, frequency-specific, and phase-locked activity that may persist beyond stimulation[35,64]. In contrast, event-related potentials (ERPs) arise from transient, time-locked responses whose repetition can mimic oscillatory activity without engaging endogenous generators[76,77]. In the present paradigm, a complete differentiation between the two effects is difficult due to inherent methodological and physiological constraints of rhythmic sensory stimulation. Each luminance modulation necessarily evokes a transient visual response, which overlaps temporally and spectrally with the ongoing oscillatory activity. As both processes produce power increases and phase locking at the stimulation frequency, it is difficult to fully disentangle them based on spectral and temporal measures of EEG recordings alone[35,76]. Moreover, the relatively brief but continuous 2-s stimulation epochs do not provide sufficient inter-stimulus intervals to assess post-stimulation persistence, which can be considered a strong indicator of actual entrainment[78]. Finally, the limited spatial resolution of EEG measurements prevents a reliable separation of concurrent neural sources, since early visual areas could generate evoked responses while distributed cortical networks support oscillatory synchronization. Therefore, both processes are likely reflected within the recorded signal, and the observed behavioral effects clearly argue for a functional relevance of the modulated neural activity in the pre-stimulus period. Although sensory entrainment and evoked responses cannot be fully dissociated in EEG, the pattern of frequency-specific power increases observed here aligns with partial entrainment of intrinsic oscillatory activity.

In sum, our results highlight the distinct functional roles of alpha and theta oscillations in multisensory learning and memory. Alpha oscillations appear to serve as a gating mechanism that can be externally modulated to optimize sensory processing and attentional filtering[9,11], with our findings providing causal evidence that externally driven alpha rhythms prior to encoding facilitate associative memory performance. In contrast, the unsuccessful behavioral impact of theta entrainment highlights the importance of time specificity and multisensory synchronization for the mnemonic functions of theta oscillations[7,45]. These insights contribute to a nuanced understanding of how tailored oscillatory modulation can differentially influence neural states underpinning successful memory formation, emphasizing the potential of targeted neurostimulation techniques, personalized cognitive interventions, and novel therapeutic approaches for memory disorders. This is highlighting the significant clinical potential of utilizing specific oscillatory pathways to enhance learning and memory.

Methods

Participants

In total, 176 healthy young adults were recruited for this pre-registered study (http://osf.io/5gprt). Participants were required to have normal or corrected-to-normal vision and hearing ability. We had to exclude several participants from the analysis due to unsuccessful entrainment (21.59%). Further exclusions were the result of false positive rates above the predetermined threshold (14.77%). An additional 3.98% were excluded for both failure to entrain and high false positive rate. Taken together, a sample of $n = 105$ (72.38% female) participant data sets were submitted to the analysis, with a group size of $k = 35$ for each experimental group. On average, participants were 24.8 years old (SD = 4.17), with the age ranging from 18 to 35 years. All participants gave their informed consent and received either financial reimbursement or course credit for taking part in the study, which was approved by the ethics committee of the Hamburg Medical Council (PV5893). We confirm that all experiments were performed in accordance with relevant guidelines and regulations.

Experimental design

The Subsequent Memory Effects task (SME) implemented in this study is a slight variation from the design used in[26]. The pre-stimulus interval in the encoding task was modified to accommodate the entrainment procedure, while the recognition task remained the same. Participants received the same instructions as in the previous study, with the addition that they were made aware of the presence of an oscillating image. For this study, a between-subjects design was employed, with *entrainment condition* serving as the independent variable with three groups: 5 Hz (theta group), 9 Hz (alpha group), and arhythmic (control group). To take advantage of the Bayesian framework, we implemented an open-ended sequential design for gathering evidence, but added the additional constraint of a maximum group size k[79]. Thus, data collection was carried out evenly between the groups until a group size with $k = 15$ usable data sets was reached. Subsequent statistical hypothesis testing was conducted incrementally for each additional usable data set, using the pre-registered dependent variable (sensitivity index), with changes in evidence being continuously monitored across all groups. Data collection would stop either when statistical testing showed moderate support for either the alternative or null hypothesis ($BF_{10} > 3$ or $BF_{10} < 1/3$)[80,81] or when group size reached k = 35 for each group. This resulted in group sizes of k = 35 for the theta, alpha, as well as the control group.

Stimulus material

Stimulus pairs consisting of one image and one sound were selected randomly from an internal database, and the selection was unique for each experimental run. All images featured a resolution of 640 x 480 pixels and a 24-bit color depth. Each image depicted a photograph of either natural or man-made scenes. An additional neutral image depicting a photograph of Earth in space was chosen as the entrainment stimulus to be shown in every trial. We inverted the colors of the entrainment stimulus to increase contrast, thereby increasing the intensity of the stimulation. According to the principle of the Arnold tongue[82,83], higher stimulation intensity might compensate for a slight frequency mismatch between the entraining signal and the ongoing oscillations in the brain, thus increasing the probability of a successful entrainment. The sounds were real-life recordings of either sounds from nature (e.g. animal calls) or from man-made or artificial environments (e.g. a honk of a car). All sounds were cropped to a duration of 2 s, and featured a bit rate of 1411 kBit/s. All pairings were created in a manner so that no effects of semantic congruency would arise[84]. While it was possible that e.g. animal images could be paired with animal sounds, pairings containing an image of an animal and the corresponding sound of that animal were excluded.

Sensory entrainment

Sensory stimulation was used during the pre-stimulus intervals of encoding trials to manipulate narrow-band oscillatory activity and investigate its effects on subsequent encoding. The entrainment stimulus, which was the same for all participants and all groups, was presented for 2 s before stimulus onset. Specifically, its luminance varied in a sinusoidal manner, resulting in a rhythmic oscillation of 5 Hz in the theta group and 9 Hz in the alpha group. The choice of stimulation frequency was based on the results from an earlier study[26], where we reported pre-stimulus SMEs in the theta and alpha range. We extracted the frequencies in the respective bands that showed the maximum effect in the contrast between later remembered and later forgotten associations, which were then chosen as entrainment frequencies. To achieve high temporal resolution of the luminance sine curve, we used a monitor with a frame rate of 240 Hz (Alienware 27 AW2723DF, Dell Technologies, Round Rock, USA). This enabled us to change luminance every 4.2 ms, resulting in luminance change that closely followed a sine curve instead of a box car function. While the luminance in the theta and alpha groups was kept at a steady rhythm in the respective frequencies, the luminance waveforms in the control condition were arhythmic. The waveforms consisted of single cycles of differing frequencies pulled randomly from the interval of 13 to 24 Hz. Importantly, we excluded frequencies of 15 Hz, 18 Hz, and 20 Hz, as these are harmonic frequencies of the entrainment frequencies in the other entrainment conditions. Each participant in the control group was presented with a unique arhythmic waveform with a duration comparable to the 2 s of entrainment in the other groups (M = 1.976 s, SD = 0.022). Notably, the luminance waveform for every group always started and ended at zero luminance (image not visible). To ensure that the stimulus pair would be presented in line with the entrainment rhythm, we implemented a gap of 100 ms between the end of stimulation and stimulus onset in the theta group (56 ms in the alpha group, respectively), which constitutes half of a cycle in the entrainment frquency. In the control condition, this gap was set to 50 ms.

Task and procedure

The experimental procedure was the same regardless of experimental group. After giving informed consent and receiving a short introduction by the experimenter, participants were seated in a sound-attenuated chamber. The experimental session started with a recording of 3.5 minutes of resting-state activity, during which participants were told to fixate a fixation cross on the screen. This was followed by the SME task, which consisted of a short training session and three experimental runs that only differed in the stimulation material presented to the participants. Each experimental run included an encoding phase, an intermission, and a subsequent recognition phase (see **Figure 1**). One encoding phase consisted of 47 trials. During each trial, participants were simultaneously presented with an image and a sound for 2 s. A white fixation cross was visible during stimulus presentation and remained on the screen for 3 to 5 s after stimulus offset. Before stimulus onset, the entrainment stimulus was presented in the respective frequency. Participants were instructed to memorize the combination of image and sound from every trial. Furthermore, participants should indicate whether both the image and sound represented an animal (right mouse button) or not (left mouse button). Button presses were registered as a valid response during the first 3 s after stimulus onset but were otherwise counted as a missed response. The experimental trials were followed by four survey questions measuring the participants' perception of the entrainment procedure. Specifically, the questions measured salience, attention, fatigue, and distractive qualities in relation to the entrainment procedure. During the subsequent intermission of approximately 3 minutes, the participants were asked to count down aloud from 100 (115 and 125 in the second and third run, respectively) in steps of 7 (9 and 13 in the other runs, respectively).

In the recognition phase, the 47 audiovisual pairings from the preceding encoding phase were presented again but intermixed with 47 new pairings, which were created by randomly shuffling the original ones. Note that the individual images and sounds used for the combinations remained the same within each experimental run. All stimulus pairs were again presented for 2 s, with a small white fixation cross layered on top of the image. The fixation cross remained on the screen after stimulus onset. The participants were asked to indicate via button-press whether the current pair had already been presented in the preceding encoding phase (left mouse button) or not (right mouse button). They were further encouraged to press the right mouse button when they felt highly uncertain about a stimulus pair. As in the encoding phase, valid responses were recorded up to 3 s after stimulus onset, and otherwise labeled as a missed response trial. The subsequent inter-trial interval was set to 4 s, during which the white fixation cross was visible on the screen. Across all three experimental runs, participants were presented with 141 unique encoding trials and 282 recognition trials. At the end of the experimental session, resting-state activity was measured again for 3.5 minutes while participants fixated the middle of the screen.

EEG data acquisition and preprocessing

We used a 64-channel electrode setup (ActiCap, BrainProducts, Gilching, Germany) to record EEG. Four of those electrodes were placed on the left and right temple, as well as above and below the left eye, to record vertical and horizontal EOG. The signal was referenced online to *FCz* and re-referenced offline to a common average. The ground electrode was placed at *Iz* below *Oz*, and electrode impedences were kept below 10 kΩ. The signal was amplified with a low cut-off frequency of 0.53 Hz (0.3 s time constant) and recorded at a sampling rate of 500 Hz. EEG activity was recorded during all encoding and recognition phases, but not during intermissions. These settings were used for resting-state recordings as well as for the recordings during the SME task.

Offline preprocessing was done using the Fieldtrip[85] and EEGLAB[86] toolboxes for MATLAB (Release 2023a, The Mathworks Inc., Natick, Massachusetts, USA). For the data from the encoding task, an automated approach was used to epoch and clean the data for further processing. The raw data was divided into segments from -3.4 s to 2.5 s relative to the onset of the stimulus pair. A bandpass filter was used to filter out all frequencies outside the range of 0.5 Hz to 40 Hz. Next, trials containing temporally distinct artifacts based on muscular activity or related to electronics were rejected in an automated pipeline using the *ft_artifact_zvalue* function from Fieldtrip. The trial data was filtered, z-transformed, and averaged over channels. An accumulated z-score was computed for each trial based on the types of artifacts. The cutoff value was set to z = 60 for jump artifacts and z = 30 for artifacts caused by phasic muscular activity. Trials were then rejected if the accumulated z-score was larger than the corresponding threshold value. The resulting data was submitted to an automated Independent Component Analysis (ICA) to remove underlying noise from muscular activity as well as artifacts resulting from blinks and eye movements using the *ICLabel* plugin for EEGLAB[87]. Components that showed at least a probability of 80% of being related to eye-movements, noise caused by muscular activation, or line noise were flagged for removal. On average, 6.37 (SD = 3.8) independent components were removed from the data of the theta group, 6.17 (SD = 3.99) for the alpha group, and 6.63 (SD = 3.32) for the control group. The data was then re-referenced again to the common average. After preprocessing, 4.74 trials (SD = 4.9) out of 141 encoding trials were removed from data sets in the theta group. In the alpha group, an average of 5.14 trials (SD = 3.84) was rejected per participant, while 3.77 trials (SD = 2.65) were rejected in the control group. As the data from the previous study were also analyzed again in the context of the present investigation[26], all corresponding EEG data were submitted to the same processing pipeline to ensure comparability. After ICA, 4.79 (SD = 2.19) independent components were rejected from the data on average per participant. After preprocessing, an average of 6.42 trials (SD = 4.67) per participant was removed from the data.

From the 3.5 minutes of recorded resting-state activity before and after the experiment, the first and last 15 seconds were omitted for offline processing. Pre- and post-experiment data were processed separately. From this point, we will refer to the data as RestPre and RestPost, respectively. We used a bandpass filter to remove activity below 0.5 Hz and above 40 Hz from the remaining 3-minute interval. The data were then divided into 90 epochs with a length of 2 s each and cleaned from temporally distinct artifacts with the same automated pipeline that was used with the experimental data. Epochs containing artifacts were then removed from the data. The results were submitted to an automated ICA using the same parameters as for the experimental data. On average, 1.11 epochs (SD = 1.3) were removed from RestPre data in the theta group per participant (alpha: 0.91, SD = 1.07; control: 1.2, SD = 1.45). After ICA, 2.91 (SD = 1.8) independent components were rejected per participant in the theta group (alpha: 2.97, SD = 2.35; control: 3.17, SD = 2.16). For RestPost, an average of 1.4 epochs (SD = 2.24) were removed in the theta group per participant (alpha: 0.89, SD = 1.47; control: 1.14, SD = 1.57). On average, 3.74 (SD = 2.78) independent components were rejected (alpha: 3.54, SD = 2.76; control: 5.51, SD = 3.78).

Entrainment validation

As a first step, the pre-processed experimental data from the theta and alpha groups were decomposed into the time-frequency domain. We chose a frequency range of 1 to 40 Hz with frequency bins of 1 Hz, and a time interval of -3.1 s to 2.2 s relative to the onset of the stimulus pairs. Fieldtrip's *mtmconvol* method[85] was used in conjunction with a Hanning window of 500 ms and a step size of 100 ms. The additional 300 ms before and after the chosen time interval that were retained during preprocessing served as padding to avoid edge artifacts from the decomposition process. After conducting the decomposition for every trial, the resulting oscillatory power was then averaged over trials for every participant. Next, the data was normalized using a measure of change percentage relative to baseline activity that was defined as the activity from -3.1 s to -2.1 s before stimulus onset. For every individual data set from the theta and alpha group, an average was computed from the data of occipital electrodes (O1, O2, and Oz). As the sensory entrainment took place in the visual domain, the most prominent response should be expected in the electrodes adjacent to the visual cortex. Separate frequency envelopes were chosen for the theta group (5 Hz ± 1 Hz) and the alpha group (9 ± 1 Hz), with a common time interval of interest ranging from -1.1 s to - 0.1 s relative to stimulus onset. We used the latter half of the entrainment interval to estimate entrainment success, as phase alignment and entrainment typically develop over time and tend to plateau after an initial adjustment period[88,89]. Assessing the full interval may underestimate entrainment strength due to lower power at the beginning of the stimulation. The entrainment was deemed successful if a relative change in power of at least 10 % could be observed for at least 500 ms within the time interval of interest.

Statistical analysis

Behavioral data

We used a Bayesian framework to test the hypotheses relating to behavioral effects, utilizing the *BayesFactor* package for *R* (v.4.3.3). In line with the signal detection theory[90,91], four percentage measures were extracted for every participant from the recognition data: Correctly remembered old pairings (*hits*), not remembered old pairings (*misses*), new pairings correctly rejected as new (*correct rejections*), and new pairings seemingly remembered as old (*false alarms*). Our main dependent variable, the sensitivity index *d'*, was computed by calculating the difference between the z-transformed hit and false alarm rates for every participant. When group size reached $k = 15$, we used the Bayesian version of a *t*-test to statistically compare memory performance between groups. Testing was then repeated every time *k* increased by one for each group. Specifically, one-sided tests were computed to compare performance between the theta group and controls (H2a), as well as between the alpha group and controls (H2b). For estimating differences between both entrainment groups (H2c), a two-sided test was performed. In all cases, a Cauchy distribution of medium width was used as prior, i.e. with an *r* scale of $\sqrt{2}/2$.

For the comparison of the experimental groups from the current study with the data from the previous investigation (H3), the NE group data was processed in the same manner. To keep in line with our exclusion criteria, participants with a false positive rate > 25% were not considered in the analysis, resulting in a sample size of k = 45 for the NE group. Due to the difference in group size, a sampling approach was chosen in which a subsample was randomly pulled from the NE data set that matched the group size of the entrainment groups. The average sensitivity was calculated from that subsample and compared to the mean of the full NE sample. This procedure was repeated 50 times. Ultimately, we chose the subsample where the difference in means was minimal, ensuring that the subsample would be representative of the original NE sample. We then conducted one-sided Bayesian t-tests to compare memory performance between both entrainment groups and the previous data set using the same settings as in testing for H2.

Bayesian statistical approaches were further used to explore differences between groups in secondary behavioral variables. A Bayesian one-way ANOVA with the factor *entrainment condition* (theta, alpha, control, NE) was used to assess differences in accuracy and response times from the categorization task during encoding. Changes in memory sensitivity over the course of the experiment were investigated using a mixed-design Bayesian ANOVA with the factors *entrainment condition* and *experimental run* (a, b, c). Furthermore, Bayesian one-way ANOVAs with the factor *entrainment condition* were used to assess group differences for every response category of reaction times. To investigate, whether the entrainment condition modulated the discrepancy in response time between correct and incorrect trials, a mixed-design Bayesian ANOVA with the factors *entrainment condition* and *correctness* was utilized. Finally, Bayesian mixed-design ANOVAs with the factors *entrainment condition* and *experimental run* were used to assess differences in the subjective perception of the entrainment procedure, as well as state of attention and fatigue. The analyses were conducted separately for each survey item. To estimate the relative likelihood of the interactions in the these analyses, the ratio of Bayes factors corresponding to the full model and the model containing only the main effects was computed. For all analyses, a Cauchy distribution with an *r* scale of $\sqrt{2}/2$ was used as prior.

EEG data

To statistically test the success of entrainment, we compared oscillatory activity from the theta and alpha groups with activity from the control group. Specifically, the baseline-normalized time-frequency data was restricted to the latter half of the entrainment period (-1.1 s to -0.1 s relative to stimulus onset), and the frequency range was set to 1 to 40 Hz. We used a non-parametric permutation testing approach with a cluster-based correction for multiple comparisons as implemented in Fieldtrip[85]**.** Independent-samples *t*-tests were computed for every data point across participants from the channel-time-frequency space. Data points that showed significant differences between conditions ($p < .05$) were organized into clusters based on temporal, spatial, and spectral proximity. For each cluster, statistical values were summed to yield a cluster-level statistic, and the highest of these sums was selected as the principal test statistic for condition comparisons. To construct a reference distribution, a Monte Carlo approach was employed: all trials from both conditions were merged into a single dataset and randomly split into two groups. Statistical testing was performed again at the level of individual data points within these shuffled groups, and cluster-level statistics were recalculated. This randomization process was repeated 4000 times. During each iteration, the largest cluster-level statistics were recorded to generate the null distribution, separately for positive and negative clusters. The final *p*-value for condition differences was obtained by determining the proportion of randomizations that produced a test statistic greater than that observed in the original data. This method was applied across all detected clusters, yielding a *p*-value for each cluster's comparison between conditions. The same statistical approach was used for the comparison of pre-stimulus activity from the theta and alpha groups to activity from the NE group. In addition, this approach was also used to assess differences between the entrainment groups (theta, alpha, control) in brain activity during stimulus presentation. However, an independent-samples *F*-test was used on sample level in this case.

A similar statistical approach was used for the exploration of resting-state data. For every entrainment group, the preprocessed RestPre and RestPost data were decomposed into the frequency domain by using the Fast Fourier Transform on single epochs for a frequency range of 1 to 40 Hz. All epoch spectra were then averaged to a subject-specific mean frequency spectrum. This was done separately for RestPre and RestPost. For each of the entrainment groups, we compared RestPre and RestPost with a paired-samples *t*-test on sample level. To further assess whether these differences varied between groups, difference scores were computed between RestPre and RestPost data and submitted to cluster-based permutation testing using an independent-samples *F*-test on sample level. Thresholds for *p*-values were kept as laid out above.

To determine each participant's Individual Alpha Frequency (IAF) and Individual Theta Frequency (ITF), we analyzed resting state EEG data acquired prior to the experimental task. Preprocessed data underwent spectral analysis using a multitaper Fast Fourier Transform (FFT) approach implemented in FieldTrip. Spectral power was computed across frequencies from 1 to 40 Hz in 1 Hz steps, with a 2 Hz smoothing kernel applied. For each participant, we extracted the mean power spectrum across a set of posterior electrodes (Pz, POz, Oz, O1, O2, P3, P4, PO3, PO4). The IAF was identified as the frequency within the alpha range (8–12 Hz) exhibiting the maximum spectral power across these electrodes. Conversely, the ITF was defined as the frequency within the theta range (3–7 Hz) with the highest spectral power. We calculated the absolute differences between each participant's IAF and ITF and their corresponding entrainment frequencies (theta: 5 Hz; alpha: 9 Hz). To assess whether the proximity of an individual's intrinsic frequencies to the stimulation frequencies influenced entrainment efficacy, we conducted Pearson correlation analyses between these frequency-distance measures and the maximum relative change in spectral power at the individual peak channel during stimulation.

References

1. Dickerson, B. C. & Eichenbaum, H. The Episodic Memory System: Neurocircuitry and Disorders. *Neuropsychopharmacology* **35**, 86–104 (2010).
2. Gasser, C. & Davachi, L. Cross-Modal Facilitation of Episodic Memory by Sequential Action Execution. *Psychol. Sci.* **34**, 581–602 (2023).
3. Klimesch, W., Fellinger, R. & Freunberger, R. Alpha oscillations and early stages of visual encoding. *Front. Psychol.* **2**, (2011).
4. Rudoler, J. H., Herweg, N. A. & Kahana, M. J. Hippocampal Theta and Episodic Memory. *J. Neurosci.* **43**, 613–620 (2023).
5. Staudigl, T. & Hanslmayr, S. Theta Oscillations at Encoding Mediate the Context-Dependent Nature of Human Episodic Memory. *Curr. Biol.* **23**, 1101–1106 (2013).
6. Buzsáki, G. & Moser, E. I. Memory, navigation and theta rhythm in the hippocampal-entorhinal system. *Nat. Neurosci. 2013 162* **16**, 130–138 (2013).
7. Herweg, N. A., Solomon, E. A. & Kahana, M. J. Theta Oscillations in Human Memory. *Trends Cogn. Sci.* **24**, 208–227 (2020).
8. Terada, S., Sakurai, Y., Nakahara, H. & Fujisawa, S. Temporal and Rate Coding for Discrete Event Sequences in the Hippocampus. *Neuron* **94**, 1248-1262.e4 (2017).
9. Foxe, J. J. & Snyder, A. C. The Role of Alpha-Band Brain Oscillations as a Sensory Suppression Mechanism during Selective Attention. *Front. Psychol.* **2**, (2011).
10. Jensen, O. & Mazaheri, A. Shaping Functional Architecture by Oscillatory Alpha Activity: Gating by Inhibition. *Front. Hum. Neurosci.* **4**, (2010).
11. Waldhauser, G. T., Johansson, M. & Hanslmayr, S. Alpha/Beta Oscillations Indicate Inhibition of Interfering Visual Memories. *J. Neurosci.* **32**, 1953–1961 (2012).
12. Lindenbaum, L., Steppacher, I., Mehlmann, A. & Kissler, J. M. The effect of neural pre-stimulus oscillations on post-stimulus somatosensory event-related potentials in disorders of consciousness. *Front. Neurosci.* **17**, (2023).
13. Roberts, B. M., Clarke, A., Addante, R. J. & Ranganath, C. Entrainment enhances theta oscillations and improves episodic memory. *Cogn. Neurosci.* **9**, 181–193 (2018).
14. Salari, N. & Rose, M. Dissociation of the functional relevance of different pre-stimulus oscillatory activity for memory formation. *NeuroImage* **125**, 1013–1021 (2016).
15. Taesler, P. & Rose, M. Multivariate prediction of pain perception based on pre-stimulus activity. *Sci. Rep.* **12**, 1–9 (2022).
16. Van Dijk, H., Schoffelen, J. M., Oostenveld, R. & Jensen, O. Prestimulus Oscillatory Activity in the Alpha Band Predicts Visual Discrimination Ability. *J. Neurosci.* **28**, 1816–1823 (2008).
17. Zazio, A., Ruhnau, P., Weisz, N. & Wutz, A. Pre-stimulus alpha-band power and phase fluctuations originate from different neural sources and exert distinct impact on stimulus-evoked responses. *Eur. J. Neurosci.* **55**, 3178–3190 (2022).
18. Addante, R. J., Watrous, A. J., Yonelinas, A. P., Ekstrom, A. D. & Ranganath, C. Prestimulus theta activity predicts correct source memory retrieval. *Proc. Natl. Acad. Sci. U. S. A.* **108**, 10702–10707 (2011).
19. Schneider, S. L. & Rose, M. Intention to encode boosts memory-related pre-stimulus EEG beta power. *NeuroImage* **125**, 978–987 (2016).
20. Scholz, S., Schneider, S. L. & Rose, M. Differential effects of ongoing EEG beta and theta power on memory formation. *PLOS ONE* **12**, e0171913 (2017).
21. Sweeney-Reed, C. M. *et al.* Pre-stimulus thalamic theta power predicts human memory formation. *NeuroImage* **138**, 100–108 (2016).
22. Winterling, S. L., Shields, S. M. & Rose, M. Reduced memory-related ongoing oscillatory activity in healthy older adults. *Neurobiol. Aging* **79**, 1–10 (2019).
23. Cruzat, J. *et al.* The phase of Theta oscillations modulates successful memory formation at encoding. *Neuropsychologia* **154**, 107775 (2021).

24. Strunk, J. & Duarte, A. Prestimulus and poststimulus oscillatory activity predicts successful episodic encoding for both young and older adults. *Neurobiol. Aging* **77**, 1–12 (2019).
25. Zoefel, B. & VanRullen, R. Oscillatory Mechanisms of Stimulus Processing and Selection in the Visual and Auditory Systems: State-of-the-Art, Speculations and Suggestions. *Front. Neurosci.* **11**, (2017).
26. Ostrowski, J. & Rose, M. Increases in pre-stimulus theta and alpha oscillations precede successful encoding of crossmodal associations. *Sci. Rep.* **14**, 7895 (2024).
27. Amil, A. F., Albesa-González, A. & Verschure, P. F. M. J. Theta oscillations optimize a speed-precision trade-off in phase coding neurons. *PLOS Comput. Biol.* **20**, e1012628 (2024).
28. Terporten, R., Schoffelen, J.-M., Dai, B., Hagoort, P. & Kösem, A. The Relation between Alpha/Beta Oscillations and the Encoding of Sentence induced Contextual Information. *Sci. Rep.* **9**, 20255 (2019).
29. Yeh, N. & Rose, N. S. How Can Transcranial Magnetic Stimulation Be Used to Modulate Episodic Memory?: A Systematic Review and Meta-Analysis. *Front. Psychol.* **10**, 993 (2019).
30. Bree, S. van, Sohoglu, E., Davis, M. H. & Zoefel, B. Sustained neural rhythms reveal endogenous oscillations supporting speech perception. *PLOS Biol.* **19**, e3001142 (2021).
31. Neuling, T. *et al.* Friends, not foes: Magnetoencephalography as a tool to uncover brain dynamics during transcranial alternating current stimulation. *NeuroImage* **118**, 406–413 (2015).
32. Neuling, T., Ruhnau, P., Weisz, N., Herrmann, C. S. & Demarchi, G. Faith and oscillations recovered: On analyzing EEG/MEG signals during tACS. *NeuroImage* **147**, 960–963 (2017).
33. Veniero, D., Vossen, A., Gross, J. & Thut, G. Lasting EEG/MEG Aftereffects of Rhythmic Transcranial Brain Stimulation: Level of Control Over Oscillatory Network Activity. *Front. Cell. Neurosci.* **9**, (2015).
34. Duecker, K. *et al.* Challenges and Approaches in the Study of Neural Entrainment. *J. Neurosci.* **44**, (2024).
35. Notbohm, A., Kurths, J. & Herrmann, C. S. Modification of Brain Oscillations via Rhythmic Light Stimulation Provides Evidence for Entrainment but Not for Superposition of Event-Related Responses. *Front. Hum. Neurosci.* **10**, (2016).
36. Notbohm, A. & Herrmann, C. S. Flicker Regularity Is Crucial for Entrainment of Alpha Oscillations. *Front. Hum. Neurosci.* **10**, (2016).
37. Thut, G., Schyns, P. & Gross, J. Entrainment of Perceptually Relevant Brain Oscillations by Non-Invasive Rhythmic Stimulation of the Human Brain. *Front. Psychol.* **2**, (2011).
38. Michael, E., Covarrubias, L. S., Leong, V. & Kourtzi, Z. Learning at your brain's rhythm: individualized entrainment boosts learning for perceptual decisions. *Cereb. Cortex* https://doi.org/10.1093/cercor/bhac426 (2022) doi:10.1093/cercor/bhac426.
39. Wang, D., Marcantoni, E., Clouter, A., Shapiro, K. L. & Hanslmayr, S. Rhythmic sensory stimulation as a noninvasive tool to study plasticity mechanisms in human episodic memory. *Curr. Opin. Behav. Sci.* **58**, 101412 (2024).
40. Grover, S., Nguyen, J. A. & Reinhart, R. M. G. Synchronizing Brain Rhythms to Improve Cognition. *Annu. Rev. Med.* **72**, 29–43 (2021).
41. Köster, M. & Gruber, T. Rhythms of human attention and memory: An embedded process perspective. *Front. Hum. Neurosci.* **16**, (2022).
42. Singer, W. Synchronization of cortical activity and its putative role in information processing and learning. *Annu. Rev. Physiol.* 349–374 (1993).
43. Wälti, M. J., Woolley, D. G. & Wenderoth, N. Assessing Rhythmic Visual Entrainment and Reinstatement of Brain Oscillations to Modulate Memory Performance. *Front. Behav. Neurosci.* **14**, (2020).
44. Hanslmayr, S., Axmacher, N. & Inman, C. S. Modulating Human Memory via Entrainment of Brain Oscillations. *Trends Neurosci.* **42**, 485–499 (2019).
45. Wang, D., Clouter, A., Chen, Q., Shapiro, K. L. & Hanslmayr, S. Single-trial phase entrainment of theta oscillations in sensory regions predicts human associative memory performance. *J. Neurosci.* **38**, 6299–6309 (2018).

46. Hsieh, L. T. & Ranganath, C. Frontal midline theta oscillations during working memory maintenance and episodic encoding and retrieval. *NeuroImage* **85**, 721–729 (2014).
47. Zaehle, T., Rach, S. & Herrmann, C. S. Transcranial Alternating Current Stimulation Enhances Individual Alpha Activity in Human EEG. *PLOS ONE* **5**, e13766 (2010).
48. Janssens, S. E. W., Sack, A. T., Ten Oever, S. & de Graaf, T. A. Calibrating rhythmic stimulation parameters to individual electroencephalography markers: The consistency of individual alpha frequency in practical lab settings. *Eur. J. Neurosci.* **55**, 3418–3437 (2022).
49. Kasten, F. H., Duecker, K., Maack, M. C., Meiser, A. & Herrmann, C. S. Integrating electric field modeling and neuroimaging to explain inter-individual variability of tACS effects. *Nat. Commun.* **10**, 5427 (2019).
50. Klimesch, W. Alpha-band oscillations, attention, and controlled access to stored information. *Trends Cogn. Sci.* **16**, 606–617 (2012).
51. Stecher, H. I., Pollok, T. M., Strüber, D., Sobotka, F. & Herrmann, C. S. Ten Minutes of α-tACS and Ambient Illumination Independently Modulate EEG α-Power. *Front. Hum. Neurosci.* **11**, (2017).
52. Uncapher, M. R., Hutchinson, J. B. & Wagner, A. D. Dissociable Effects of Top-Down and Bottom-Up Attention during Episodic Encoding. *J. Neurosci.* **31**, 12613–12628 (2011).
53. Kizuk, S. A. D. & Mathewson, K. E. Power and Phase of Alpha Oscillations Reveal an Interaction between Spatial and Temporal Visual Attention. *J. Cogn. Neurosci.* **29**, 480–494 (2017).
54. Leske, S. *et al.* Beta oscillations predict the envelope sharpness in a rhythmic beat sequence. *Sci. Rep.* **15**, 3510 (2025).
55. Morrow, A., Elias, M. & Samaha, J. Evaluating the Evidence for the Functional Inhibition Account of Alpha-band Oscillations during Preparatory Attention. *J. Cogn. Neurosci.* **35**, 1195–1211 (2023).
56. Palva, S., Monto, S. & Palva, J. M. Graph properties of synchronized cortical networks during visual working memory maintenance. *NeuroImage* **49**, 3257–3268 (2010).
57. Parish, G., Hanslmayr, S. & Bowman, H. The Sync/deSync Model: How a Synchronized Hippocampus and a Desynchronized Neocortex Code Memories. *J. Neurosci.* **38**, 3428–3440 (2018).
58. Raud, L. *et al.* Hippocampal-cortical functional connectivity during memory encoding and retrieval. *NeuroImage* **279**, 120309 (2023).
59. Tian, Y., Zhou, H., Zhang, H. & Li, T. Research on Differential Brain Networks before and after WM Training under Different Frequency Band Oscillations. *Neural Plast.* **2021**, 6628021 (2021).
60. de Pesters, A. *et al.* Alpha power indexes task-related networks on large and small scales: a multimodal ECoG study in humans and a non-human primate. *NeuroImage* **134**, 122–131 (2016).
61. Fell, J. *et al.* Medial temporal theta/alpha power enhancement precedes successful memory encoding: Evidence based on intracranial EEG. *J. Neurosci.* **31**, 5392–5397 (2011).
62. Park, H. *et al.* Blocking of irrelevant memories by posterior alpha activity boosts memory encoding. *Hum. Brain Mapp.* **35**, 3972–3987 (2014).
63. Nenert, R., Viswanathan, S., Dubuc, D. M. & Visscher, K. M. Modulations of ongoing alpha oscillations predict successful short-term visual memory encoding. *Front. Hum. Neurosci.* **6**, (2012).
64. Zoefel, B., ten Oever, S. & Sack, A. T. The Involvement of Endogenous Neural Oscillations in the Processing of Rhythmic Input: More Than a Regular Repetition of Evoked Neural Responses. *Front. Neurosci.* **12**, (2018).
65. Nyhus, E. & Curran, T. Functional role of gamma and theta oscillations in episodic memory. *Neurosci. Biobehav. Rev.* **34**, 1023–1035 (2010).
66. Köster, M., Martens, U. & Gruber, T. Memory entrainment by visually evoked theta-gamma coupling. *NeuroImage* **188**, 181–187 (2019).
67. Boran, E. *et al.* Persistent hippocampal neural firing and hippocampal-cortical coupling predict verbal working memory load. *Sci. Adv.* **5**, eaav3687 (2019).
68. Etter, G., Carmichael, J. E. & Williams, S. Linking temporal coordination of hippocampal activity to memory function. *Front. Cell. Neurosci.* **17**, (2023).

69. Figueiro, M., Nagare, R. & Price, L. Non-visual effects of light: How to use light to promote circadian entrainment and elicit alertness. *Light. Res. Technol.* **50**, 38–62 (2018).
70. Lok, R., Smolders, K. C. H. J., Beersma, D. G. M. & de Kort, Y. A. W. Light, Alertness, and Alerting Effects of White Light: A Literature Overview. *J. Biol. Rhythms* **33**, 589–601 (2018).
71. Weinbach, N. & Henik, A. The relationship between alertness and executive control. *J. Exp. Psychol. Hum. Percept. Perform.* **38**, 1530–1540 (2012).
72. Golmohammadi, R., Yousefi, H., Safarpour Khotbesara, N., Nasrolahi, A. & Kurd, N. Effects of Light on Attention and Reaction Time: A Systematic Review. *J. Res. Health Sci.* **21**, e00529 (2021).
73. Nieuwenhuis, S. & de Kleijn, R. The impact of alertness on cognitive control. *J. Exp. Psychol. Hum. Percept. Perform.* **39**, 1797–1801 (2013).
74. Poirel, N. *et al.* Do You Want to See the Tree? Ignore the Forest. *Exp. Psychol.* https://econtent.hogrefe.com/doi/10.1027/1618-3169/a000240 (2014).
75. Albouy, P., Weiss, A., Baillet, S. & Zatorre, R. J. Selective Entrainment of Theta Oscillations in the Dorsal Stream Causally Enhances Auditory Working Memory Performance. *Neuron* **94**, 193-206.e5 (2017).
76. Nuttall, R. *et al.* Evoked responses to rhythmic visual stimulation vary across sources of intrinsic alpha activity in humans. *Sci. Rep.* **12**, 5986 (2022).
77. Damsma, A., de Roo, M., Doelling, K., Bazin, P.-L. & Bouwer, F. L. Tempo-dependent selective enhancement of neural responses at the beat frequency can be mimicked by both an oscillator and an evoked model. *Cereb. Cortex* **35**, bhaf258 (2025).
78. Menétrey, M. Q. & Pascucci, D. Spectral tuning and after-effects in neural entrainment. *Behav. Brain Funct.* **20**, 29 (2024).
79. Schönbrodt, F. D. & Wagenmakers, E.-J. Bayes factor design analysis: Planning for compelling evidence. *Psychon. Bull. Rev.* **25**, 128–142 (2018).
80. Jeffreys, Harold. *Theory of Probability*. (Oxford University Press, 1998).
81. Lee, M. D. & Wagenmakers, E.-J. *Bayesian Cognitive Modeling: A Practical Course*. (Cambridge University Press, 2014).
82. Pikovsky, A., Rosenblum, M. & Kurths, J. Synchronization: A Universal Concept in Nonlinear Sciences. *Synchronization Arkady Pikovsky Michael Rosenblum Jürgen Kurths Pp 432 ISBN 052153352X Camb. UK Camb. Univ. Press May 2003* **2**, (2003).
83. Tass, P. *et al.* Detection of N:m Phase Locking from Noisy Data: Application to Magnetoencephalography. *Phys. Rev. Lett.* **81**, 3291–3294 (1998).
84. Parise, C. V. & Spence, C. Audiovisual crossmodal correspondences and sound symbolism: a study using the implicit association test. *Exp. Brain Res.* **220**, 319–333 (2012).
85. Oostenveld, R., Fries, P., Maris, E. & Schoffelen, J. FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. *Comput. Intell. Neurosci.* https://doi.org/10.1155/2011/156869 (2011) doi:10.1155/2011/156869.
86. Delorme, A. & Makeig, S. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Methods* **134**, 9–21 (2004).
87. Pion-Tonachini, L., Kreutz-Delgado, K. & Makeig, S. ICLabel: An automated electroencephalographic independent component classifier, dataset, and website. *NeuroImage* **198**, 181–197 (2019).
88. Riecke, L., Sack, A. T. & Schroeder, C. E. Endogenous Delta/Theta Sound-Brain Phase Entrainment Accelerates the Buildup of Auditory Streaming. *Curr. Biol.* **25**, 3196–3201 (2015).
89. Wacker, M. *et al.* A Time-Variant Processing Approach for the Analysis of Alpha and Gamma MEG Oscillations During Flicker Stimulus Generated Entrainment. *IEEE Trans. Biomed. Eng.* **58**, 3069–3077 (2011).
90. Pastore, R. E. & Scheirer, C. J. Signal detection theory: Considerations for general application. *Psychol. Bull.* **81**, 945–958 (1974).
91. Stanislaw, H. & Todorov, N. Calculation of signal detection theory measures. *Behav. Res. Methods Instrum. Comput.* **31**, 137–149 (1999).

Acknowledgements

We thank Leonie Lambertz, Sebastian Heeren, Michele Frerichs, and Lennart May for their invaluable assistance during data acquisition.

Funding Declaration

The present research was financially supported by the German Research Foundation (DFG; SFB/Transregio 169, Project B3 and DFG RO 2653/9-1)

Author Contributions

M.R., J.O. and M.M. designed the study. J.O. and M.M. performed data acquisition. J.O. and M.M. analyzed the data. M.R. acquired funding, conceptualized, and supervised the project. J.O., M.M. and M.R. wrote the original manuscript. J.O., M.M., and M.R. reviewed and edited the manuscript and approved the final manuscript.

Data availability

The raw EEG and behavioral data underlying our findings have been uploaded to an open repository of the University of Hamburg for accessibility (https://doi.org/10.25592/uhhfdm.17620).

Competing interests

The authors declare no competing interests.

Additional Information

Correspondence and requests for materials should be addressed to M.R.

Disentangling the Functional Roles of Pre-Stimulus Oscillations in Crossmodal Associative Memory Formation via Sensory Entrainment

Supplementary material

Jan Ostrowski[1†], **Marike C. Maack**[1†], **Michael Rose**[1*]

1 *Department of Systems Neuroscience, University Medical Center Hamburg-Eppendorf, Hamburg, Germany; j.ostrowski@uke.de, m.maack@uke.de, rose@uke.de*

† Equal contributions

** Correspondence: rose@uke.de*

16-digit ORCID:
JO: 0000-0001-9928-272X
MM: 0000-0002-6960-4465
MR: 0000-0002-9789-7066

Supplementary 1. Contrasting pre-stimulus activity from theta and alpha groups to activity from the control and NE groups

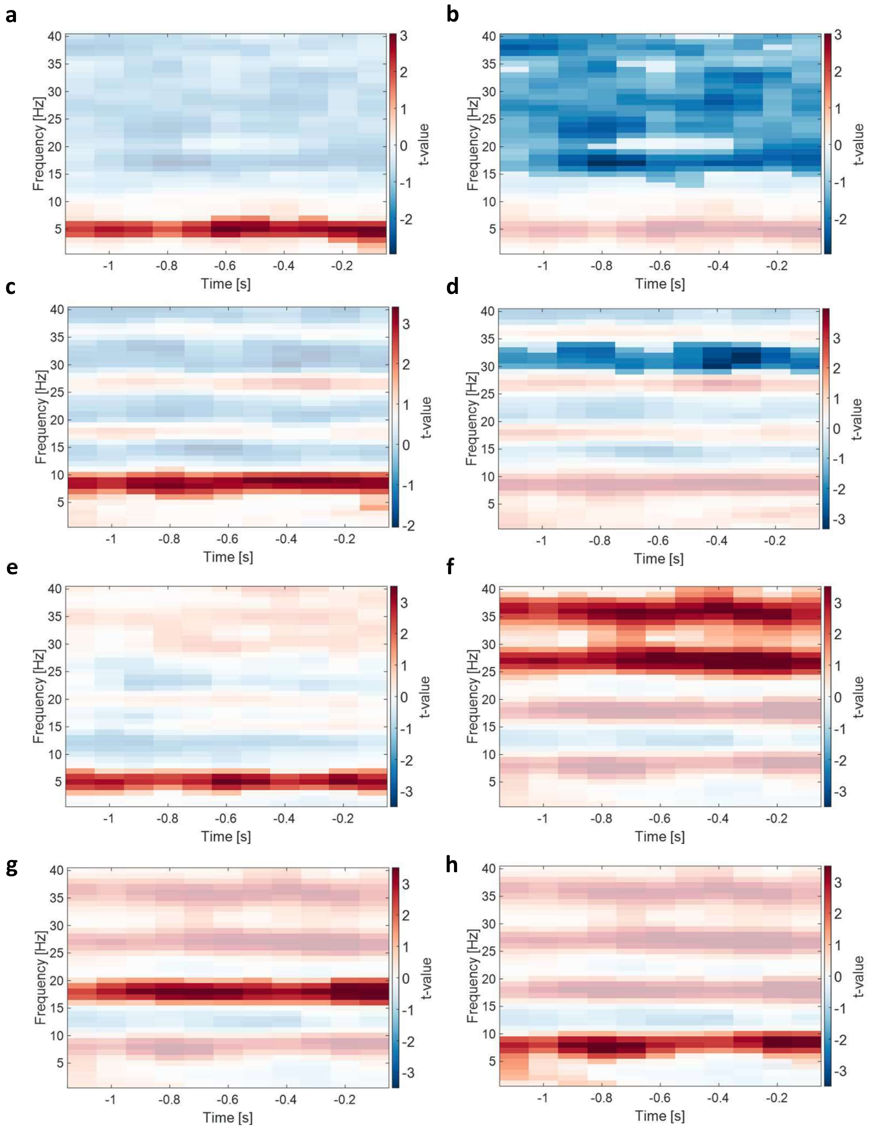


Figure S1. Results of EEG data contrasts of entrainment groups with the control and NE groups. The figure shows time-frequency plots depicting the results of the statistical comparison of relative change in pre-stimulus activity. **(a)** and **(b)** show the two significant clusters from the comparison of the theta group with the control group. **(c)** and **(d)** depict the two significant clusters resulting from contrasting the alpha group with the control group. **(e)** shows the positive cluster revealed by comparing activity from the theta group with the NE group. **(f) – (g)** depict the statistical results comparing the alpha group with the NE group. In all time-frequency plots, positive *t*-values signify greater relative change in the theta or alpha groups, respectively. Opaque data points show the extent of a statistically significant cluster ($p < .025$, corrected). Each subplot shows one distinct cluster and depicts the *t*-values averaged over the electrodes comprising the cluster.

Oscillatory power in the late entrainment period (-1.1 s to -0.1 s relative to stimulus onset) from the theta and alpha group was each contrasted with the activity from the NE group in the same time period. We used a cluster-based permutation approach to account for multiple comparisons, and two-tailed independent-samples *t*-tests on sample level. The frequency range for this analysis was set to 1 to 40 Hz, and all electrodes were included. Comparing the theta entrainment condition with the NE group, the analysis yielded one significant positive cluster in the frequency range of 3 to 7 Hz, spanning the whole analysis window (*p* < .025, corrected). This suggests significantly increased oscillatory power in the envelope around 5 Hz for the theta group as compared to the NE group **(Figure S2e)**. Contrasting activity from the alpha group with the NE group revealed three distinct positive clusters, each spanning the whole analysis window. The clusters covered the frequency ranges of 24 to 40 Hz and 16 to 20 Hz. Importantly, the third cluster ranged from 1 to 10 Hz up until -0.8 s relative to stimulus onset and was centered one the 9 Hz envelope for the remaining part of the analysis time window (**Figure S2h**).

Supplementary 2. Analysis of oscillatory activity in the stimulus presentation window during encoding

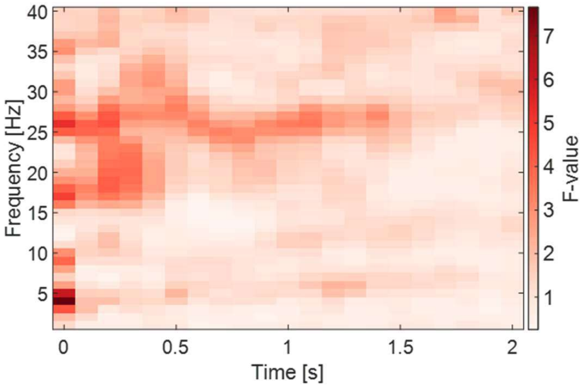


Figure S2. Difference in post-stimulus activity between entrainment groups. The figure shows a time-frequency plot of the stimulus presentation time window from the encoding task over a frequency range of 1 to 40 Hz. The color dimension displays the F-values from the independent-samples F-test.

In order to assess potential differences in oscillatory activity during stimulus presentation between groups, we compared oscillatory power from the post-stimulus interval (0 s to 2s relative to stimulus onset) among the entrainment groups (theta, alpha, and control) using an independent-samples *F*-test on sample level. Data was included for a frequency range of 1 to 40 Hz and all electrodes, and cluster-based permutation was used for multiple-comparison corrections. However, the analysis showed only a tendency for a significant cluster in the electrode-frequency-time space, suggesting that there are no significant differences in post-stimulus power between the entrainment groups (*p* = .069, corrected).

Supplementary 3. Analysis of categorization task performance during encoding

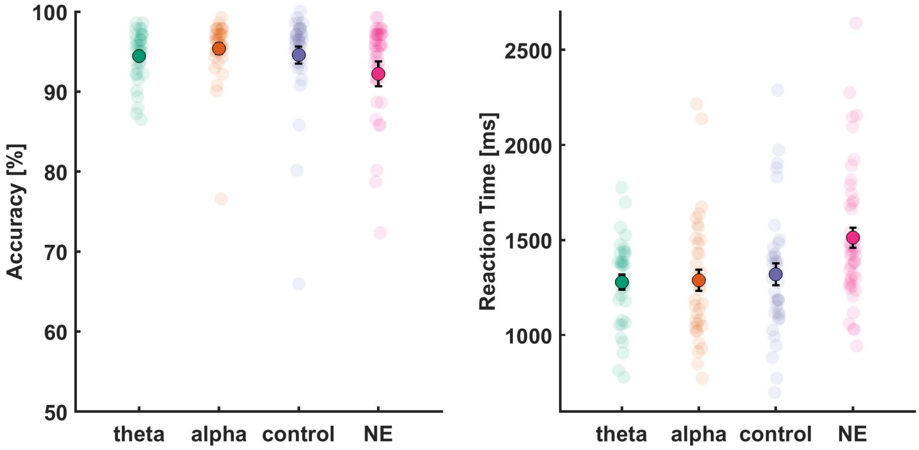


Figure S3. Performance in the categorization task during encoding. *Left*: Accuracy values for the categorization task during encoding for each group. *Right:* Average response time for the categorization task during encoding. Transparent data points mark individual task accuracy, and the black error bars signify the standard error of means.

In the categorization task from the encoding phase, participants showed high accuracy across all entrainment conditions, 94.45% (SD = 3.23) for theta, 95.38% (SD = 3.88) for alpha, and 94.57% (SD = 6.27) for control condition. Accuracy in the NE condition as an additional control was slightly lower at 92.21% (SD = 10.43). The overall accuracy across all four conditions was 94.02% (SD = 6.97). Using a Bayesian one-way ANOVA model yielded a Bayes factor of BF_{10} = 0.381, suggesting moderate evidence in support of the null hypothesis of no significant differences among the groups. These results suggest that participants in the current study maintained high compliance with task demands throughout the experiment, which was essential for accurately assessing the subsequent impact of oscillatory activity on memory performance. Reaction times showed a similar pattern. Participants responded fastest in the entrainment conditions (theta: 1279.4 ms, SD = 230.3; alpha: 1288.9 ms, SD = 327.6; control: 1320.4 ms, SD = 343.7), with slower responses in the NE condition (1512.6 ms, SD = 355.3). The overall average reaction time was 1361.11 ms (SD = 333.1). However, a Bayesian one-way ANOVA indicated moderate evidence for the alternative hypothesis, BF_{10} = 5.0737, indicating measurable differences among the groups. Individual group contrasts revealed that there was likely no difference in response times between the entrainment groups (theta vs control: BF_{10} = 0.2849; alpha vs control: BF_{10} = 0.2628; theta vs alpha: BF_{10} = 0.248). However, the evidence suggests a moderate-to-strong effect for differences between the theta and alpha groups and the NE group (theta vs NE: BF_{10} = 19.1684; alpha vs NE: BF_{10} = 5.7022). The comparison between the control and the NE group yielded only weak evidence for significant difference, BF_{10} = 2.3366.

Supplementary 4*. Changes in performance over the course of the experiment*

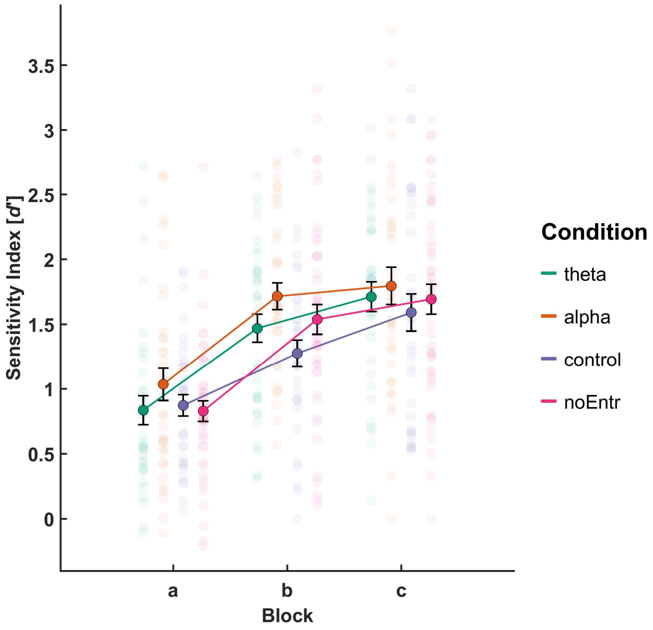


Figure S4. Changes in sensitivity indices across experimental runs. The plot depicts mean sensitivity indices (*d'*) over participants for every group and the three experimental runs. Every transparent data point marks the individual sensitivity index of one participant. Black error bars indicate the standard error of means.

To assess changes in behavioral performance over time, we conducted a mixed-design Bayesian ANOVA with the within-subjects factor *block* (a, b, c) and the between-subjects factor *entrainment condition* (theta, alpha, control, NE), both as fixed factors. The participant ID was included as a random effect. The best-supported model included *block* and the participant ID, BF = 1.58×10^{35}, indicating extreme evidence for a main effect of *block*. Adding *entrainment condition* reduced model support by a factor of approximately 4.6 (BF = 3.43×10^{34}), while including the *block* x *entrainment condition* interaction further reduced support by a factor of approximately 135, BF = 1.17×10^{33}. The model with only *entrainment condition* and participant ID was 7.3 times less likely than the null model (BF = 0.14), providing strong evidence against a main effect of *entrainment condition*. This indicates that the improvement in memory performance over the course of the experiment was consistent across entrainment conditions and was not modified by the type of entrainment.

Supplementary 5. ***Individual group and variable contrasts for response times during recognition***

Table S1

Individual group comparisons of RTs for all response categories

Response category	Group 1	M [ms]	SD	Group 2	M [ms]	SD	*BF*^{a}
hit	alpha	1405	165	control	1450	206	0.3789
	alpha	1405	165	NE	1612	272	47.4767**
	alpha	1405	165	theta	1427	156	0.2825
	control	1450	206	NE	1612	272	4.279*
	control	1450	206	theta	1427	156	0.2773
	NE	1612	272	theta	1427	156	18.9926**
miss	alpha	1580	257	control	1519	271	0.3652
	alpha	1580	257	NE	1771	344	3.3256*
	alpha	1580	257	theta	1573	283	0.2472
	control	1519	271	NE	1771	344	19.4755**
	control	1519	271	theta	1573	283	0.326
	NE	1771	344	theta	1573	283	3.3623*
CR	alpha	1397	174	control	1417	236	0.265
	alpha	1397	174	NE	1609	296	31.4731**
	alpha	1397	174	theta	1414	185	0.2642
	control	1417	236	NE	1609	296	6.9499*
	control	1417	236	theta	1414	185	0.2463
	NE	1609	296	theta	1414	185	13.1874**
FA	alpha	1669	222	control	1675	309	0.2469
	alpha	1669	222	NE	1885	310	37.8379**
	alpha	1669	222	theta	1718	230	0.3493
	control	1675	309	NE	1885	310	9.4932*
	control	1675	309	theta	1718	230	0.2961
	NE	1885	310	theta	1718	230	5.2933*

Note. This table shows the results from the statistical analysis of reaction times based on entrainment group differences. CR = correct rejection, FA = false alarm, M = mean (arithmetic), SD = standard deviation, df = degrees of freedom

a The depicted Bayes factor values are equivalent to BF_{10}, estimating the evidence for the alternative hypothesis (statistical difference) relative to the null hypothesis (no difference). A Cauchy distribution of medium width was used as prior for each comparison.

* at least moderate evidence for H_1, ** at least strong evidence for H_1

Supplementary 6. *Resting State*

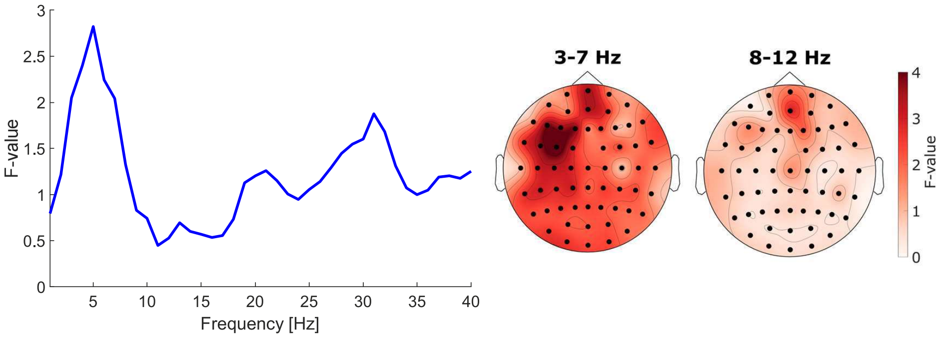


Figure S5. Group contrast for differences in resting-state activity before and after the experiment. *Left*: F-values for the analysis window of 1 to 40 Hz from a cluster-based permutation test with an independent-samples *F*-test on sample level assessing group differences in pre- and post-experiment resting-state discrepancies. *Right*: Topographical distribution of *F*-values averaged across the 3–7 Hz (theta) and 8–12 Hz (alpha) bands. No significant clusters were observed in this analysis (p = .2972, corrected).

As some studies report lingering oscillatory effects due to entrainment procedures **[Kasten & Herrmann, 2022; Gallina et al., 2023)**, we explored differences in resting-state spectra that were recorded once before (RestPre) and once after the SME task (RestPost) to determine whether traces of the entrainment could be observed even after the experiment. For the analysis, we used power spectra in the frequency range of 1 to 40 Hz and submitted the data to a cluster-based permutation test with two-tailed paired-samples t-tests on the sample level. Note that this analysis was conducted separately for the theta group, alpha group, as well as the control group. For the theta group, one negative cluster was found in the alpha band (8 to 12 Hz), indicating increased power after the experiment (p < .025, corrected). Similarly, a negative cluster ranging from 7 to 18 Hz was observed for the comparison in the alpha group (p < .025, corrected), while the analysis in the control revealed a negative cluster in the alpha band (8 - 12 Hz, p < .025, corrected). Interestingly, the control group analysis yielded a second negative cluster in the beta band, ranging from 17 to 33 Hz (p < .025, corrected). As the effect in the alpha band and, to a certain degree, in the beta band was observed in all three groups, we were interested in whether the effect magnitude differed between the groups.

Supplementary 7. *No differences in subjective perception of entrainment*

Survey items (translated from German into English):

I1 (pleasentness): How pleasant did you find the flickering of the image?

I2 (distraction): To what extent did you feel distracted by the flickering of the image while trying to remember the pairs?

I3 (attention): How would you rate your level of attention during the task?

I4 (fatigue): How exhausted do you feel at the moment?

Participants rated on a scale from 0 (*not at all*) to 5 (*very much*) in steps of 0.5.

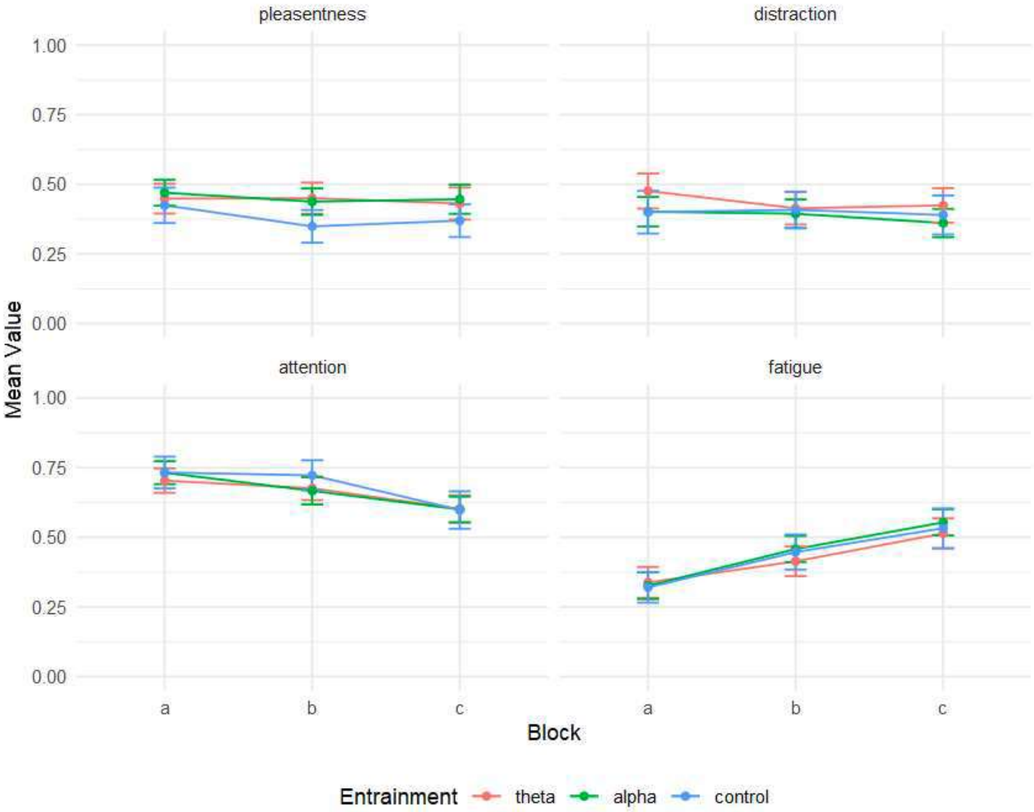


Figure S6. Subjective ratings of task-related experience across blocks and entrainment conditions. The data points depict group and block averages across participants. The error bars mark the standard error of means.

As individual perception qualities of images with oscillating luminance may vary, we investigated whether the subjective perception of the sensory stimulation might differ between the entrainment groups to control for salience effects. Participants received four survey items after each encoding phase, measuring the *pleasantness* and the *distracting qualities* of the entrainment procedure, as well as *attention* and *fatigue*. We conducted a Bayesian mixed-design ANOVA for every item, with a between-subjects factor *pre-stimulus condition* (theta, alpha, control) and a within-subjects factor *block* (A, B, C). Scores from every item did not significantly differ between levels of *pre-stimulus condition* ($BF_{\text{pleasentness}}$ = 0.3099, $BF_{\text{distraction}}$ = 0.3853 , $BF_{\text{attention}}$ = 0.1132 , BF_{fatigue} = 0.1279), indicating that the type of entrainment procedure had no differential effect. However, the analysis revealed an effect of *block* for the variables *distraction, attention,* and *fatigue* ($BF_{\text{distraction}}$ = 7.8834, $BF_{\text{attention}}$ = 1.855 x 10^{9}, BF_{fatigue} = 1.3415 x 10^{15}). No interactions of *pre-stimulus condition* and *block* were observed ($BF_{\text{pleasentness}}$ = 0.0732, $BF_{\text{distraction}}$ = 0.0578, $BF_{\text{attention}}$ = 0.195, BF_{fatigue} = 0.0552. Participants felt less distracted by the entrainment in block C of the experiment (M = 0.382, SD = 0.224) than in block A (M = 0.45, SD = 0.243). Conversely, participants rated their level of attention in block C (M = 0.573, SD = 0.203) consistently lower than in block A (M = 0.694, SD = 0.186). This was accompanied by increased fatigue ratings in block C (M = 0.528, SD = 0.223) as compared to block A (M = 0.338, SD = 0.197). In sum, evidence from the survey data indicates that the entrainment procedures were received equally pleasant and distracting, suggesting no confound of the behavioral results due to subjective perception.

10.3 Study 3: The order of multisensory associative sequences is reinstated as context feature during successful recognition

Maack, M. C., Ostrowski, J., & Rose, M. (2025). The order of multisensory associative sequences is reinstated as context feature during successful recognition. Scientific Reports, 15(1), 18120. https://doi.org/10.1038/s41598-025-02553-3

www.nature.com/scientificreports

scientific reports

OPEN

The order of multisensory associative sequences is reinstated as context feature during successful recognition

Marike Christiane Maack, Jan Ostrowski & Michael Rose

The ability of the human brain to encode and recognize sequential information from different sensory modalities is key to memory formation. The sequence in which these modalities are presented during encoding critically affects recognition. This study investigates the encoding of sensory modality sequences and its neural impact on recognition using multivariate pattern analysis (MVPA) of oscillatory EEG activity. We examined the reinstatement of multisensory episode-specific sequences in $n = 32$ participants who encoded sound-image associations (e.g., the image of a ship with the sound of a frog). Images and sounds were natural scenes and 2-second real-life sounds, presented sequentially during encoding. During recognition, stimulus pairs were presented simultaneously, and classification was used to test whether the modality sequence order could be decoded as a contextual feature in memory. Oscillatory results identified a distinct neural signature during successful retrieval, associated with the original modality sequence. Furthermore, MVPA successfully decoded neural patterns of different modality sequences, hinting at specific memory traces. These findings suggest that the sequence in which sensory modalities are encoded forms a neural signature, affecting later recognition. This study provides novel insights into the relationship between modality encoding and recognition, with broad implications for cognitive neuroscience and memory research.

The ability to remember episodes from the past is a cornerstone of human memory. Episodes consist of multiple features that may stem from different modalities (e.g., visual, auditory), reaching us in specific sequences. In line, it has been shown that humans encode not only the semantic content but also the temporal order (sequence) of features, which is crucial for recalling the flow of a past episode[1,2]. The capacity to encode and retrieve sequential information allows us to mentally rebuild the dynamic structure of events, highlighting the role of temporal context in episodic memory[1,3]. Recalling the order that features of an episode were originally encoded in, is based on sequential reinstatement[4].

Episodic memory relies on the integration of contextual information during encoding, with the hippocampus playing a key role in binding event features such as sensory modality and spatial-temporal context[5–7]. Prior research has investigated how we remember the temporal order of events, including the role of unimodal cueing[8–10]. Evidence suggests that episodic memory involves temporal compression and event segmentation, where the hippocampus supports memory organization by structuring event sequences and contextual boundaries[9,11]. Temporal compression refers to the tendency of episodic memory to condense events during recall, influenced by event segmentation and goal-directed actions[12–15]. Event segmentation, in turn, affects how temporal order is remembered, as events chunked at perceptual boundaries enhance object-context binding but may reduce precise temporal order memory[9,16]. The hippocampus further supports the encoding and retrieval of event sequences, integrating spatial and temporal contexts essential for remembering event order[17,18]. In line, episodic memory retrieval is shaped by the availability of contextual information at encoding, with reinstatement of encoding context enhancing recognition in providing characteristic cues that mitigate interference[19–21]. Sensory modality sequences, as part of contextual information, contribute to the organization of memory representations[22,23]. The hippocampus is crucial for integrating these contextual elements, facilitating recognition by reactivating modality-based associations rather than strictly reconstructing event sequences in order[18,24,25].

While previous studies have explored unimodal cueing and temporal order memory, the current study specifically investigates whether the modality sequence acts as a contextual feature that influences encoding and

Department of Systems Neuroscience, University Medical Center Hamburg-Eppendorf, Martinistr. 52, Building W34, 20248 Hamburg, Germany. ✉email: rose@uke.de

recognition rather than sequential recall per se. Contextual cues, including sensory modality sequences, can mitigate interference effects and improve memory performance by reinstating elements of the original encoding context[21,26,27]. Conversely, mismatches between encoding and retrieval contexts may lead to competition between overlapping memory traces, impairing recall[4,28,29]. Both physical and mental reinstatement of contextual information facilitate episodic retrieval, with mental reconstruction yielding comparable benefits to direct environmental cues[30,31]. Furthermore, cognitive control plays a role in sustaining contextual reinstatement, as individuals with higher working memory capacity are better able to maintain contextual associations through strategic memory processes[32].

Beyond unimodal sequences, results from the animal, as well as human studies, suggest that sequential information plays a critical role in recalling multisensory episodes, where encoded features from different sensory modalities (e.g., an image-sound pair) are reinstated during retrieval[33–36]. Multisensory features enable the brain to store and retrieve information across various perceptual domains, enhancing our ability to recall past experiences and make informed decisions[37–39]. As such, the human memory has evolved to function optimally under multisensory conditions[40]. Interestingly, multisensory memories can be cued by unimodal features upon remembering, suggesting that multisensory encoding enhances subsequent recognition[39,41]. This means that one modality may serve as a cue to retrieve the complete episode, even if it includes features from different modalities[42]. It is, however, unclear so far whether and how one modality (i.e., auditory) relates to the reinstatement of another (i.e., visual). The Scene Reconstruction Theory suggests that especially the hippocampus helps to reconstruct memories by integrating various sensory details associated with an event[4]. This integration is supposed to allow richer, and more detailed, memory formation, as the brain can draw upon multiple sensory inputs to create a coherent narrative of the event[11,43].

While neural plasticity allows multisensory learning[44], understanding the neural reinstatement of sequential information across sensory modalities remains crucial for elucidating the broader mechanisms of remembering. Recall generally involves the activation and reconstruction of neural pathways tied to previously encoded details[45]. This process is influenced by retrieval cues and familiarity with the material[46]. Beyond sequential and multisensory reinstatement, the recollection of contextual details surrounding past events, such as where and when they occurred, significantly contribute to the liveliness and specificity of the memory representation[47–50]. The Context Maintenance and Retrieval (CMR) model here provides a framework to understand how the brain organizes memories around contextual and temporal cues, facilitating the accurate retrieval of episode-specific feature sequences[51,52], propelling the reconstruction of the correct order and updating of associations. In line, previous research has highlighted that the process of episodic remembering involves not only recalling specific items but also reinstating the contextual details of the original event[53–55]. These studies have demonstrated that the success of memory retrieval is closely associated with the reactivation of the encoding-related memory trace[52,56–58]. Interestingly, it has been shown that during memory reactivation, not only episode-specific features but also contextual features, that were not directly related to the current memory task, are reinstated[29,59–65]. However, the precise neural mechanisms underlying this sequential reinstatement, especially in multisensory contexts, remain elusive.

EEG is a powerful tool to track these reinstatement processes including multisensory episode-specific feature sequences. Here, especially multivariate temporal-pattern analysis has emerged as the gold-standard to examine how neural activity during retrieval reflects (sequential) reinstatement. Moreover, it represents a tool for investigating the role of context reinstatement in memory processes, revealing the (beneficial) effects of reinstating neural encoding patterns in memory retrieval[30,64]. Accordingly, multivariate pattern analysis (MVPA) has been used to decode oscillatory activity patterns during memory retrieval, successfully classifying specific neural signatures tied to remembering[30,64]. Here, low-frequency activity (e.g., beta (13–30 Hz) and theta (3–7 Hz) oscillations) have been shown to be particularly important for episodic memory processes, facilitating successful retrieval[66–70]. Multisensory inputs from different modalities as well as their sequential encoding thereby enrich the formation of stable memory traces[39,41]. As multivariate approaches have shown that neural pattern reinstatement is indeed associated with episode-specific feature sequences, this study aims to investigate the oscillatory mechanisms underlying the retrieval of sequential information in human memory, focusing on whether the modality sequence in which information was presented during encoding is reinstated during recognition. Specifically, we utilize EEG and MVPA to classify the neural patterns associated with modality sequence reinstatement, providing new insights into the role of oscillatory activity in organizing and retrieving sequential memories across different sensory modalities. Importantly, the current study aims to demonstrate how modality sequence functions as a contextual feature during encoding and recognition (but not temporal reinstatement in the sense of reactivating the sequential order during retrieval; i.e., first visual, second auditory). This design offers a novel perspective on context memory in representing a sharp contrast to previous designs, which employed a parallel presentation of modalities during encoding[71,72].

Methods

Participants

Thirty-six healthy participants were recruited for the experiment. Data from four participants were excluded due to a high number of missing trials ($n = 1$) and poor behavioral performance ($n = 3$). Outliers in terms of memory performance (d') were identified and excluded if they exceeded ± 3 absolute deviations from the median (MAD;[73]. Therefore, the final sample included $n = 32$ participants (19 females, 52.77% female) with a mean age of 24.25 years (SD = 3.34), ranging from 18 to 33 years. All participants had normal or corrected-to-normal vision and hearing ability and reported no neurological or psychiatric diseases. They gave written informed consent and received financial reimbursement for participating in the study. The Hamburg Medical Council ethics committee (PV5893) approved this investigation. We confirm that all research was performed in accordance with relevant guidelines and regulations.

Task and procedure

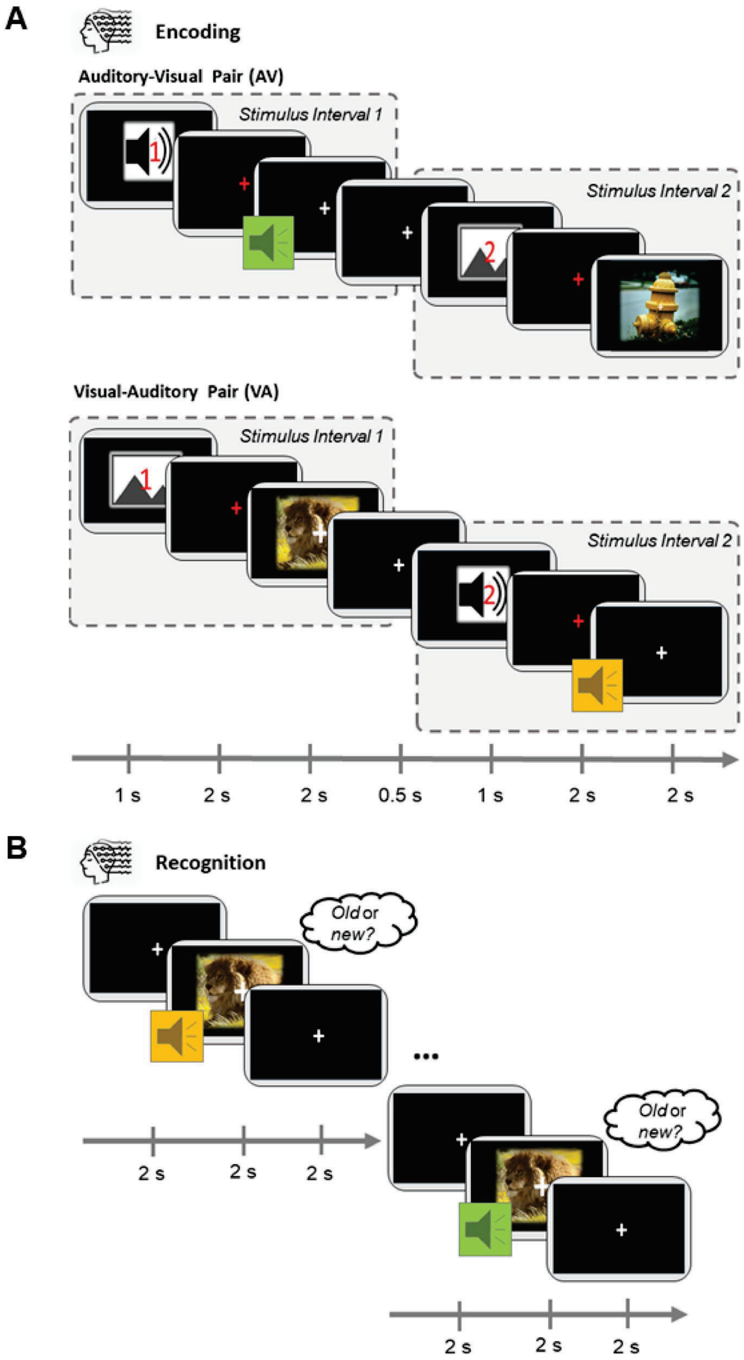
We implemented an explicit sequential associative memory task consisting of an encoding task, a short intermission, and a subsequent recognition task. In order to measure associative multisensory memory, participants were presented sequential image-sound pairs during the encoding task. The images (resolution: 640 × 480 pixels; 24-bit color depth) and sounds (length: 2 s; bitrate: 1411kBit/s) were randomly selected from an internal stimulus database, presenting real-life objects, animals, and landscapes. The individual stimuli were paired pseudo-randomly (semantically congruent stimuli pairs were excluded). Each pair was presented once during the encoding task. In each encoding trial, the stimulus pairs were presented sequentially. Each trial started with a 1-second *modality cue* indicating whether a visual or an auditory stimulus would be presented as the first pair component (Fig. 1). The *modality cue* was represented as an icon, cueing the following modality (image or tone). Additionally, the icon involved a red number, stating whether the next stimulus would be the first or second stimulus of the pair. The *modality cue* was followed by a red fixation cross for 2 s, which served as a visual cue for the upcoming stimulus. Afterwards, the first stimulus was presented, followed by a 500 ms Inter-Stimulus-Interval (ISI). Complementary to the first stimulus presentation, a second *modality cue* indicated whether a visual or an auditory stimulus would be presented as the second stimulus. Again, a red fixation cross served as a visual cue for the upcoming stimulus followed by the announced stimulus and the inter-trial interval (ITI). The ITI was jittered between 3 s and 5 s. Trials were counterbalanced for *modality-order*, such that the encoding task consisted of the same number of visual-auditory (VA) as auditory-visual (AV) trials. We applied a modality cueing procedure, including both modality-specific cues and numerical indicators, to clearly signal the upcoming auditory and visual pairings, thereby facilitating robust and explicit encoding of the stimulus associations. All participants were explicitly instructed to memorize the stimulus pairs, and not to focus on the individual images or sounds. This ensured that subsequent memory would later reflect associative memory, but not item memory. We divided the experiment into three consecutive blocks, each consisting of an encoding and subsequent recognition task. During each encoding task, 47 stimulus pairs were presented. After the encoding task, a short 3-minute intermission followed, during which participants were asked to count down aloud from 100 (115 and 125 in the second and third run, respectively) in steps of 7 (9 and 13 in the second and third run, respectively). In the subsequent recognition task, participants were presented with the 47 stimulus pairs shown during the previous encoding phase, as well as 47 new pairs. Both components of a pair were presented in parallel, in sharp contrast to the encoding task, where the components were shown sequentially. New pairs consisted of the same individual components that rendered the pairs from the encoding task, but were shuffled to create 47 new pairs. The participants were asked to indicate via button press whether the presented pairs were already known from the encoding task or not. Stimulus presentation lasted for 2 s, and no cue was used. The inter-trial interval was fixed to 5 s. The recognition task was followed by a short break of 3 to 5 min, followed by the encoding task of the next run. Across the three blocks, 141 stimulus pairs were presented during encoding, and 282 were presented during recognition in total.

EEG data acquisition

EEG data were collected using a 64-channel Ag/AgCl active electrode system (ActiCap64; BrainProducts, Gilching, Germany), arranged in accordance with the extended 10–20 system[74]. Sixty electrodes were positioned at the most central scalp locations. To facilitate offline artifact removal, a bidirectional bipolar electrooculogram (EOG) was concurrently recorded using the remaining four electrodes. These bipolar EOG electrode pairs were positioned above and below the left eye, as well as at the lateral ends of the bicanthal plane. FCz served as the reference electrode for data acquisition, while the ground electrode was situated at position Iz. Signals were digitized at a sampling rate of 500 Hz and was amplified with a low cut-off frequency of 0.53 (0.3 s time constant). Impedances were maintained below 10 kΩ throughout the recording session.

EEG preprocessing and time-frequency decomposition

The acquired EEG data were preprocessed offline using the FieldTrip toolbox[75] in MATLAB (Release 2022a, The MathWorks Inc., Natick, Massachusetts, USA). For each participant, the encoding and the recognition task were analyzed separately. For the recognition task, epochs were extracted from − 2500 ms to 3500 ms relative to stimulus onset, resulting in a trial duration of 5 s. A high-pass filter at 0.5 Hz was applied to remove extreme low-frequency fluctuations. The data were visually inspected, and trials containing artifacts, such as high-frequency noise indicating muscular activity or spikes resembling poor electrode connections, were removed. Independent Component Analysis (ICA) was used to identify components corresponding to blinks and other ocular activity, and the data were corrected accordingly. On average, 4.8 components (SD = 3.31) were removed per subject. The data were then visually inspected again, and trials with artefacts were excluded. The remaining trials for each subject were split into correct old (remembered; mean = 83.11; SD = 26.40), incorrect old (forgotten; mean = 46.94; SD = 24.08), correctly rejected (mean = 112.46; SD = 17.05) and false alarm (mean = 18.60; SD = 14.78) trials. The correct old trials were additionally split for the "visual-auditory" (VA) and "auditory-visual" (AV) conditions according to modality order in the encoding task, resulting in a similar number of trials in each condition (44 trials on average in each condition; AV: mean = 44.75, SD = 10.79; VA: mean = 44.41, SD = 11.02). Time-frequency decomposition was performed from − 1 to 2 s relative to stimulus onset, covering the 1 to 40 Hz frequency range. This was achieved using a multitaper convolution approach with a sliding Hanning window of 500 ms and a 100 ms step size. Although a 500 ms window has an intrinsic frequency resolution of 2 Hz (1/0.5 s), we applied zero-padding to the maximum trial length, which interpolated the spectrum to a 1 Hz grid, thereby effectively balancing temporal precision with frequency resolution. No baseline correction was applied for the recognition tasks, as the primary focus was on within-subject differences in oscillatory power between the remembered and forgotten pairs. We did not apply baseline correction to preserve potential pre-stimulus effects, which have been implicated in learning and memory processes. Additionally, baseline correction assumes a proportional scaling



of oscillatory and non-oscillatory (1/f) activity, an assumption that may not always hold. As a result, the reported effects should be interpreted in terms of relative power changes rather than absolute polarity shifts. Additionally, for the data of the recognition task, the resulting frequency spectra (electrode × frequency × time) from stimulus onset onward, reflecting the processing phase, were used to predict the modality order in the encoding task for each participant and condition. Only trials with successfully remembered items were included in the analysis, while pre-stimulus activity was not included. For the multivariate analyses, the Matlab toolbox for classification and regression of multi-dimensional data (MVPA-Light;[76] was used. A support vector machine (SVM) with a

◀**Fig. 1**. Schematic overview of the encoding task in both sequence variations as well as the following recognition task. (**A**) The two different modality order sequences in the encoding task. Stimuli were presented sequentially. The trial started with a cue, indicating which stimulus modality is presented first followed by a red fixation cross. The red fixation cross indicated that a stimulus would be presented in the next 2 s. Afterwards, a complex natural image was presented. The presentation of the second stimulus of the pair followed the same procedure. We utilized two different encoding sequence orders: either the sound was present first and the image afterwards (auditory-visual; AV-condition or the image was presented first and the sound afterwards (visual-auditory; VA-condition). For the analysis of the encoding task, the task was subdivided into Stimulus Intervals 1 and 2, indicated by the dashed boxes. (**B**) One example trial from the recognition task. Unlike the encoding phase, stimulus pairs were presented simultaneously. Participants had to identify whether the pair **had** been presented during encoding (old) or not (new) within 4 s. The recognition task pairs were composed of the stimuli from the encoding resulting in new and old pairs.

k = 5-fold cross-validation was used for classification with a five-time repetition. The classifier was trained on all electrodes using single-trial frequency spectra.

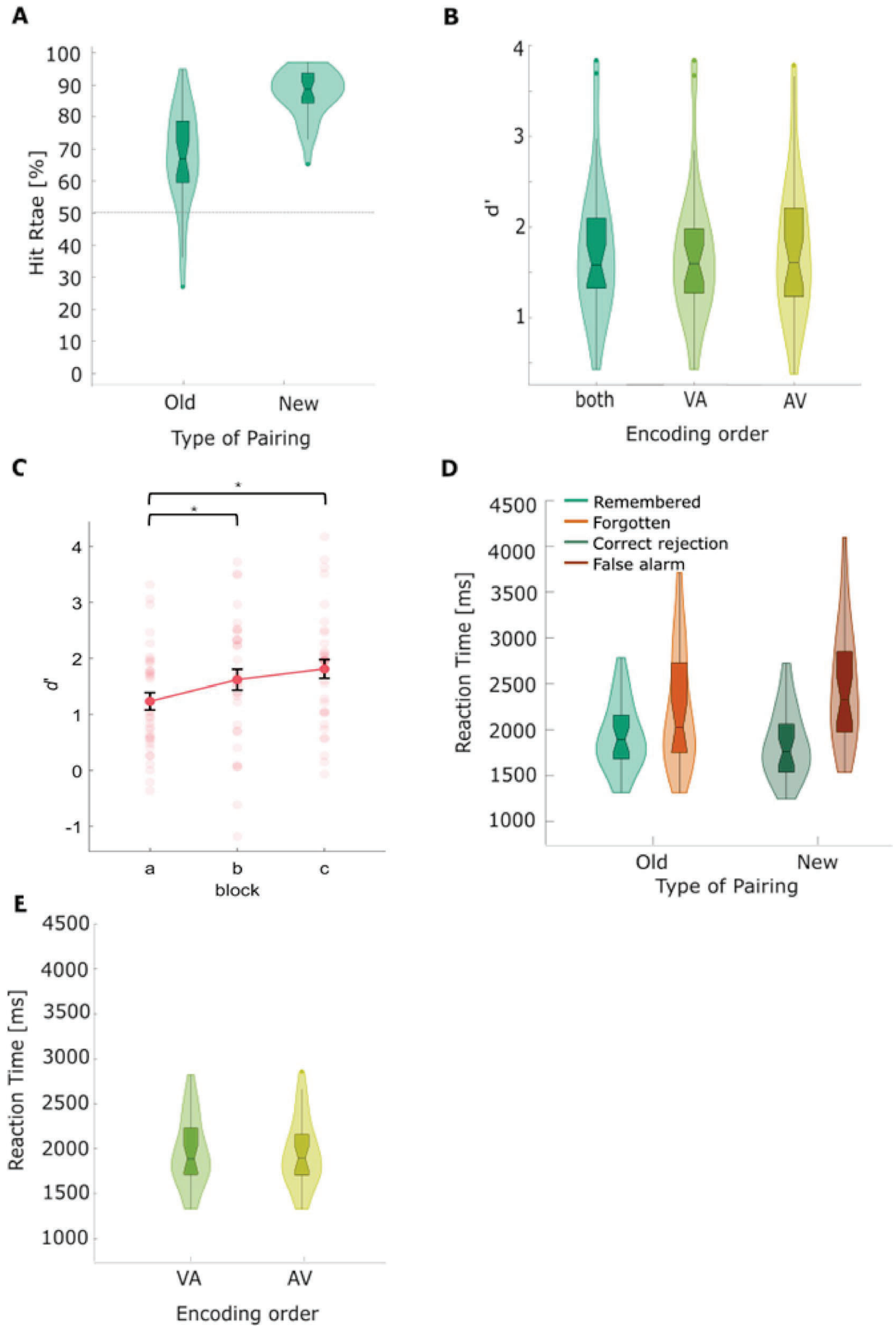
The preprocessing routine and the time-frequency analysis for the encoding task were the same as for the recognition task, with deviations during epoching. The deviation in epoching procedure resulted from the difference in presentation mode. While sound-image associations were presented simultaneously in the recognition task, the associations were presented sequentially in the encoding task. Epochs were extracted from the first modality cue until 2 s after the onset of the second stimulus, resulting in a trial duration of 10.5 s. Using ICA, on average 4.8 independent components were rejected from each individual data set (SD = 2.61). After preprocessing, the remaining trials for each subject were split into a “visual-auditory” and “auditory-visual” condition according to modality order in the encoding task, resulting in a similar number of trials in each condition. These trials were then used in the subsequent analyses of later remembered and forgotten trials (55 trials on average in each condition). After time-frequency decomposition, data were averaged separately for remembered and forgotten trials for each participant.

Statistical analysis

In the recognition task, the percentages of remembered old pairs (hits), correctly rejected new pairs, forgotten old pairs, and falsely remembered new pairs (false alarms) were extracted. In order to index memory performance, we utilized the sensitivity measure d’, which is the difference between the z-transformed hit and false alarm rates[77–79]. A one-sample t-test against zero was conducted to probe associative memory formation with *d’* as dependent variable. Additionally, a repeated-measures ANOVA was used to analyze reaction times during the recognition task, with the within-subject factors *Pairing* (old vs. new) and *Correctness* (correct: remembered or correct rejection vs. incorrect: forgotten or false alarm).

Statistical analysis of the time-frequency EEG data acquired during the recognition phase of the experiment was conducted to explore the potential effect of remembered and forgotten trials within the low-frequency spectrum. This analysis was further differentiated by modality-independent sequence order during encoding, as well as sequential auditory-visual and visual-auditory presentations. Employing a non-parametric permutation testing approach with cluster-based correction for multiple comparisons, as implemented in the FieldTrip toolbox[75], we statistically compared time-frequency representations corresponding to remembered trials against those of forgotten trials. The cluster-based permutation test defines a cluster as a set of contiguous significant points in a three-dimensional space comprising electrode location (spatial dimension), frequency, and time. A significant point is identified when the test statistic at a specific electrode, frequency, and time point surpasses a predefined threshold ($p < .01$, uncorrected). These significant points are then grouped into clusters based on their adjacency. This means that a cluster can extend across multiple electrodes, frequency bands, and time points, rather than being restricted to a single dimension. We used the electrode neighbourhood structure defined by Fieldtrip function ft_prepare_neighbours to determine adjacency, ensuring that spatially close electrodes are considered neighbors. In the frequency and time dimensions, adjacency is defined by consecutive frequency bins and time points. To be classified as a cluster, an effect needed to span at least two neighbouring electrodes., preventing isolated effects in one electrode from being classified as clusters. Multiple comparison correction was applied using the cluster-based permutation test (*cfg.correctm = ‘cluster’*, *cfg.method = ‘montecarlo’*), which controls the family-wise error rate (FWER). This means that while individual points initially pass a cluster-forming threshold ($p < .01$, uncorrected), the final significance of a cluster is determined via a permutation-based correction ($p < .05$ two-tailed, cluster-corrected). Thus, only clusters that survived this multiple comparison correction are reported as significant. Subsequently, Monte Carlo method was utilized to generate a distribution of t-values[80].

The main focus of the study was to probe neuronal reinstatement of the stimulus modality order (visual-auditory, auditory-visual) during subsequent recognition via MVPA. To investigate this effect, we employed MVPA in the time-frequency domain of the recognition task. The SVM classifier distinguished between the two different encoding stimulus modality orders (AV/VA) based on the EEG data from the recognition task in which the previously encoded associations were presented simultaneously. To comprehensively capture neural processing during the recognition phase, we applied MVPA to the entire a priori defined dataset, analyzing the full trial period during recognition from 0 to 2 s relative to stimulus onset, across the 1–40 Hz frequency range and all 60 electrodes. Classification accuracy was assessed using a single–subject k = 5-fold cross-validation procedure, ensuring that model training and testing were performed on separate data splits within each subject to reduce overfitting and improve generalization. We conducted the MVPA on remembered trials of the



recognition task to classify the two different modality orders in which the stimulus pairs were presented during the encoding task (*Modality Sequence Classifier*). To assess the statistical significance of the accuracy achieved by the *Modality Sequence Classifier*, we conducted a one-sample *t*-test (one-tailed) comparing the overall classifier accuracy against chance-level (50%) The classifier accuracy was determined by averaging the individual classifier performance within the entire analysis window. This methodology enabled us to assess whether the performance of the *Modality Sequence Classifier* significantly exceeds the chance classification level, thus providing insight into the presence of meaningful patterns associated with memory retrieval as opposed to random classification. Subsequently, to probe statistically significant accuracy of the *Modality Sequence Classifier* across the entire

◀**Fig. 2**. Behavioral results from the recognition task. (**A**) Hit-rate in the recognition task for old and newly rearranged pairs. Within the boxplots, the horizontal lines indicate the median of the subset, while the notch around the median represents its 95% confidence interval. The upper and lower edges indicate quartiles 1 and 3. (**B**) The distribution of memory performance (*d'*) overall, as well as separated between the two modality-order sequences during the encoding task (VA = visual-auditory, AV = auditory-visual). (**C**) The block effect for memory performance (d'). Asterisks indicate significant differences between blocks. $p < .05$(*). (**D**) Distribution of reaction times for the respective response categories from the recognition task, split for remembered, forgotten, correct rejection and false alarm trials. (**E**) Distribution of reaction times for the respective response categories from the recognition task, split between the two modality-order sequences during the encoding task (VA = visual-auditory, AV = auditory-visual) for the remembered trials.

analysis window, we performed a cluster-based permutation t-test, comparing the accuracy values from the *Modality Sequence Classifier* to chance level (50%). To further examine frequency-specific effects, accuracy values were averaged within predefined frequency bands: theta (3–7 Hz), alpha (8–13 Hz), low beta (13–21 Hz), high beta (22–32 Hz), beta (13–32 Hz), and gamma (32–40 Hz). We determined the electrode with the highest mean t-value for each band and computed individual mean accuracy values at these electrodes.

Furthermore, a correlational analysis was conducted to examine the relationship between the oscillatory power contrast between remembered and forgotten trials during encoding task and d' (memory performance) estimates from the recognition task. This analysis is expected to yield valuable insights into multisensory processing during associative learning and memory. Drawing on previous research[81,82], we expected power differences to correlate with the memory performance within the low-frequency bands during the presentation of the first and second stimuli. Specifically, these power differences were expected to vary according to the modality sequence order (AV vs. VA condition). To accomplish this objective, we employed a non-parametric cluster-based permutation technique for the correlation analysis to control for alpha-error inflation. Here, we calculated the neuronal activity power differences (remembered > forgotten; AV/VA condition) and correlated these with the behavioural measure d'. Cluster-based permutation t-tests were conducted for each time-frequency data point across channels and participants. Significant differences between conditions ($p < .05$) resulted in adjacent data points being grouped into clusters based on temporal, spatial, and spectral criteria.

Results

Successful acquisition of sequentially encoded multisensory associative pairs

Participants completed one recognition task after each encoding task, which consisted of 47 multisensory associative pairs (Fig. 1). In the recognition task, participants were presented pairs of images and sounds in parallel, which were sequentially presented during previous encoding. This task included previously presented pairs (*old*) and tested memory specificity by presenting newly formed pairs, consisting of old stimuli elements (*new*). Participants had to indicate whether they remembered the presented stimulus pair from the encoding task (old) or whether it was a newly rearranged pair, consisting of an old image with a sound previously paired with another image (new). Overall, participants performed very well in remembering *old* pairs, with an average hit rate of M(SD) = 67.19 (± 15.29%; Fig. 2A). Although the *new* pairs consisted of images and sounds from encoding that were now rearranged, the false alarm rate was low (M(SD) = 12.12 (± 7.68%)). Accordingly, signal detection theory-based analysis confirmed robust learning, expressed by an average associative d' of M(SD) = 1.76 (± 0.76) independent of stimulus modality order ($t_{(30)} = 12.69$, $p < .001$, *cohen's* $d = 0.59$). The d' estimates of auditory-visual (AV; M(SD) = 1.74 ± 0.76) and visual-auditory stimuli (VA; M(SD) = 1.77 ± 0.77) did not differ significantly ($t_{(30)}$ = -0.14, $p = .884$, see Fig. 2B). Taken together, behavioral results confirmed the successful acquisition of sequentially encoded multisensory associative pairs, with no differences in performance due to modality order.

Our study was intentionally designed as an explicit learning and memory paradigm, where participants were specifically instructed to remember the pairs. Given the experimental structure, it was expected that participants adapt their strategies over time, mainly as they were aware that a recognition test followed each block. Crucially, due to the design, these improvements were likely to occur consistently across participants, regardless of their overall performance. Therefore, this effect should not be seen as a systematic bias but rather as an inherent characteristic of explicit learning. To assess whether behavioural performance changed across blocks, we conducted a repeated measures ANOVA on the performance measure d′, which revealed a significant main effect of Block, $F_{(2, 70)} = 8.92$, $p < .001$, $\eta^2 = 0.05$. Given that Mauchly's test indicated a violation of sphericity ($W = 0.92$, $p = .239$), we applied the Greenhouse-Geisser correction ($\varepsilon = 0.925$), yielding a corrected significance value of $p < .001$. Post hoc tests further revealed that performance significantly differed between Block A and Block B ($p = .025$) as well as Block A and Block C ($p = .002$; Fig. 2C).

Next, we compared participants' reaction times during recognition as an index of memory confidence[83,84]. A two-way repeated-measures ANOVA revealed a significant main effect of the factor Correctness ($F_{(1,31)} = 69.84$, $p < .001$, $\eta^2 = 0.69$; Fig. 2D), indicating faster responses during remembered pairs, compared to forgotten. Furthermore, this analysis revealed a main effect of Pairing ($F_{(1,31)} = 9.24$, $p = .005$, $\eta^2 = 0.23$; Fig. 2D), indicating faster responses to old pairs, compared to new. Critically, we observed a significant Pairing × Correctness interaction ($F_{(1,31)} = 15.56$, $p = .001$, $\eta^2 = 0.33$; see Table 1). The post-hoc *t*-test revealed a significant decrease in reaction times for correctly recognised old pairs ($t_{(126)}$ = -0.90, $p < .001$, *Cohen's* $d = -0.44$), indicating an increase in memory confidence in light of correctly retrieved associations compared to forgotten. The reaction time corresponding to auditory-visual (AV; RT = 1944.6 ± 381.7 ms) and visual-auditory stimuli (VA; RT = 1959.4 ± 385.9 ms) did not differ significantly ($t_{(62)} = 0.15$, $p = .877$, see Fig. 2E)**.** Interestingly, participants correctly rejected new pairs significantly faster compared to mistakenly categorizing them as old (false alarm;

Effect	F(df)	p	Partial η^2
Pairing (Old vs. New)	9.23(1,31)	0.005	0.23
Correctness (Correct vs. Incorrect)	69.84(1,31)	< 0.001	0.69
Pairing × Correctness	15.56(1,31)	< 0.001	0.33

Table 1. Repeated-Measures ANOVA results for reaction times.

Comparison	t(df)	p	p_{corr}
Remembered vs. forgotten	-2.26(62)	0.027	0.162
Remembered vs. correct rejected	0.81(62)	0.421	1
Remembered vs. false alarm	-4.30(62)	< 0.001***	< 0.001***
Correct rejected vs. forgotten	-2.83(62)	0.006**	0.036*
Correct rejected vs. false alarm	-4.88(62)	< 0.001***	< 0.001***
Forgotten vs. false alarm	-1.63(62)	0.110	0.660

Table 2. Post-hoc t-test results for reaction times. p_{corr} relates to p-values after Bonferroni correction. $p < .05$(*), $p < .01$(**), $p < .001$ (***).

$t_{(62)}$ = -4.88, $p < .001$), supporting the idea that decision confidence might influence RTs in recognition memory. Also, the response in correctly rejected trials were significantly faster as compared to response in forgotten trials, $t_{(62)}$ = -2.84, $p = .006$, suggesting that correctly detecting novel information is easier than failing to recognize old pairs. Responses to forgotten trials did not significantly differ in reaction times as compared to false alarm trials ($t_{(62)}$ = -1.63, $p = .110$; Table 2).

Successful recognition of multisensory associations relies on alpha/beta oscillations

In the next step, we investigated the oscillatory power differences between remembered and forgotten multisensory pairs within the recognition task, which presented the previously sequentially encoded pairs simultaneously. Here, participants had to indicate whether the presented pair was previously shown in sequential order during encoding. In the following analysis, we split the recognition trials according to their modality-sequence during encoding (VA/AV), and conducted time-frequency analyses. In VA associations (remembered > forgotten) we observed a significant negative cluster of oscillatory activity covering the high theta to low beta frequency range (0.8–1.2 s after stimulus onset; 7–23 Hz; negative cluster: $p < .003$, SD = 0.001). This indicates that remembered pairs, which were represented in a VA sequence order during encoding, were associated with alpha and beta power during memory retrieval as compared to forgotten pairs. This effect was primarily driven by activity differences in frontotemporal and lateral-occipital areas (0.8–1.2 s after stimulus onset, 7–23 Hz; Fig. 3A). Interestingly, AV trials showed a different pattern, including a negative cluster in the theta and alpha range (0.5–1.9 s; 6–13 Hz; negative **c**luster 1: $p < .002$, SD = 0.009; negative **c**luster 2: $p < .045$, SD = 0.005), indicating that remembered pairs, which were represented in an AV sequence order during encoding, were associated with theta and alpha power during memory retrieval as compared to forgotten pairs. This effect was primarily driven by activity differences in parietal-occipital areas (0.5–1.9 s after stimulus onset, 6–13 Hz; Fig. 3B). The results indicate differential processes concerning the oscillatory processing of modality-sequences during recognition and were used to restrict the following MVPA analysis. When analyzing both conditions (combining AV and VA) together as an independent modality-sequence condition, we observed similar significant neuronal activity effects, further reinforcing the underlying processing patterns across modalities. The results revealed a negative cluster covering the theta (median cluster size = 10), alpha (median cluster size = 27), and beta (median cluster size = 18) bands, occurring 0.9 to 1.8 s after stimulus onset (negative cluster: $p < .001$, SD = 0.004; see Fig. 3C). This indicates that remembered pairs were associated with lower theta, alpha, and beta power during memory retrieval as compared to forgotten pairs. This effect was primarily driven by activity differences in frontotemporal and lateral-central areas (1.0 to 1.7 s after stimulus onset, 3–7 Hz) and in lateral parietal regions (0.9 to 1.7 s after stimulus onset, 8–18 Hz; see Fig. 3C).

Modality-sequences are reinstated as context-features during recognition

The neuronal signature within the recognition task indicated differential processing of the stimulus modality order, which we hypothesized to also be expressed as context-specific features of the underlying memory trace (i.e. the temporal sequence of the stimulus from different modalities). Accordingly, our main hypothesis stated that the neural signature during the recognition task would reflect the modality sequence in which the pairs were presented during the encoding task. To probe this effect, we employed MVPA, moving beyond the univariate comparisons of oscillatory power. The *Modality Sequence Classifier* distinguished between the two different encoding stimulus modality orders (AV/VA) based on the EEG data from the recognition task in which the previously encoded associations were presented simultaneously. Classification accuracy was assessed using a cross-validation (k = 5) procedure. The overall mean classifier performance for the *Modality Sequence Classifier* was 52.26%, which significantly exceeded the chance level of 50% ($t_{(31)} = 4.28$, $p < .001$, *cohen's d* = 0.76).

For the more detailed classification analyses, we calculated the classification accuracy over all electrodes for each frequency band within the significant data points, as well as the average classification accuracy for the electrode with the maximum mean *t*-value of the entire time within the specific frequency range. The cluster-based permutation test comparing MVPA accuracy values for remembered trials when decoding the two modality orders against chance level (50%) revealed eight significant positive clusters (most prominent cluster: $p < .001$, cluster-level statistic $t = 29.069$, SD = 0.0003, CI range = 0.0006). This cluster encompassed 45.302 data points out of a total of 50.400 (60 channels × 40 frequency × 21 time), covering approximately 89.88% of the analyzed search space. This significant cluster extended from stimulus onset to 2 s post-stimulus, spanning frequencies from 1 to 40 Hz, and was distributed across all electrodes, with the lowest representation in P7 (84.28%) and the highest in FC4 (93.69%). The remaining clusters had *p*-values ranging from 0.017 to 0.047, with their respective cluster statistics and confidence intervals indicating robust effects across multiple frequency bands and time points. No significant negative clusters were detected.

To further interpret the decoding performance, average accuracy values were computed over the significant time points identified by the cluster-based permutation test, focusing on time points and electrodes with the highest mean *t*-values. To identify the electrodes exhibiting the strongest effects, we computed the mean *t*-value for each electrode by averaging all significant *t*-values ($p < .05$) across frequency bands and time points. This metric served as an index of the relative effect size at each electrode, highlighting regions that consistently demonstrated robust neural discrimination effects in the cluster-based permutation test. By focusing on electrodes with the highest mean *t*-values, we aimed to characterize the spatial distribution of the most pronounced neural decoding effects during the recognition task. The overall mean accuracy across all frequencies (1–40 Hz) was 52.26%, with the highest mean *t*-value observed at electrode F4 ($t = 4.18$). The mean individual accuracy at this electrode was 52.32%, while the highest individual accuracy value reached 62.38% at 0.8 s and 30 Hz. The maximal *t*-value was reached at F4 ($t = 6.58$).

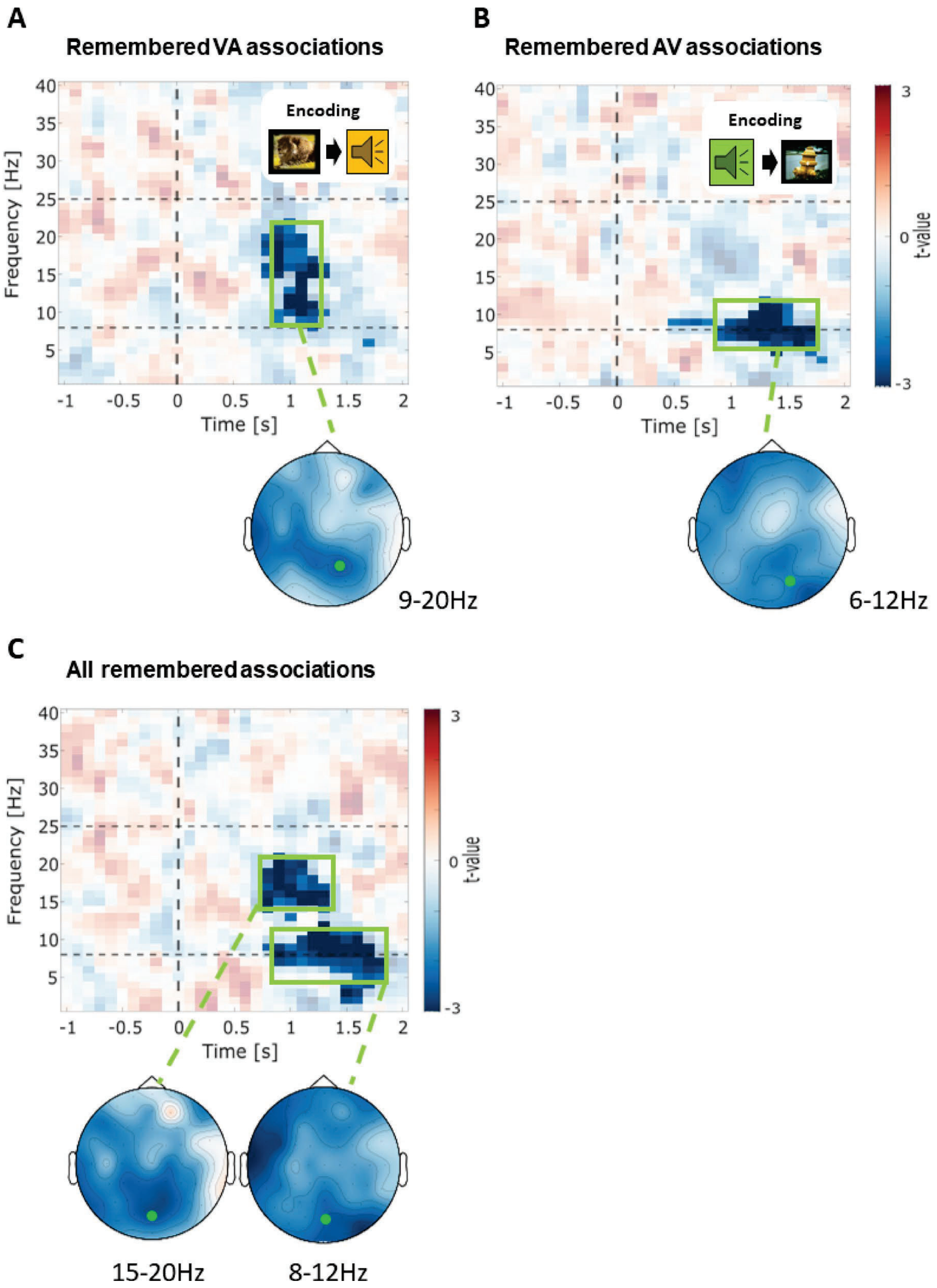
When examining specific frequency bands, the theta range (3–7 Hz) yielded the highest mean accuracy of 52.49%, with the strongest effect at electrode AF7 ($t = 4.22$), and an individual peak accuracy of 58.80% at 0.4 s and 7 Hz. The maximal *t*-value was reached at AF7 ($t = 6.29$). In the alpha band (8–13 Hz), the mean accuracy was 52.40%, with the highest *t*-value recorded at electrode Fpz ($t = 3.92$), and an individual maximum accuracy of 58.67% at 0.1 s and 11 Hz. The maximal *t*-value was reached at F4 ($t = 6.58$). The low beta range (13–21 Hz) showed a mean accuracy of 52.29%, with the most significant effect at electrode Fpz ($t = 3.80$) and a peak accuracy of 58.63% at 0.4 s and 21 Hz. The maximal *t*-value was reached at FC2 ($t = 5.93$). Similarly, the high beta range (22–32 Hz) demonstrated a mean accuracy of 52.22%, with the strongest effect at electrode P1 ($t = 4.27$) and a peak accuracy of 58.29% at 1.9 s and 24 Hz. The maximal *t*-value was reached at CP2 ($t = 6.31$).

When considering the full beta range (13–32 Hz), the mean accuracy was 52.24%, with the highest *t*-value at P1 ($t = 4.07$) and an individual maximum accuracy of 61.00% at 1.9 s and 24 Hz. The maximal *t*-value was reached at CP2 ($t = 6.31$). The mean accuracy in the gamma band (32–40 Hz) was 52.23%, with the effect at electrode P2 ($t = 4.69$) and an individual peak accuracy of 52.98% at 0.1 s and 33 Hz. The maximal t-value was reached at PO8 ($t = 6.18$). All results are summarised in Table 3. These findings suggest that decoding performance was significantly above chance level across multiple time points, frequencies, and electrode locations, with particularly strong effects in the theta, alpha, and beta bands.

To further explore the spatial distribution of significant effects, we visualized topographical maps of *t*-values obtained from the cluster-based permutation test for different frequency bands (theta, alpha, low beta, high beta, and gamma) over the trial time course (Fig. 4). Interestingly, the higher beta and gamma frequency range (21–40 Hz) exhibited pronounced discriminative power between the two conditions during the entire stimulus presentation over the centro-parietal electrodes, specifically strongest at the beginning (0.4 to 1.3 s) and the end (1.7 to 2.0 s). Additionally, also early (0 to 1.0 s to stimulus onset) centro-frontal electrode cluster in the lower frequency range (3 to 20 Hz) showed a significant classification performance. The results demonstrate a convergence between the neural activity patterns during successful recognition and retrospective discrimination between the modality order of the sequential encoding during recognition. In sum, these findings highlight the ability to encode and differentiate VA from AV sequences during the retrieval task, as evidenced by the distinct neural patterns observed in the EEG data during subsequent recognition. In addition to the averaged accuracy values from electrodes with the highest mean *t*-values, time-resolved decoding accuracy (MVPA) for remembered trials is shown at exemplary electrodes across different frequency bands (Fig. 5).

Successful recognition of multisensory associations relies on low-frequency oscillations during encoding

As an explorative analysis, we analyzed the dynamics between the neuronal activity from the encoding task and the recognition performance. Thus, we asked whether specific oscillations during encoding propel successful memory formation. First, we computed the differences in oscillatory power between later remembered and forgotten trials separately for the presentation of the first and second stimulus of each pair. Therefore, we focused on the 2-s period before and after each stimulus onset for the VA and AV conditions, resulting in two analysis time windows (Stimulus Interval 1 and Stimulus Interval 2; Fig. 1). Initially, we analyzed oscillatory data independent of the stimulus modality order, dividing Stimulus intervals 1 (SI1) and 2 (SI2). The differential time-frequency spectra between remembered and forgotten pairs were computed in each participant. These difference values were correlated with associative d' values from the recognition task. Results revealed significant correlations within SI2 for both encoding sequence conditions. During the visual stimulus of AV pairs, two clusters of significant negative correlation between associative d' and average power differences (remembered > forgotten) were revealed at multiple electrodes in the parietal and central region in the alpha band (pre-stimulus positive cluster: $p < .042$, SD < 0.005; post-stimulus negative cluster: $p < .013$, SD = 0.003, Fig. 6A) at multiple electrodes in the central-parietal region (Fig. 6A) within the alpha range. In VA pairs, however, during the presentation of



the auditory stimulus, we observed a significant positive post-stimulus correlation ($p < .006$, SD = 0.002; Fig. 6B) and negative pre-stimulus correlation ($p < .018$, SD = 0.003) at multiple electrodes in the parietal-occipital region (Fig. 6B) within the alpha and beta range.

Discussion

Successful retrieval of events is strongly bound to the context of encoding[55,85,86]. While it is well established that context can be reflected as the surrounding environment[31,87,88], it can also be represented differentially, i.e. as the sequence of episode-specific features. In line, context feature reinstatement (of sequential information)

◀**Fig. 3**. Memory effects on time-frequency power before and during recognition for electrodes with maximal t-value for corresponding encoding stimulus modality order. (**A**) Time-frequency plot of the statistical comparison of REMEMBERED > FORGOTTEN oscillatory power at P2 for recognized associations, which were presented in the visual-auditory sequence during encoding. Opaque data points show a significant difference at $p < .05$ (corrected). The lower panel shows the topographical distribution within the significant cluster during stimulus presentation in the theta-alpha range (0.9 to 1.2 s; left). The green marker illustrates P2. (**B**) Time-frequency plot of the statistical comparison of REMEMBERED > FORGOTTEN oscillatory power at PO4 for recognized associations, which were presented in the auditory-visual sequence during encoding. Opaque data points show a significant difference at $p < .05$ (corrected). The lower panel shows the topographical distribution within the significant cluster during stimulus in the alpha/beta range (0.8 to 1.4 s). The green marker illustrates P2. (**C**) Top: Time-frequency plot of the statistical comparison of REMEMBERED > FORGOTTEN oscillatory power at POz, independent of modality order presentation during encoding. The vertical line marks the stimulus onset, and the horizontal lines mark the frequency bins alpha and beta (8 Hz and 25 Hz). Opaque data points show a significant difference at $p < 0.\ 5$ (corrected). Negative t-values signify higher power in FORGOTTEN trials. The lower panel shows the topographical distribution within the significant cluster during stimulus in the beta range (0.8 to 1.3 s; left) and the significant cluster in the alpha range (0.9 to 1.8 s, right). The marker illustrates POz.

Frequency range [Hz]	Mean Accuracy [%]	Peak mean t-value Electrode	Time [s]	Frequency [Hz]	Peak mean t-value Max. [%]
Overall [1 40]	52.26	F4	0.8	30	62.38
Theta [3 7]	52.49	AF7	0.4	7	58.80
Alpha [8 13]	52.40	Fpz	0.1	11	58.67
Beta [13 21]	52.29	Fpz	0.4	21	58.63
Beta [22 32]	52.22	P1	1.9	24	58.29
Beta [13 32]	52.24	P1	1.9	24	61.00
Gamma [32 40]	52.23	P2	0.1	33	52.98

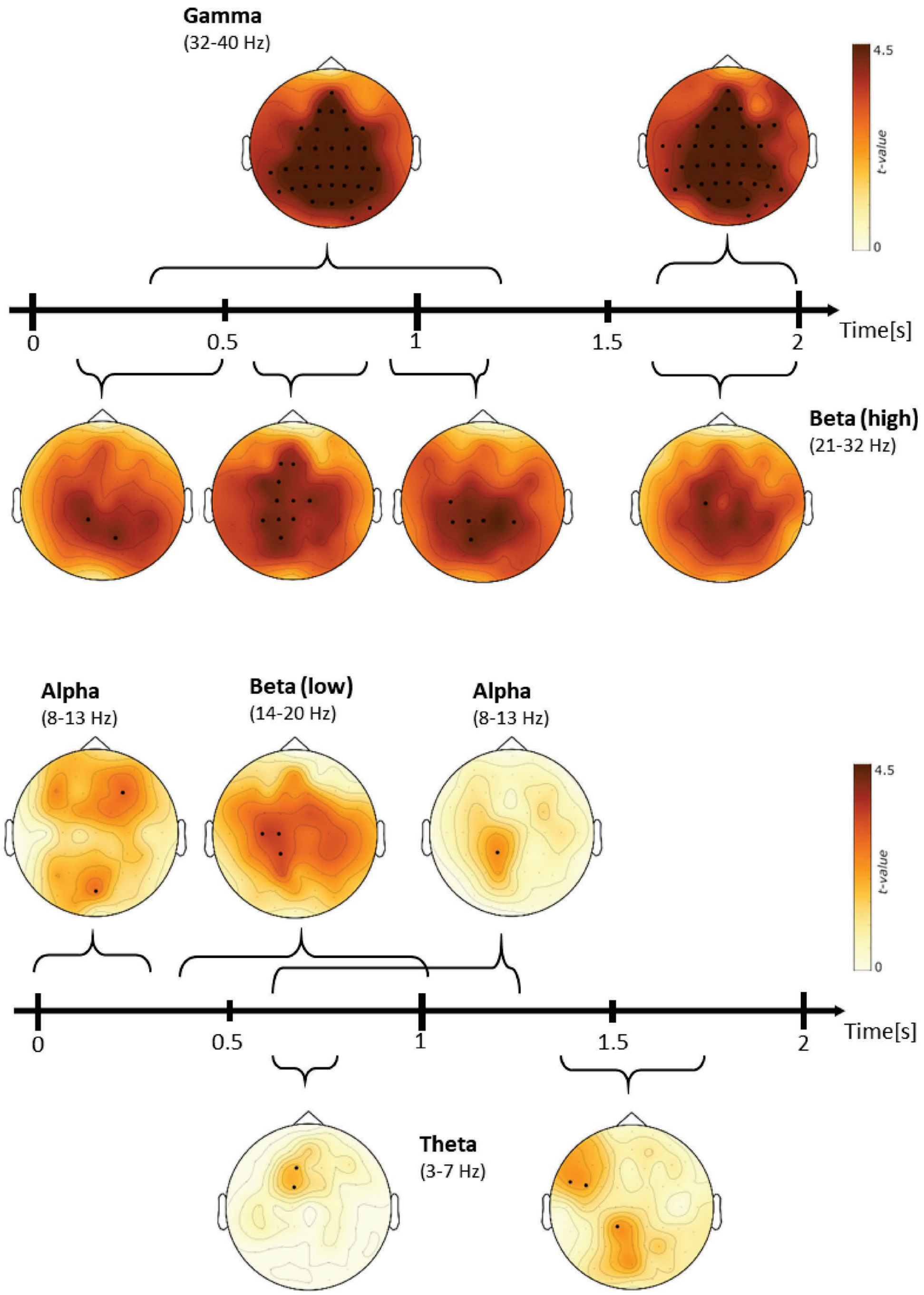
Table 3. Average Accuracy for each frequency range and at the electrode with the maximummean t-value.

has been shown to be of central importance for memory encoding and retrieval processes[51,88–91]. The role of contextual reinstatement of multisensory features that stem, i.e. from the auditory and visual domain, remains so far unexplored. Here we aimed to shed light on the oscillatory mechanisms underlying the recognition of sequentially encoded multisensory episodes. Our findings show that modality sequences are (incidentally) encoded within the memory trace and serve as a context feature that drives recognition based on theta, alpha and beta frequency pattern reinstatement.

It is well established that context reinstatement plays a crucial role in memory retrieval, allowing the brain to access the temporal and environmental cues associated with past events[51,52]. However, previous research has largely focused on unimodal stimuli, rendering our understanding about how complex multisensory sequences are encoded and retrieved incomplete. In the current study, participants acquired and retrieved the image-sound/sound-image associations overall very well, with recognition performance as measured by d' being comparable to similar study designs[72,92–94]. Importantly, recognition performance did not differ when comparing AV (auditory-visual) vs. VA (visual-auditory) pairs, suggesting that the order of features itself did not influence memory formation. While we did not test for incidental stimulus acquisition, several studies report reinstatement of encoding specific features in memory tasks[29,95,96].

MVPA of EEG data revealed distinct neural signatures depending on the modality sequence presented during encoding, even though overall memory performance for both conditions was the same. This suggests that the brain encodes the order of multisensory episodes as part of the contextual memory trace, which aids in the retrieval process. This finding is consistent with prior work demonstrating context-specific temporal patterns during both encoding and retrieval processes[97]. Furthermore, it aligns with the Context Maintenance and Retrieval (CMR) model, which states that temporal and contextual features of episodes are essential components of the memory trace[52]. Our study extends this model by showing that modality order, as a contextual feature, can be decoded from oscillatory activity during memory retrieval.

Our multivariate results from EEG recordings suggest that decoding performance went significantly above chance level across multiple time points, frequencies, and electrode locations, with particularly strong effects in the theta, alpha, and beta bands. Theta oscillations have been associated with the binding of information into coherent memory traces and are crucial for organizing sequentially ordered working memory items[60,68,98]. These oscillations are thought to coordinate neural activity across different brain regions, facilitating the binding of sensory inputs into a coherent memory trace[97–99], acting as the “glue”[100]. Alpha oscillations have been generally related to the inhibition of irrelevant information and are involved in processing incoming information relevant to memory[101,102]. Decreases in alpha power during memory tasks have been associated with enhanced memory performance, particularly in semantic encoding tasks[103,104], while beta oscillations have been linked to memory formation, with elevated pre-stimulus beta power associated with successful memory encoding[105,106]. This activity is thought to reflect a memory-promoting state, possibly moderated by attentional or inhibitory processes[105]. In sum, theta, alpha, and beta oscillations play distinct yet interconnected roles in



memory processing[107,108]. Taken together, the fact that the MVPA analysis revealed significant classification of modality order across different oscillatory bands provides strong evidence that sequential information in the form of a context feature is retained and reinstated during retrieval rather than merely reflecting general associative activation. Thus, our results suggest that encoding processes are sequence-specific, with VA pairs potentially engaging greater anticipatory processing due to the nature of auditory stimulus processing. One may speculate, that the reinstatement of the observed oscillatory patterns may facilitate the synchronization of neural activity across sensory processing regions, ensuring that the original modality sequence is represented during recognition within the specific memory trace, which has been suggested by several human studies[4,11,82,109,110].

◀**Fig. 4**. Topographical plots of *t*-values from the cluster-based permutation test comparing MVPA accuracy for remembered trials against the chance level of 50%. The plots illustrate the distribution of significant effects across the scalp for different frequency bands (theta, alpha, low beta, high beta, and gamma) over the trial time course. Highlighted electrodes indicate regions with the highest number of neighbouring significant data points), reflecting areas with the strongest decoding effects. The gamma band showed significant effects between 400–1300 ms and 1700–2000 ms, with strong activations in centro-posterior regions. The high beta band displayed significant clusters in multiple time windows (100–500 ms, 600–800 ms, 900–1200 ms, and 1700–2000 ms), predominantly in centro-parietal areas. The low beta band exhibited significant effects between 400–1000 ms, mainly over central electrodes. The alpha band showed spatially distributed effects in early (0–300 ms) and later (600–1300 ms) time windows, particularly in partial-occipital and fronto-central sites. The theta band revealed significant clusters in two discrete time windows (600–700 ms and 1400–1700 ms), with the strongest effects observed in frontal and central regions. The results suggest that significant decoding effects are not uniformly distributed across the scalp but are concentrated in specific electrode regions, particularly in central and parietal areas in the beta and gamma range and frontal areas in the theta and alpha range.

Considering the potential cognitive processes elicited by the experimental design, one could argue that the initial stimulus might evoke visual or auditory mental imagery, creating an expectation of the second stimulus. In fact, there is evidence showing that mental imagery could also influence associative memory retrieval by engaging both modality-specific and modality-independent neural networks[111,112], thereby aiding in overcoming potential modality mismatches during encoding induced by incongruent association pairs[113]. This process involves the activation of sensory-specific regions, such as the visual and auditory cortices, alongside a modality-independent core network, including the default mode network, which supports imagery across different sensory domains[111,112,114]. The overlap between brain regions involved in mental imagery and those supporting retrieval suggests that successful retrieval relies on the same neural mechanisms that facilitate imagery[111,115]. Furthermore, encoding specificity plays a critical role in remembering, as the reactivation of encoding-related neural patterns benefits retrieval when there is a match between encoding and retrieval modalities but can impair memory under mismatch conditions[116]. However, individuals can flexibly employ mental imagery to compensate for mismatches, generating and maintaining mental representations even when encoding involves incongruent audiovisual information[117]. Moreover, imagery-based strategies, such as integrating items into interactive mental images, have been shown to enhance associative memory, emphasizing the functional significance of mental imagery in retrieval processes[118].

While these findings demonstrate that mental imagery is connected to memory encoding and retrieval, prior research also suggests that multisensory, sequential encoding can enhance memory through encoding variability, introducing competition effects that alter retrieval dynamics[28,29]. This interpretation gains support from our univariate oscillatory findings, suggesting a modality-specific influence of alpha and beta oscillations during the encoding of sequentially presented audiovisual stimuli. Specifically, for auditory-visual (AV) pairs, increased pre-stimulus alpha and beta power before the visual stimulus and a subsequent decrease during stimulus presentation may indicate a preparatory state followed by active sensory processing. In contrast, the pattern is reversed for visual-auditory (VA) pairs: pre-stimulus decreases in alpha and beta before the auditory stimulus, and increased power during its presentation suggests a shift in processing demands between modalities. Previous research has linked decreased alpha-band activity in the prefrontal and occipital cortex to successful visual encoding, indicating that lower alpha power facilitates visual information processing and enhances memory formation[119–122]. Similarly, increased pre-stimulus beta power has been associated with improved memory formation, potentially reflecting attentional or inhibitory processes that aid in binding stimulus components[105,123]. The observed pre-stimulus increases in beta power in AV pairs may, therefore, indicate an anticipatory mechanism supporting visual encoding, whereas the decrease in VA pairs might reflect a shift in sensory dominance from vision to audition. Alpha and beta oscillations have further been implicated in the processing of expectations and prediction errors. An alpha-to-beta desynchronization (ERD) has been linked to expected stimulus valence, suggesting that these frequency bands contribute to prediction mechanisms that influence encoding efficiency[124]. In audiovisual tasks, alpha oscillations modulate sensory processing and attention, influencing the temporal integration of stimuli[125]. However, alpha activity does not solely predict auditory stimulus detection consistently due to its interaction with broadband neural activity[126]. Beta oscillations, on the other hand, are associated with top-down control processes and enhance memory formation across sensory modalities, including auditory processing[105]. Taken together, these findings suggest that alpha and beta oscillations in sequential encoding are modality-dependent rather than purely memory-driven. The observed pre-stimulus shifts in power may reflect preparatory mechanisms that optimize encoding by modulating attention and sensory processing demands across modalities. Specifically, lower alpha power in occipital-parietal regions has been associated with improved perceptual sensitivity and the enhancement of stimulus representations[127], supporting the idea that modality-dependent oscillatory changes may reflect the differential engagement of sensory and integrative processes during retrieval. Finally, theta oscillations play a critical role in cross-modal binding, supporting associative memory by synchronizing neural activity across sensory regions[128]. Given the angular gyrus' role in multimodal integration[129] and the contribution of multisensory cues to episodic retrieval[130–132], it is likely that power changes across frequency bands reflect both modality-specific processing and memory-related mechanisms in an interactive manner. Thus, the observed oscillatory dynamics align with well-established mechanisms of sensory reactivation, cortical excitability, and associative memory retrieval.

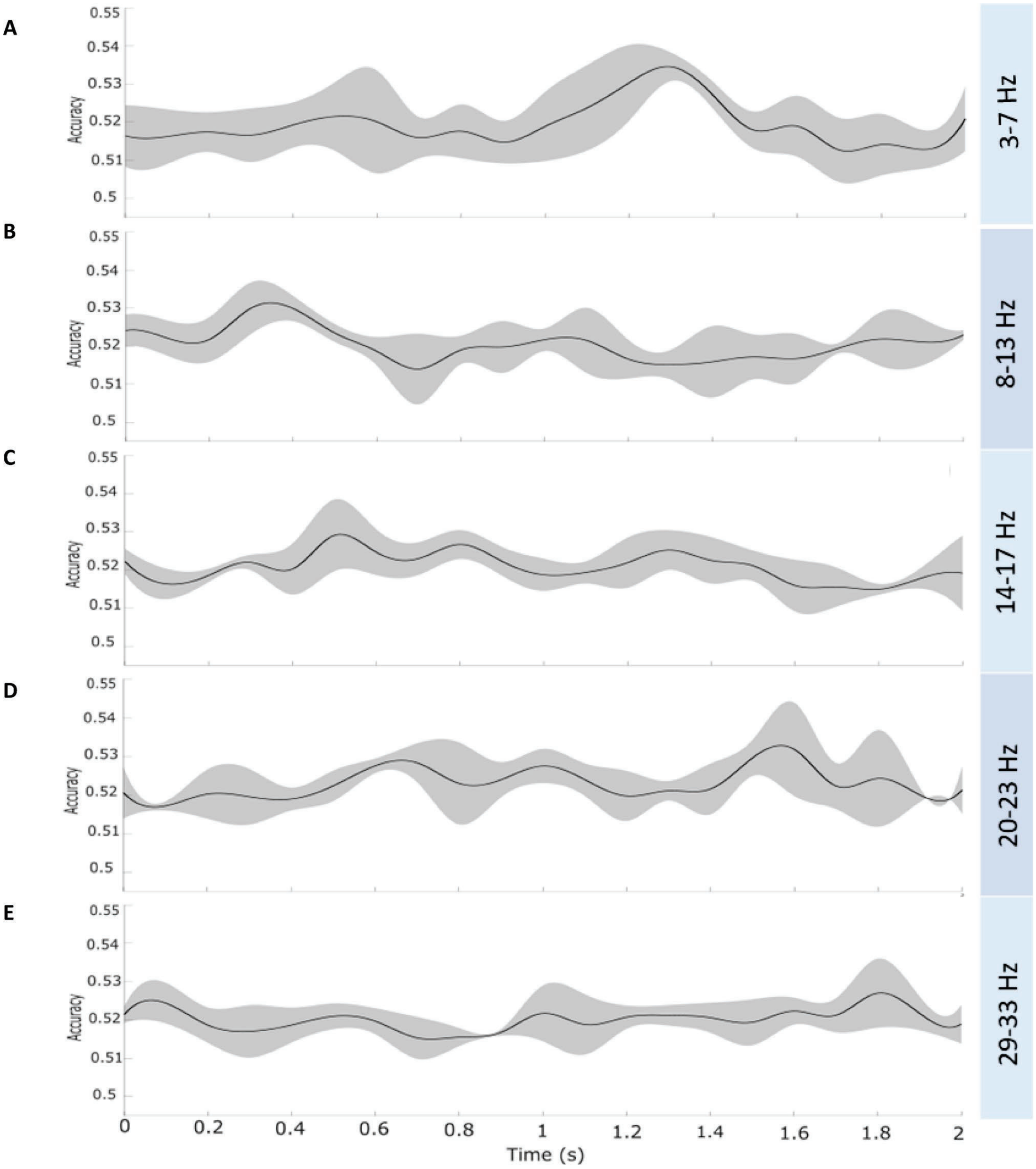
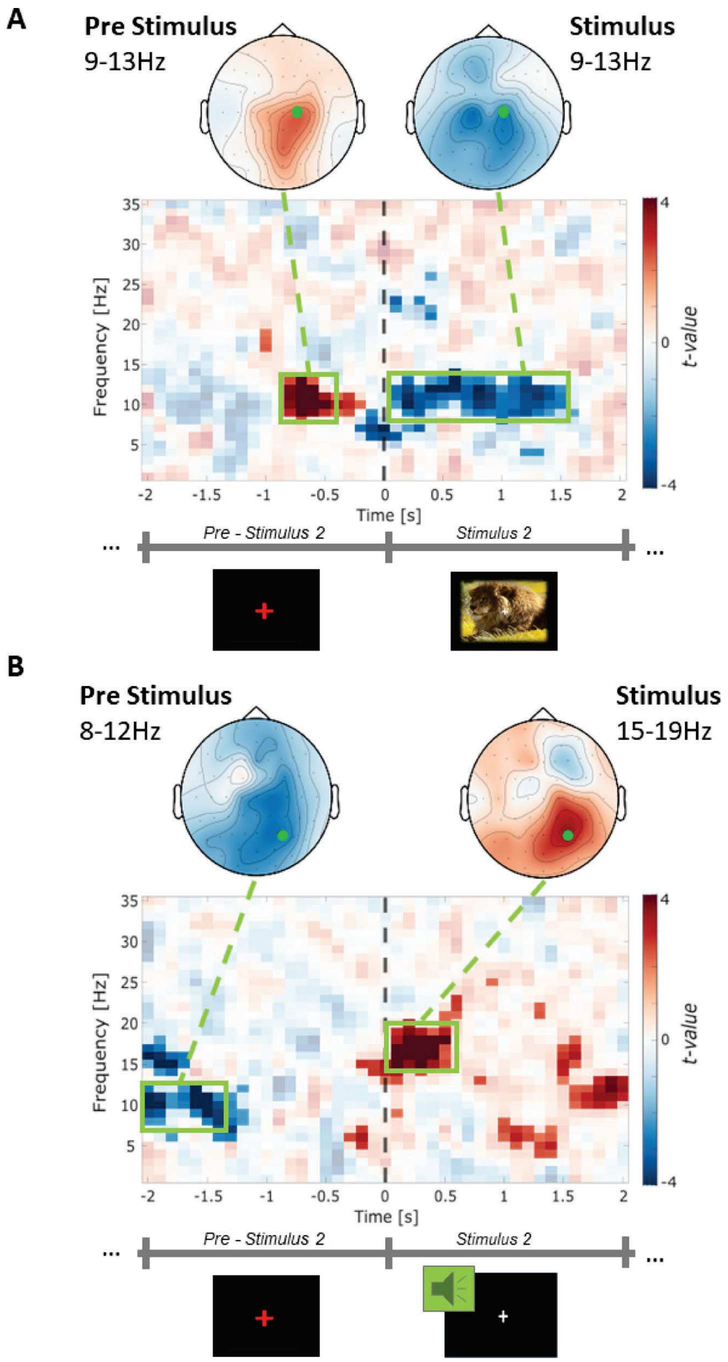


Fig. 5. Full-time courses of accuracy values from exemplary electrodes for each frequency range. Time-resolved decoding accuracy (MVPA) for remembered trials to classify modality order from 0 to 2 s relative to stimulus onset is shown at exemplary electrodes. Accuracy values, averaged within the respective frequency bands, range from 51–54%. (**A**) Theta (3–7 Hz) at Cz exhibits a subtle peak around 1.3 s. (**B**) Alpha (8–13 Hz) at F4 shows a slight peak around 0.3 s. (**C**) Decoding accuracy in the low beta (14–17 Hz) at Fz, (**D**) high beta (20–23 Hz) at C3, and (**E**) gamma (29–33 Hz) at F4 bands fluctuates over time but did not reveal distinct classification peaks. Caution should be exercised, as the averaging of accuracy estimates over multiple time points and across participants may have contributed to an overall reduction in classification performance.



The role of modality order in retrieval is further supported by the finding that above-chance decoding of modality order from EEG activity during retrieval indicates its integration into the memory trace. If one modality had dominated encoding, successful decoding of modality order would not be expected. Prior research supports the idea that encoding modality order contributes to retrieval by providing structured cues that facilitate reconstruction of past experiences[133]. Contextual information is a well-established component of episodic memory, with hippocampal mechanisms playing a crucial role in binding sensory details into coherent memory representations[22,85,103,134,135]. Our study extends this body of work by demonstrating that modality order, as a contextual feature, can be decoded from oscillatory activity during retrieval. While our data do not conclusively establish a causal link between modality order encoding and retrieval success, they provide novel

◀ **Fig. 6**. Correlation between the power difference of remembered vs forgotten trials in Stimulus interval 2 and the memory performance (d') from the recognition task. (**A**) The correlation between the power differences and the memory performance as measured by d' during visual stimuli presentation (AV pair) at C2. Topographical distribution within the significant cluster in the pre stimulus (-0.8 to -0.1 s; left) and the significant cluster in the stimulus presentation (0 to 1.5 s) in the alpha range (9 to 13 Hz, right) during visual stimuli presentation. The marker illustrates C2. (**B**) The correlation between the power differences and the memory performance as measured by d' during auditory stimulus presentation (VA pair) at P4. Topographical distributions are shown for the pre-stimulus cluster (-2 to -1.3 s; 8–12 Hz) and stimulus presentation cluster (0–0.5 s; 15–19 Hz). The green marker illustrates P4.

insights into the neural dynamics supporting multisensory sequential memory. Although no behavioural data confirm explicit retrieval of order information, the significant decoding results indicate that modality order was included in the memory trace and reinstated during retrieval. Future studies should explore the extent to which such reinstatement contributes to explicit order memory and whether implicit representations influence retrieval performance.

Finally, we observed modality effects in parietal locations during both, encoding, and recognition tasks. This might reflect multisensory association processes[136,137], as the parietal cortex is crucial for integrating information from various sensory modalities[138–141]. Interestingly, our findings align well with recent work around multisensory processing, which shows that information from different sensory modalities is integrated within several cortical regions (e.g. the parietal lobe;[139,141,142]). While the intraparietal sulcus (IPS) is known to process multisensory information[143–145], the angular gyrus has been shown to be centrally involved in binding information into coherent narratives[131]. In our results, classifier accuracy derived from MVPA was highest at centro-parietal electrodes (e.g., CP1), covering the superior parietal lobe. This might suggest a distinct role of the superior parietal cortex in multisensory sequential reinstatement processes, which supports the hypothesis that the neural systems for sequence encoding and multisensory integration are closely linked to facilitate the binding of presented items, thereby forming an episode.

In conclusion, our study provides new insights into the neural mechanisms underlying multisensory memory retrieval. The findings of this study yield important implications for our understanding of memory processes. First, the (incidental) encoding of modality sequence order as a context feature suggests that the brain actively integrates temporal and sensory information during memory formation. This has important implications for models of episodic memory, particularly those that emphasize the role of context[52]. Our findings suggest that the neural mechanisms underlying context-feature retrieval are not limited to unimodal tasks[4,51,64,146]. Instead, they extend to more complex multisensory episodes, during which we encode and integrate sequences of different sensory modalities. Crucially, the sequence of modalities as a contextual feature within the memory trace directly affects memory retrieval, cognitive control, and learning processes[147–150]. Prior research suggests that different sensory modalities contribute uniquely to encoding and retrieval mechanisms, with auditory and visual sequences influencing attentional engagement and memory consolidation in distinct ways (e.g.,[151,152]. Auditory sequences, for instance, have been linked to more durable temporal structuring, while visual sequences often benefit from spatial organization[71]. Recognizing modality sequence as a contextual feature allows us to investigate how the structure of sensory input shapes memory representations rather than focusing solely on content-based associations. Understanding these effects can help optimize learning and memory strategies by leveraging the strengths of different modalities. This might offer insights into educational and rehabilitative applications where multimodal integration plays a key role. Our findings provide new insights into how the brain encodes and retrieves complex episodic memories, particularly those that involve multisensory information.

Data availability

The raw EEG and behavioral data underlying our findings have been uploaded to an open repository (https://www.fdr.uni-hamburg.de/; https://www.fdr.uni-hamburg.de/record/17120) for accessibility.

Received: 28 October 2024; Accepted: 14 May 2025

References

1. Dannenberg, H., Alexander, A. S., Robinson, J. C. & Hasselmo, M. E. The role of hierarchical dynamical functions in coding for episodic memory and cognition. *J. Cogn. Neurosci.* **31**, 1271–1289 (2019).
2. Sheldon, S., Farb, N., Palombo, D. J. & Levine, B. Intrinsic medial Temporal lobe connectivity relates to individual differences in episodic autobiographical remembering. *Cortex* **74**, 206–216 (2016).
3. Sadeh, S. & Clopath, C. Theory of neuronal perturbome in cortical networks. *Proc. Natl. Acad. Sci.* **117**, 26966–26976 (2020).
4. Kim, J. S. & Lee, S. A. Hippocampal orchestration of associative and sequential memory networks for episodic retrieval. *Cell. Rep.* **42**, 112989 (2023).
5. Yonelinas, A. P., Ranganath, C., Ekstrom, A. D. & Wiltgen, B. J. A contextual binding theory of episodic memory: systems consolidation reconsidered. *Nat. Rev. Neurosci.* **20**, 364–375 (2019).
6. Pronier, É., Morici, J. F. & Girardeau, G. The role of the hippocampus in the consolidation of emotional memories during sleep. *Trends Neurosci.* **46**, 912–925 (2023).
7. Cooper, R. A. & Ritchey, M. Progression from Feature-Specific brain activity to hippocampal binding during episodic encoding. *J. Neurosci.* **40**, 1701–1709 (2020).
8. Crystal, J. D. Temporal foundations of episodic memory. *Learn. Behav.* **52**, 35–50 (2024).
9. Clewett, D. & Davachi, L. The ebb and flow of experience determines the Temporal structure of memory. *Curr. Opin. Behav. Sci.* **17**, 186–193 (2017).

10. Horner, A. J., Bisby, J. A., Wang, A., Bogus, K. & Burgess, N. The role of Spatial boundaries in shaping long-term event representations. *Cognition* **154**, 151–164 (2016).
11. Eichenbaum, H. Time (and space) in the hippocampus. *Curr. Opin. Behav. Sci.* **17**, 65–70 (2017).
12. Leroy, N., Majerus, S. & D'Argembeau, A. Working memory capacity for continuous events: the root of Temporal compression in episodic memory? *Cognition* **247**, 105789 (2024).
13. Jeunehomme, O., Folville, A., Stawarczyk, D., Van Der Linden, M. & D'Argembeau, A. Temporal compression in episodic memory for real-life events. *Memory* **26**, 759–770 (2018).
14. Jeunehomme, O. & D'Argembeau, A. Event segmentation and the Temporal compression of experience in episodic memory. *Psychol. Res.* **84**, 481–490 (2020).
15. D'Argembeau, A., Jeunehomme, O. & Stawarczyk, D. Slices of the past: how events are temporally compressed in episodic memory. *Memory* **30**, 43–48 (2022).
16. Riegel, M., Granja, D., Amer, T., Vuilleumier, P. & Rimmele, U. Opposite effects of emotion and event segmentation on Temporal order memory and object-context binding. *Cogn. Emot.* **39**, 117–135 (2025).
17. Thavabalasingam, S., O'Neil, E. B. & Lee, A. C. H. Multivoxel pattern similarity suggests the integration of Temporal duration in hippocampal event sequence representations. *NeuroImage* **178**, 136–146 (2018).
18. Liu, C., Ye, Z., Chen, C., Axmacher, N. & Xue, G. Hippocampal representations of event structure and Temporal context during episodic Temporal order memory. *Cereb. Cortex*. **32**, 1520–1534 (2022).
19. Rey, L. et al. Episodic memory and recognition are influenced by cues' sensory.
20. Tamminen, J. & Mebude, M. Reinstatement of odour context cues veridical memories but not false memories. *Memory* **27**, 575–579 (2019).
21. Sorokowska, A., Nord, M., Stefańczyk, M. M. & Larsson, M. Odor-based context-dependent memory: influence of olfactory cues on declarative and nondeclarative memory indices. *Learn. Mem.* **29**, 136–141 (2022).
22. Marks, W. D., Yokose, J., Kitamura, T. & Ogawa, S. K. Neuronal ensembles organize activity to generate contextual memory. *Front. Behav. Neurosci.* **16**, 805132 (2022).
23. Noyce, A. L., Cestero, N., Shinn-Cunningham, B. G. & Somers, D. C. Short-term memory stores organized by information domain. *Atten. Percept. Psychophys*. **78**, 960–970 (2016).
24. Dimsdale-Zucker, H. R. et al. Representations of complex contexts: A role for Hippocampus. *J. Cogn. Neurosci.* **35**, 90–110 (2022).
25. Bird, C. M. The role of the hippocampus in recognition memory. *Cortex* **93**, 155–165 (2017).
26. Robin, J. & Moscovitch, M. Familiar real-world Spatial cues provide memory benefits in older and younger adults. *Psychol. Aging*. **32**, 210–219 (2017).
27. Wälti, M. J., Woolley, D. G. & Wenderoth, N. Assessing rhythmic visual entrainment and reinstatement of brain oscillations to modulate memory performance. *Front. Behav. Neurosci.* **14**, 118 (2020).
28. Zhang, M. & Hupbach, A. The effects of variable encoding contexts on item and source recognition. *Mem. Cognit*. **51**, 391–403 (2023).
29. Bramão, I., Jiang, J., Wagner, A. D. & Johansson, M. Encoding contexts are incidentally reinstated during competitive retrieval and track the Temporal dynamics of memory interference. *Cereb. Cortex.* **32**, 5020–5035 (2022).
30. Bramão, I. & Johansson, M. Neural Pattern Classification Tracks Transfer-Appropriate Processing in Episodic Memory. *eneuro* 5, ENEURO.0251-18.2018 (2018).
31. Wheeler, R. L. & Gabbert, F. Using Self-Generated cues to facilitate recall: A narrative review. *Front. Psychol.* **8**, 1830 (2017).
32. Unsworth, N. & Spillers, G. J. Variation in working memory capacity and episodic recall: the contributions of strategic encoding and contextual retrieval. *Psychon Bull. Rev.* **17**, 200–205 (2010).
33. Versace, R. et al. Act-In: an integrated view of memory mechanisms. *J. Cogn. Psychol.* **26**, 280–306 (2014).
34. Duarte, S. E., Ghetti, S. & Geng, J. J. Object memory is multisensory: Task-irrelevant sounds improve recollection. *Psychon Bull. Rev.* **30**, 652–665 (2023).
35. Versace, R., Labeye, É., Badard, G. & Rose, M. The contents of long-term memory and the emergence of knowledge. *Eur. J. Cogn. Psychol.* **21**, 522–560 (2009).
36. Juan, C. et al. The variability of multisensory processes of natural stimuli in human and non-human primates in a detection task. *PLOS ONE*. **12**, e0172480 (2017).
37. Lehmann, S. & Murray, M. M. The role of multisensory memories in unisensory object discrimination. *Cogn. Brain Res.* **24**, 326–334 (2005).
38. Moran, J. K. et al. Multisensory processing can compensate for Top-Down attention deficits in schizophrenia. *Cereb. Cortex*. **31**, 5536–5548 (2021).
39. Thelen, A., Talsma, D. & Murray, M. M. Single-trial multisensory memories affect later auditory and visual object discrimination. *Cognition* **138**, 148–160 (2015).
40. Murray, C. A. & Shams, L. Crossmodal interactions in human learning and memory. *Front. Hum. Neurosci.* **17**, 1181760 (2023).
41. Tovar, D. A., Murray, M. M. & Wallace, M. T. Selective enhancement of object representations through multisensory integration. *J. Neurosci.* **40**, 5604–5615 (2020).
42. Benini, E., Koch, I., Mayr, S., Frings, C. & Philipp, A. M. Contextual features of the cue enter episodic bindings in task switching. *J. Cogn.* **5**, 29 (2022).
43. Karacsony, S. & Abela, M. R. L. Stimulating sense memories for people living with dementia using the Namaste care programme: what works, how and why? *J. Clin. Nurs.* **31**, 1921–1932 (2022).
44. Shams, L. & Seitz, A. R. Benefits of multisensory learning. *Trends Cogn. Sci.* **12**, 411–417 (2008).
45. Dudai, Y. Molecular bases of long-term memories: a question of persistence. *Curr. Opin. Neurobiol.* **12**, 211–216 (2002).
46. Sridhar, S., Khamaj, A. & Asthana, M. K. Cognitive neuroscience perspective on memory: overview and summary. *Front. Hum. Neurosci.* **17**, 1217093 (2023).
47. Brainerd, C. J., Gomes, C. F. A. & Nakamura, K. Dual recollection in episodic memory. *J. Exp. Psychol. Gen.* **144**, 816–843 (2015).
48. Chang, M. et al. Spatial context scaffolds long-term episodic richness of weaker real-world autobiographical memories in both older and younger adults. *Memory* **32**, 431–448 (2024).
49. Dobbins, I. G. & Wagner, A. D. Domain-general and Domain-sensitive prefrontal mechanisms for recollecting events and detecting novelty. *Cereb. Cortex*. **15**, 1768–1778 (2005).
50. King, D. R., De Chastelaine, M., Elward, R. L., Wang, T. H. & Rugg, M. D. Recollection-Related increases in functional connectivity predict individual differences in memory accuracy. *J. Neurosci.* **35**, 1763–1772 (2015).
51. Lohnas, L. J., Healey, M. K. & Davachi, L. Neural Temporal context reinstatement of event structure during memory recall. *J. Exp. Psychol. Gen.* **152**, 1840–1872 (2023).
52. Polyn, S. M., Norman, K. A. & Kahana, M. J. A context maintenance and retrieval model of organizational processes in free recall. *Psychol. Rev.* **116**, 129–156 (2009).
53. Clewett, D., DuBrow, S. & Davachi, L. Transcending time in the brain: how event memories are constructed from experience. *Hippocampus* **29**, 162–183 (2019).
54. Davachi, L. & DuBrow, S. How the hippocampus preserves order: the role of prediction and context. *Trends Cogn. Sci.* **19**, 92–99 (2015).
55. DuBrow, S. & Davachi, L. Temporal binding within and across events. *Neurobiol. Learn. Mem.* **134**, 107–114 (2016).

56. Gordon, A. M., Rissman, J., Kiani, R. & Wagner, A. D. Cortical reinstatement mediates the relationship between Content-Specific encoding activity and subsequent recollection decisions. *Cereb. Cortex.* **24**, 3350–3364 (2014).
57. Jafarpour, A., Horner, A. J., Fuentemilla, L., Penny, W. D. & Duzel, E. Decoding oscillatory representations and mechanisms in memory. *Neuropsychologia* **51**, 772–780 (2013).
58. Staresina, B. P. & Davachi, L. Mind the Gap: binding experiences across space and time in the human Hippocampus. *Neuron* **63**, 267–276 (2009).
59. Folkerts, S., Rutishauser, U. & Howard, M. W. Human episodic memory retrieval is accompanied by a neural contiguity effect. *J. Neurosci.* **38**, 4200–4211 (2018).
60. Herweg, N. A., Solomon, E. A. & Kahana, M. J. Theta oscillations in human memory. *Trends Cogn. Sci.* **24**, 208–227 (2020).
61. Koen, J. D. & Rugg, M. D. Memory reactivation predicts resistance to retroactive interference: evidence from multivariate classification and pattern similarity analyses. *J. Neurosci.* **36**, 4389–4399 (2016).
62. Leiker, E. K. & Johnson, J. D. Pattern reactivation co-varies with activity in the core recollection network during source memory. *Neuropsychologia* **75**, 88–98 (2015).
63. Miller, J. E., Carlson, L. A. & McAuley, J. D. When what you hear influences when you see: listening to an auditory rhythm influences the Temporal allocation of visual attention. *Psychol. Sci.* **24**, 11–18 (2013).
64. Staudigl, T., Vollmar, C., Noachtar, S. & Hanslmayr, S. Temporal-Pattern similarity analysis reveals the beneficial and detrimental effects of context reinstatement on human memory. *J. Neurosci.* **35**, 5373–5384 (2015).
65. Yu, J. Y., Liu, D. F., Loback, A., Grossrubatscher, I. & Frank, L. M. Specific hippocampal representations are linked to generalized cortical representations in memory. *Nat. Commun.* **9**, 2209 (2018).
66. Ratcliff, R., Sederberg, P. B., Smith, T. A. & Childers, R. A single trial analysis of EEG in recognition memory: tracking the neural correlates of memory strength. *Neuropsychologia* **93**, 128–141 (2016).
67. Rugg, M. D. & Wilding, E. L. Retrieval processing and episodic memory. *Trends Cogn. Sci.* **4**, 108–115 (2000).
68. Staudigl, T., Hanslmayr, S. & Bäuml, K. H. T. Theta oscillations reflect the dynamics of interference in episodic memory retrieval. *J. Neurosci.* **30**, 11356–11362 (2010).
69. Tan, R. J., Rugg, M. D. & Lega, B. C. Direct brain recordings identify hippocampal and cortical networks that distinguish successful versus failed episodic memory retrieval. *Neuropsychologia* **147**, 107595 (2020).
70. Waldhauser, G. T., Braun, V. & Hanslmayr, S. Episodic memory retrieval functionally relies on very rapid reactivation of sensory information. *J. Neurosci.* **36**, 251–260 (2016).
71. Cowan, N. & Guitard, D. Encoding colors and tones into working memory concurrently: A developmental investigation. *Dev. Sci.* **27**, e13552 (2024).
72. Ostrowski, J. & Rose, M. Increases in pre-stimulus theta and alpha oscillations precede successful encoding of crossmodal associations. *Sci. Rep.* **14**, 7895 (2024).
73. Leys, C., Ley, C., Klein, O., Bernard, P. & Licata, L. Detecting outliers: do not use standard deviation around the mean, use absolute deviation around the median. *J. Exp. Soc. Psychol.* **49**, 764–766 (2013).
74. Klem, G. H., Lüders, H. O. & Elger, C. *The ten-twenty Electrode System of the International Federation* (The International Federation of Clinical Neurophysiology, 1999).
75. Oostenveld, R., Fries, P., Maris, E., Schoffelen, J. M. & FieldTrip Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. *Comput. Intell. Neurosci.* 1–9 (2011). (2011).
76. Treder, M. S. & MVPA-Light A classification and regression toolbox for Multi-Dimensional data. *Front. Neurosci.* **14**, 289 (2020).
77. Artuso, C., Palladino, P. & Belacchi, C. Sensitivity detection in memory recognition: interference control as index of taxonomic memory development? *Memory* **28**, 187–195 (2020).
78. Haatveit, B. C. et al. The validity of *d* prime as a working memory index: results from the Bergen *n* -back task. *J. Clin. Exp. Neuropsychol.* **32**, 871–880 (2010).
79. Shermohammed, M., Davidow, J. Y., Somerville, L. H. & Murty, V. P. Stress impacts the fidelity but not strength of emotional memories. *Brain Cogn.* **133**, 33–41 (2019).
80. Marinari, E. Optimized Monte Carlo methods. in Advances in Computer Simulation (eds Kertész, J. & Kondor, I.) vol. 501 50–81 (Springer Berlin Heidelberg, (1998).
81. Kalafatovich, J., Lee, M. & Lee, S. W. Decoding declarative memory process for predicting memory retrieval based on source localization. *PLOS ONE.* **17**, e0274101 (2022).
82. Osipova, D. et al. Theta and gamma oscillations predict encoding and retrieval of declarative memory. *J. Neurosci.* **26**, 7523–7531 (2006).
83. Sikora-Wachowicz, B. et al. False recognition in Short-Term Memory – Age-Differences in confidence. *Front. Psychol.* **10**, 2785 (2019).
84. Weidemann, C. T. & Kahana, M. J. Assessing recognition memory using confidence ratings and response times. *R Soc. Open. Sci.* **3**, 150670 (2016).
85. Staudigl, T. & Hanslmayr, S. Theta oscillations at encoding mediate the Context-Dependent nature of human episodic memory. *Curr. Biol.* **23**, 1101–1106 (2013).
86. Sols, I., DuBrow, S., Davachi, L. & Fuentemilla, L. Event boundaries trigger rapid memory reinstatement of the prior events to promote their representation in Long-Term memory. *Curr. Biol.* **27**, 3499–3504e4 (2017).
87. Schwabe, L. & Wolf, O. T. The context counts: congruent learning and testing environments prevent memory retrieval impairment following stress. *Cogn. Affect. Behav. Neurosci.* **9**, 229–236 (2009).
88. Bramão, I., Karlsson, A. & Johansson, M. Mental reinstatement of encoding context improves episodic remembering. *Cortex* **94**, 15–26 (2017).
89. Lu, Y., Wang, C., Chen, C. & Xue, G. Spatiotemporal neural pattern similarity supports episodic memory. *Curr. Biol.* **25**, 780–785 (2015).
90. Sutterer, D. W., Foster, J. J., Serences, J. T., Vogel, E. K. & Awh, E. Alpha-band oscillations track the retrieval of precise Spatial representations from long-term memory. *J. Neurophysiol.* **122**, 539–551 (2019).
91. Xiao, X. et al. Transformed neural pattern reinstatement during episodic memory retrieval. *J. Neurosci.* **37**, 2986–2998 (2017).
92. Jablonowski, J. & Rose, M. The functional dissociation of posterior parietal regions during multimodal memory formation. *Hum. Brain Mapp.* **43**, 3469–3485 (2022).
93. Marian, V., Hayakawa, S. & Schroeder, S. R. Cross-Modal interaction between auditory and visual input impacts memory retrieval. *Front. Neurosci.* **15**, 661477 (2021).
94. Pillai, A. S., Gilbert, J. R. & Horwitz, B. Early sensory cortex is activated in the absence of explicit input during crossmodal item retrieval: evidence from MEG. *Behav. Brain Res.* **238**, 265–272 (2013).
95. Healey, M. K. Temporal contiguity in incidentally encoded memories. *J. Mem. Lang.* **102**, 28–40 (2018).
96. Mundorf, A. M. D., Lazarus, L. T. T., Uitvlugt, M. G. & Healey, M. K. A test of retrieved context theory: dynamics of recall after incidental encoding. *J. Exp. Psychol. Learn. Mem. Cogn.* **47**, 1264–1287 (2021).
97. Michelmann, S., Bowman, H. & Hanslmayr, S. The Temporal signature of memories: identification of a general mechanism for dynamic memory replay in humans. *PLOS Biol.* **14**, e1002528 (2016).
98. Rudoler, J. H., Herweg, N. A. & Kahana, M. J. Hippocampal Theta and episodic memory. *J. Neurosci.* **43**, 613–620 (2023).
99. Karakaş, S. A review of theta Oscillation and its functional correlates. *Int. J. Psychophysiol.* **157**, 82–99 (2020).

100. Clouter, A., Shapiro, K. L. & Hanslmayr, S. Theta phase synchronization is the glue that binds human associative memory. *Curr. Biol.* **27**, 3143–3148e6 (2017).
101. Schroeder, S. C. Y., Ball, F. & Busch, N. A. The role of alpha oscillations in distractor Inhibition during memory retention. *Eur. J. Neurosci.* **48**, 2516–2526 (2018).
102. Hall, M. C. et al. Oscillatory activity in bilateral prefrontal cortices is altered by distractor strength during working memory processing. *NeuroImage* **301**, 120878 (2024).
103. Griffiths, B. J., Martín-Buro, M. C., Staresina, B. P. & Hanslmayr, S. Disentangling neocortical alpha/beta and hippocampal theta/gamma oscillations in human episodic memory formation. *NeuroImage* **242**, 118454 (2021).
104. Vogelsang, D. A., Gruber, M., Bergström, Z. M., Ranganath, C. & Simons, J. S. Alpha oscillations during incidental encoding predict subsequent memory for new foil information. *J. Cogn. Neurosci.* **30**, 667–679 (2018).
105. Scholz, S., Schneider, S. L. & Rose, M. Differential effects of ongoing EEG beta and theta power on memory formation. *PLOS ONE*. **12**, e0171913 (2017).
106. Winterling, S. L., Shields, S. M. & Rose, M. Reduced memory-related ongoing oscillatory activity in healthy older adults. *Neurobiol. Aging*. **79**, 1–10 (2019).
107. Elmers, J., Yu, S., Talebi, N., Prochnow, A. & Beste, C. Neurophysiological effective network connectivity supports a threshold-dependent management of dynamic working memory gating. *iScience* **27**, 109521 (2024).
108. Siebenhühner, F., Wang, S. H., Palva, J. M. & Palva, S. Cross-frequency synchronization connects networks of fast and slow oscillations during visual working memory maintenance. *eLife* 5, e13451 (2016).
109. Engel, A. K. & Singer, W. Temporal binding and the neural correlates of sensory awareness. *Trends Cogn. Sci.* **5**, 16–25 (2001).
110. Pennartz, C. M. A. Identification and integration of sensory modalities: neural basis and relation to consciousness. *Conscious. Cogn.* **18**, 718–739 (2009).
111. Huijbers, W., Pennartz, C. M. A., Rubin, D. C. & Daselaar, S. M. Imagery and retrieval of auditory and visual information: neural correlates of successful and unsuccessful performance. *Neuropsychologia* **49**, 1730–1740 (2011).
112. Caenegem et al. Multisensory approach in mental imagery: ALE meta-analyses comparing motor, visual and auditory imagery. *Neurosci Biobehav Rev* **167**.
113. Tian, X., Zarate, J. M. & Poeppel, D. Mental imagery of speech implicates two mechanisms of perceptual reactivation. *Cortex* **77**, 1–12 (2016).
114. Daselaar, S. M., Porat, Y., Huijbers, W. & Pennartz, C. M. A. Modality-specific and modality-independent components of the human imagery system. *NeuroImage* **52**, 677–685 (2010).
115. Spagna, A. et al. Visual mental imagery: evidence for a heterarchical neural architecture. *Phys. Life Rev.* **48**, 113–131 (2024).
116. Staudigl, T. & Hanslmayr, S. Reactivation of neural patterns during memory reinstatement supports encoding specificity. *Cogn. Neurosci.* **10**, 175–185 (2019).
117. Umar, H., Mast, F. W., Cacchione, T. & Martarelli, C. S. The prioritization of visuo-spatial associations during mental imagery. *Cogn. Process.* **22**, 227–237 (2021).
118. Sahadevan, S. S., Chen, Y. Y. & Jeremy, B. C. Imagery-based strategies for memory for associations. *Memory* **29**:10, 1275–1295 .
119. Yin, Q. et al. Direct brain recordings reveal occipital cortex involvement in memory development. *Neuropsychologia* **148**, 107625 (2020).
120. Xie, Y., Feng, Z., Xu, Y., Bian, C. & Li, M. The different Oscillation patterns of alpha band in the early and later stages of working memory maintenance. *Neurosci. Lett.* **633**, 220–226 (2016).
121. Staudigl, T., Hartl, E., Noachtar, S., Doeller, C. F. & Jensen, O. Saccades are phase-locked to alpha oscillations in the occipital and medial Temporal lobe during successful memory encoding. *PLOS Biol.* **15**, e2003404 (2017).
122. Romei, V. et al. Spontaneous fluctuations in posterior -Band EEG activity reflect variability in excitability of human visual areas. *Cereb. Cortex*. **18**, 2010–2018 (2008).
123. Schneider, S. L. & Rose, M. Intention to encode boosts memory-related pre-stimulus EEG beta power. *NeuroImage* **125**, 978–987 (2016).
124. Strube, A., Rose, M., Fazeli, S. & Büchel, C. Alpha-to-beta- and gamma-band activity reflect predictive coding in affective visual processing. *Sci. Rep.* **11**, 23492 (2021).
125. Ronconi, L., Busch, N. A. & Melcher, D. Alpha-band sensory entrainment alters the duration of Temporal windows in visual perception. *Sci. Rep.* **8**, 11810 (2018).
126. Cunningham, E., Zimnicki, C. & Beck, D. M. The influence of prestimulus 1/f-Like versus Alpha-Band activity on subjective awareness of auditory and visual stimuli. *J. Neurosci.* **43**, 6447–6459 (2023).
127. Zhou, Y. J., Iemi, L., Schoffelen, J. M., De Lange, F. P. & Haegens, S. Alpha oscillations shape sensory representation and perceptual sensitivity. *J. Neurosci.* **41**, 9581–9592 (2021).
128. Wang, D., Clouter, A., Chen, Q., Shapiro, K. L. & Hanslmayr, S. Single-Trial phase entrainment of Theta oscillations in sensory regions predicts human associative memory performance. *J. Neurosci.* **38**, 6299–6309 (2018).
129. Yazar, Y., Bergström, Z. M. & Simons, J. S. Reduced multimodal integration of memory features following continuous theta burst stimulation of angular gyrus. *Brain Stimulat*. **10**, 624–629 (2017).
130. Tibon, R., Fuhrmann, D., Levy, D. A., Simons, J. S. & Henson, R. N. Multimodal integration and vividness in the angular gyrus during episodic encoding and retrieval. *J. Neurosci.* **39**, 4365–4374 (2019).
131. Grob, A. M., Heinbockel, H., Milivojevic, B., Doeller, C. & Schwabe, L. Causal role of the angular gyrus in insight-driven memory reconfiguration. *Preprint At.* https://doi.org/10.7554/eLife.91033.1 (2023).
132. Bonnici, H. M., Richter, F. R., Yazar, Y. & Simons, J. S. Multimodal feature integration in the angular gyrus during episodic and semantic retrieval. *J. Neurosci.* **36**, 5462–5471 (2016).
133. Pierce, B. H. & Gallo, D. A. Encoding modality can affect memory accuracy via retrieval orientation. *J. Exp. Psychol. Learn. Mem. Cogn.* **37**, 516–521 (2011).
134. Thakral, P. P., Benoit, R. G. & Schacter, D. L. Characterizing the role of the hippocampus during episodic simulation and encoding. *Hippocampus* **27**, 1275–1284 (2017).
135. Foudil, S. A., Pleche, C. & Macaluso, E. Memory for spatio-temporal contextual details during the retrieval of naturalistic episodes. *Sci. Rep.* **11**, 14577 (2021).
136. Rohe, T. & Noppeney, U. Distinct computational principles govern multisensory integration in primary sensory and association cortices. *Curr. Biol.* **26**, 509–514 (2016).
137. Sereno, M. I. & Huang, R. S. Multisensory maps in parietal cortex. *Curr. Opin. Neurobiol.* **24**, 39–46 (2014).
138. Andersen, R. A. Multimodal integration for the representation of space in the posterior parietal cortex. (1997).
139. Kayser, C. & Logothetis, N. K. Do early sensory cortices integrate cross-modal information? *Brain Struct. Funct.* **212**, 121–132 (2007).
140. Lin, J. Sensory inputs guiding cognitive behaviors and decision making. *Highlights Sci. Eng. Technol.* **74**, 1399–1404 (2023).
141. Porada, D. K., Regenbogen, C., Freiherr, J., Seubert, J. & Lundström, J. N. Trimodal processing of complex stimuli in inferior parietal cortex is modality-independent. *Cortex* **139**, 198–210 (2021).
142. Lewis, J. W. & Van Essen, D. C. Corticocortical connections of visual, sensorimotor, and multimodal processing areas in the parietal lobe of the macaque monkey. *J. Comp. Neurol.* **428**, 112–137 (2000).
143. Anderson, K. L., Rajagovindan, R., Ghacibeh, G. A., Meador, K. J. & Ding, M. Theta oscillations mediate interaction between prefrontal cortex and medial Temporal lobe in human memory. *Cereb. Cortex*. **20**, 1604–1612 (2010).

144. Regenbogen, C. et al. The intraparietal sulcus governs multisensory integration of audiovisual information based on task difficulty. *Hum. Brain Mapp.* **39**, 1313–1326 (2018).
145. Sours, C. et al. Structural and functional integrity of the intraparietal sulcus in moderate and severe traumatic brain injury. *J. Neurotrauma*. **34**, 1473–1481 (2017).
146. DuBrow, S. & Davachi, L. The influence of context boundaries on memory for the sequential order of events. *J. Exp. Psychol. Gen.* **142**, 1277–1286 (2013).
147. Schmidt, M., Frings, C. & Tempel, T. Context-Dependent memory of motor sequences. *J. Cogn.* **4**, 15 (2021).
148. Kelber, P., Mackenzie, I. G. & Mittelstädt, V. Cognitive control in cross-modal contexts: abstract feature transitions of task-related but not task-unrelated stimuli modulate the congruency sequence effect. *J. Exp. Psychol. Learn. Mem. Cogn.* **50**, 902–919 (2024).
149. Pazdera, J. K. & Kahana, M. J. Modality effects in free recall: A retrieved-context account. *J. Exp. Psychol. Learn. Mem. Cogn.* **49**, 866–888 (2023).
150. Song, G. & Tan, X. Real-world Cross-modal retrieval via sequential learning. *IEEE Trans. Multimed*. **23**, 1708–1721 (2021).
151. Zhu, B. et al. Multiple interactive memory representations underlie the induction of false memory. *Proc. Natl. Acad. Sci.* **116**, 3466–3475 (2019).
152. Harrison, N. R. & Woodhouse, R. Modulation of auditory Spatial attention by visual emotional cues: differential effects of attentional engagement and disengagement for pleasant and unpleasant cues. *Cogn. Process.* **17**, 205–211 (2016).

Acknowledgements

The present research was supported by the German Research Foundation (DFG; SFB/Transregio 169, Project B3 and DFG RO 2653/9-1). We thank Michele Frerichs and Carla Mourkojannis for assistance during data acquisition.

Author contributions

M.R. and M.M. designed the study. M.M. performed data acquisition, and J.O. provided parts of the scripts for the behavioural and univariate analysis analysis. M.M. and M.R. analyzed the data. M.R. acquired funding, conceptualized, and supervised the project. M.M. and M.R. wrote the original manuscript. M.M., J.O., and M.R. reviewed and edited the paper and approved the final manuscript.

Funding

Open Access funding enabled and organized by Projekt DEAL.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

Correspondence and requests for materials should be addressed to M.R.

Reprints and permissions information is available at www.nature.com/reprints.

11 Eidesstattliche Versicherung

Ich versichere ausdrücklich, dass ich die Arbeit selbständig und ohne fremde Hilfe, insbesondere ohne entgeltliche Hilfe von Vermittlungs- und Beratungsdiensten, verfasst, andere als die von mir angegebenen Quellen und Hilfsmittel nicht benutzt und die aus den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen einzeln nach Ausgabe (Auflage und Jahr des Erscheinens), Band und Seite des benutzten Werkes kenntlich gemacht habe. Das gilt insbesondere auch für Informationen aus Internetquellen.

Soweit beim Verfassen der Dissertation KI-basierte Tools („Chatbots“) verwendet wurden, versichere ich ausdrücklich, den daraus generierten Anteil deutlich kenntlich gemacht zu haben. Die „Stellungnahme des Präsidiums der Deutschen Forschungsgemeinschaft (DFG) zum Einfluss generativer Modelle für die Text- und Bilderstellung auf die Wissenschaften und das Förderhandeln der DFG“ aus September 2023 wurde dabei beachtet.

Ferner versichere ich, dass ich die Dissertation bisher nicht einem Fachvertreter an einer anderen Hochschule zur Überprüfung vorgelegt oder mich anderweitig um Zulassung zur Promotion beworben habe.

Ich erkläre mich einverstanden, dass meine Dissertation vom Dekanat der Medizinischen Fakultät mit einer gängigen Software zur Erkennung von Plagiaten überprüft werden kann.

Datum Unterschrift