Individual differences in information processing predict sleep-based memory consolidation of complex rules

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Conflict of Interest

The authors declare no competing financial interests.

Abstract

Memory is critical for many cognitive functions, from remembering facts, to learning complex environmental rules. While memory encoding occurs during wake, memory consolidation is associated with sleep-related neural activity. Further, research suggests that individual differences in the alpha frequency band (~ 7 – 13 Hz) modulate memory processes, with higher individual alpha frequency (IAF) associated with greater memory performance. However, the relationship between wake-related EEG individual differences, such as IAF, and sleep-related neural correlates of memory consolidation has been largely unexplored, particularly in a complex rule-based memory context. Here, we aimed to investigate whether IAF and sleep neurophysiology interact to influence rule learning in a sample of 36 healthy adults (16 male; mean age = 25.4, range: 18 – 40). Participants learned rules of a modified miniature language prior to either 8hrs of sleep or wake, after which they were tested on their knowledge of the rules in a grammaticality judgement task. Results indicated that sleep and IAF modulate memory for complex linguistic rules. Phase-amplitude coupling between slow oscillations and spindles during non-rapid eye-movement (NREM) sleep also promoted memory for rules that were analogous to the canonical English word order. As an exploratory analysis, we found that theta activity during rapid eye-movement (REM) sleep predicted rule learning. Taken together, the current study provides behavioural and electrophysiological evidence for a complex role of NREM and REM sleep neurophysiology and IAF in the consolidation of rule-based information.

Keywords: memory, rule extraction, sleep, individual alpha frequency, phase-amplitude coupling

1 INTRODUCTION

An adaptive function of the brain is the extraction of rules from the environment and to generalise this information to novel sensory input. Rule learning involves forming overarching rules via the extraction of regularities from stimuli that share similar features (Frank & Gibson, 2011). For example, grammar within natural language requires rule extraction, as critical features of a sentence allow for effective categorisation and extraction of meaning (Pothos, 2007). Despite important theoretical and practical implications for understanding the consolidation of rule-based information, the underlying mechanisms that facilitate rule consolidation are poorly understood. Current understanding of rule extraction implicates sleep as an important factor (Batterink et al., 2014; Nieuwenhuis et al., 2013) as well as individual differences in baseline memory performance (Diekelmann et al., 2010). However, individual differences in neurophysiology (cf. Cross et al., 2020a; Klimesch, 1999) as related to rule extraction have yet to be explored in detail.

1.1 Memory consolidation as repeated reactivation

The consolidation and generalisation of memory occurs via repeated reactivation of new and existing memory traces (Yassa & Reagh, 2013). Generalisation refers to the process by which the brain extracts and consolidates the central features amongst multiple memory traces, often losing rich contextual details (Stark et al., 2008; Stark & Stark, 2016). It is associated with activity within hippocampus and neocortex (García-Lázaro et al., 2012; Yassa & Reagh, 2013). Generalisation likely occurs via memory traces being reactivated by a cue (e.g., a new memory trace with similar properties to an existing memory trace), thus allowing the hippocampus to instantiate the neural signature of an original, existing memory trace (Yassa & Reagh, 2013). By reactivating the shared features between both memory traces, these features are consolidated into neocortical areas (García-Lázaro et al., 2012). Some models, such as Competitive Trace Theory (Yassa & Reagh, 2013), suggest that during this process, only central features that overlap between the new memory trace and an existing memory trace are strengthened. During this process, the specific, contextual details, such as features that do not overlap with the original memory trace, compete for representation in neocortex and are less likely to be consolidated as a result of mutual inhibition (Yassa & Reagh,

2013). Therefore, over repeated reactivations of similar regularities or patterns (e.g., grammar within a language), memory traces become highly semanticised, containing important facts or rules that can be applied to future stimuli that show similarities (Yassa & Reagh, 2013). This process of consolidation occurs during both periods of wake and sleep (Humiston et al., 2019; Klinzing et al., 2019; Tucker et al., 2020; Wamsley, 2019). In particular, the systems consolidation perspective proposes that memory consolidation and reactivation relies upon slow-wave sleep (SWS; Diekelmann & Born, 2010; Lewis & Durrant, 2011).

1.2 The influence of sleep on memory and rule extraction: A systems consolidation perspective

It is now well established that sleep – and particularly cortical activity during slow-wave sleep (SWS) – benefits the consolidation of various types of information (Diekelmann et al., 2010; Diekelmann & Born, 2010; Lewis & Durrant, 2011; Nieuwenhuis et al., 2013; Stickgold & Walker, 2013; Tononi & Cirelli, 2006). According to the Active Systems Consolidation model (ASC: Diekelmann & Born, 2010), slow oscillations (SOs), thalamo-cortical spindles, and hippocampal ripples facilitate long-term memory consolidation, allowing for newly encoded memories to undergo qualitative changes (e.g., rule extraction) as they are gradually incorporated into existing neocortical memory networks (Klinzing et al., 2019; Lewis & Durrant, 2011). Work in both humans (Helfrich et al., 2018, 2019; Staresina et al., 2015) and rodents (Latchoumane et al., 2017; Maingret et al., 2016) demonstrate that SOs modulate faster oscillatory activity (e.g., spindles and hippocampal ripples), such that the phase of the SO drives spindle activity, with this coupling facilitating the controlled reactivation of neural assemblies that were active during initial encoding (Helfrich et al., 2019). Additionally, both thalamo-cortical spindles and hippocampal ripples are implicated in the controlled transfer of information, by priming cortical storage areas and modulating selective activation of neural assemblies, respectively (Girardeau & Zugaro, 2011; Staresina et al., 2015). The ASC model proposes that the phase-amplitude coupling (PAC) between SOs, spindles, and hippocampal ripples is the primary mechanism by which memories are reactivated and generalised over a period of sleep (Diekelmann & Born, 2010; Muehlroth et al., 2019). Here, PAC refers to the coupling between oscillations of differing frequencies, in which a lower frequency (e.g. a SO) is referred to as the frequency for phase and

is known to modulate the amplitude of a higher frequency, referred to as the frequency for amplitude (e.g. a spindle; (Bergmann & Born, 2018; Hülsemann et al., 2019), which has been proposed as a mechanism of cortical information transfer (Canolty & Knight, 2010). Thus, cross-frequency coupling is proposed to drive the controlled hippocampal-neocortical information transfer required for memory consolidation and more specifically, rule extraction.

Studies exploring rule extraction suggest that sleep facilitates the extraction of overarching rules from regularities within stimuli (Batterink et al., 2014; Djonlagic et al., 2009; Durrant et al., 2011; Gómez et al., 2006; Lutz et al., 2017; Nieuwenhuis et al., 2013; Wilhelm et al., 2013), such as grammar within language. Work investigating the effect of sleep on linguistic rule learning found that greater SWS duration predicted subsequent sensitivity to a hidden rule, as well as being instrumental in stabilising memory traces related to a rule (Batterink et al., 2014; Nieuwenhuis et al., 2013). Additionally, studies in non-linguistic contexts have reported similar results, in which SWS duration was positively associated with the extraction of statistical rules and subsequent performance on a task in which understanding of the rule was crucial (Djonlagic et al., 2009; Durrant et al., 2011, 2013). These findings suggest that SWS duration facilitates rule extraction, likely due to increased time allocated for essential cortical activity (e.g., SOs, thalamo-cortical spindles, and hippocampal ripples) to effectively reactivate and consolidate the central features of multiple memory traces obtained during encoding. However, only few experiments have explored how precise oscillatory events (e.g., SO-spindle coupling) that occur during SWS may predict rule extraction. The limited work in this area has found that stronger SO activity is positively associated with motor sequence learning in both children and adults (Wilhelm et al., 2013), that SO-spindle coupling increases from childhood to adolescence, and this increase predicts improvements in motor memory (Hahn et al., 2020). However, while this work provides preliminary evidence for a role of sleep-based oscillatory activity in motor memory, little is known regarding the influence of SO-spindle coupling on more complex forms of memory, such as rule learning. Due to SO-spindle coupling being linked to general memory consolidation, further investigation of such activity in a rule-based context may increase our understanding of the underlying mechanisms involved in rule extraction.

1.3 Beyond slow-wave sleep: A possible role for REM sleep in rule generalisation

In addition to cortical activity within SWS, Rapid Eye Movement (REM) sleep and its associated oscillatory activity has often been implicated in memory consolidation (Ackermann & Rasch, 2014; Boyce et al., 2016; Grosmark et al., 2012; Nishida et al., 2009; Sopp et al., 2017). REM sleep primarily occurs during the second half of the night and tends to be characterised by wake-like oscillatory activity (i.e., theta activity; ~ 4 – 7 Hz) within the hippocampus, prefrontal cortex and amygdala (Nishida et al., 2009; Schäfer et al., 2020; Sopp et al., 2017), combined with rapid-eye movements. Literature investigating the role of REM sleep indicates that REM sleep is particularly important for the processing of emotional memory and fear conditioned stimuli (Boyce et al., 2016; Cross et al., 2020a; Hutchison & Rathore, 2015; Kim et al., 2020; Nishida et al., 2009; Schäfer et al., 2020). An experimental study by Sopp et al. (2017) demonstrated that late night REM sleep and theta oscillations promoted consolidation of memories with negative emotional valence, with frontal theta activity showing the closest association with negative memory retention. Further, rodent studies have revealed fear conditioned memories are more likely to be retained with higher theta coherence between the hippocampus and the amygdala (Popa et al., 2010), and optogenetic silencing of theta activity leads to impairment in consolidation of fear-related memories (Boyce et al., 2016). Thus, there is evidence to suggest a role for REM sleep and related theta activity in the consolidation of emotional memory.

However, literature is scarce on whether REM sleep neurophysiology only benefits emotional memory processing, or whether it may extend to other types of memory, such as the extraction of complex rules. Few studies have investigated the role of REM within non-emotional memory contexts (e.g., Batterink et al., 2014; Matorina & Poppenk, 2019), such as exploring how neurophysiological activity during SWS and REM sleep affects gist extraction, which refers to the extraction of the most important elements or the general idea (Matorina & Poppenk, 2021). Here, Matorina & Poppenk, (2019) found that a higher proportion of time spent in REM sleep led to decreased performance in a statistical learning task, suggesting that REM sleep is disadvantageous to the extraction of rules. In contrast, Batterink et al. (2014) examined how REM sleep duration during a nap contributed to rule

generalisation and found increased performance relative to higher durations of REM sleep. Interestingly, this study also demonstrated that interactions between REM and SWS duration predicted rule generalisation of newly acquired rules (Batterink et al., 2014), suggesting that REM, in conjunction with SWS mechanisms may be involved in complex rule extraction. Other studies have indicated a beneficial effect of REM sleep on rule extraction, specifically when looking at acquisition of a rule for effective categorisation (Djonlagic et al., 2009) and within a task in which effective learning of sequential rules were critical (Maquet et al., 2000). In view of the conflicting evidence that the limited literature provides regarding the role of REM sleep in non-emotional contexts, further research is needed in this area.

Interestingly, work into the facilitation of memory generalisation has implicated factors other than specific sleep neurophysiology. In particular, a study by Diekelmann, Born and Wagner (2010) investigated the effect of sleep on the generalisation of memory and found that whilst sleep facilitated memory generalisation, this was influenced by individual differences in memory performance. This suggests that the accuracy of rule extraction may also be influenced by individual differences; however, individual differences in neural activity and their relation to sleep-associated memory consolidation are only just starting to be considered (Chatburn et al., 2021; Cross et al., 2020a; Fenn & Hambrick, 2012; Schabus et al., 2008).

1.4 Individual alpha frequency as a measure of individual differences in information processing

Research into inter-individual differences in cognitive processing have often focussed on the role of the alpha frequency band (~8-12Hz) and it's relation to information processing in a variety of domains, such as language and memory (Bornkessel et al., 2004; Cross et al., 2020a; Furman et al., 2018; Klimesch, 2012; Samaha & Postle, 2015). Alpha oscillations are involved in the functional inhibition of sensory areas within the brain based on current task demands (Foxe & Snyder, 2011; Jensen et al., 2012; Klimesch, 1997; Mathewson et al., 2011) and have been linked to attention, processing speed and memory (Klimesch, 1997, 1999). In addition, the individual alpha frequency (IAF), which refers to the individual dominant peak within the alpha frequency band, has been linked to various aspects of

cognition (Klimesch, 1997, 1999; Surwillo, 1961). IAF has been implicated in the controlled timing of information transmission (Klimesch, 2012; Smit et al., 2006) and it is hypothesised that those with a higher IAF have improved information transmission within the cortex, resulting in faster processing speed (Klimesch et al., 1996; Surwillo, 1961, 1963) and better performance on both tests of memory (Klimesch, 1999) and general intelligence (Grandy et al., 2013), though more recent research has demonstrated that IAF and general intelligence are unrelated (Ociepka et al., 2022). In fact, Ociepka et al., (2022) found IAF is more closely associated with processing speed, supporting previous literature proposing a role for IAF in temporal processing (Klimesch, 2012; Samaha & Postle, 2015). For example, Samaha & Postle, (2015) suggests that IAF may be related to temporal receptive windows of processing, determining the amount of information within each processing cycle. Typically, higher IAF individuals are considered to have faster cycles with less information contained within, and lower IAF individuals have slower cycles that contain more information (Samaha & Postle, 2015).

In relation to memory, research indicates that those with good memory performance tend to have an IAF of around 1 Hz higher than poor memory performers (Doppelmayr et al., 2005; Klimesch, 1997, 1999). According to Klimesch (2012), this may relate to the functional relevance of IAF as being involved in the controlled timing of information transfer within the cortex, which may interact with mechanisms of memory consolidation that draw upon hippocampal-neocortical information transfer, such as SO-spindle coupling during SWS. Whilst there is little experimental evidence for an explicit association between sleep neurophysiology and IAF, Cross et al. (2020a) investigated how these factors may interact to influence emotional memory consolidation. Results revealed complex interactions between IAF, REM theta power and SO density modulating emotional memory outcomes, indicating a relationship between individual processing capabilities and cortical activity during sleep. However, further evidence is limited and how these factors may interact in other memory-related contexts (e.g., rule extraction) is yet to be examined.

1.5 The current study

The present study is a reanalysis of Cross et al., (2021), and aimed to address whether sleep-related and intrinsic neural mechanisms, such as SO-spindle coupling and IAF, respectively, modulate rule extraction. Due to the significance of individual differences in memory performance, exploring IAF as a measure of individual differences will inform current models of sleep and memory as to how underlying electrophysiology of an individual interacts with memory consolidation and thus, rule extraction. Exploratory analyses further aimed to clarify the role of REM sleep beyond emotional memory contexts and whether REM neurophysiology is functionally involved in rule-based memory consolidation. Subjects were randomly allocated to a sleep or wake condition and were required to learn grammatical rules in a novel artificial language modelled on Mandarin Chinese (Cross et al., 2020b). Participants then completed a baseline and delayed sentence judgment task (after sleep or an equivalent period of wake) used to test knowledge about underlying grammatical rules, performance on which served as a proxy for rule extraction. The present analysis explored how SO-spindle coupling and IAF modulate the consolidation of rules. As such, based on previous literature suggesting the role of sleep and IAF in facilitating memory performance, it was hypothesised that: (H^1) those in the sleep condition will perform better on tasks assessing grammatical knowledge than those in the wake condition; (H^2) differences in memory performance relative to condition (sleep vs. wake) and grammatical rule type will be modulated by SO-spindle coupling and IAF independently. Based on literature suggesting an association between individual differences and memory performance, it was also hypothesised that (H^3) SO-spindle coupling and IAF will interact to influence memory performance. Additionally, exploratory analyses were conducted to assess whether REM sleep is associated with the extraction of complex rules.

2 METHODS

2.1 Participants

Thirty-six (17 male) healthy adults ranging from 18 to 40 years of age (*M* = 25.4, *SD* = 7.0) were randomly allocated to either a sleep (*Mean age* = 23.60 [*SD* = 5.84], 9 males) or wake (*Mean age* = 27.11 [*SD* = 7.50], 8 males) condition. Eligibility criteria included standard EEG criteria as well as additional criteria requiring

participants to be monolingual, native English speakers with no previous exposure to Mandarin Chinese. Eligible participants did not have any current conditions that affected sleep or circadian rhythms and had not undertaken shift work in the past month to ensure no influence of irregular or poor-quality sleep. Participants received an AUD$120 honorarium upon completion of the study. Ethics approval was granted by the University of South Australia's Human Research Ethics committee (I.D: 0000032556).

2.2 Materials and Measures

2.2.1 Electroencephalography (EEG)

The EEG was recorded with a 32-channel BrainCap (Brain Products GmbH, Gilching, Germany) with Ag/AgCl electrodes mounted via the International 10-20 system. The ground electrode was located at AFz and the online reference was located at FCz, with re-referencing to linked mastoids undertaken offline. The electrooculogram (EOG) was recorded using electrodes located at the side of each eye as well as above and below the left eye. All EEG and EOG channels were amplified via a BrainAmp DC amplifier (Brain Products GmbH, Gilching, Germany), band-pass filter of DC – 250Hz and a sampling rate of 1000 Hz. Impedances were kept below 10kΩ. EEG signals were recorded throughout both the sleep durations and experimental tasks.

2.2.2 Language Learning Task: Mini Pinyin

Mini Pinyin is a modified miniature language (MML) modelled on Mandarin Chinese (Cross et al., 2020b). MML paradigms contain words that are combined into sentences following grammatical rules adapted from the language they are based upon (Mueller, 2006; Wang et al., 2012). Mini Pinyin contains 16 verbs, 25 noun phrases, 2 coverbs, and 4 classifiers (for a full description of Mini Pinyin, see Cross et al., 2020b). The nouns are divided into categories of human (10 nouns), animal (10 nouns), and objects (5 nouns).

Mini Pinyin contains two coverbs that influence word order and the interpretation of the noun phrases. For example, when bǎ is present in a sentence, the first noun is the Actor (i.e., the participant instigating the event) and the second noun is the Undergoer (i.e., the participant affected by the event). The second

coverb, bèi, reverses this pattern. When either of these coverbs are used, word order becomes fixed and determines role assignment (see Table 1 for examples). Thus, bǎ constructions instantiate Actor-first word orders, while bèi instantiates an Undergoer-first word order. Additionally, verb positioning is an important element in Mini Pinyin: sentences that contain coverbs must have the verb placed at the end of the sentence, whereas sentences without coverbs (not examined here) require the verb to be positioned between the noun phrases.

Based on the linguistic parameters described above, the process of rule extraction can be explored by using the word order contingencies (e.g., the fixed word order of the Actor-Undergoer relationship) of each of the coverbs. In this instance, accurate rule extraction would allow the participant to correctly distinguish between the specific noun phrase order instantiated by Undergoer-first (bèi) and Actor-first (bǎ) constructions. Additionally, rule extraction can be explored by measuring performance on the verb positioning rule, in which the position of the verb is critical for the sentence to be considered grammatical.

Table 1. Examples of Plausible and Implausible Bèi and Bǎ Sentence Structures (adapted from Cross et al., 2020b.)

Coverb	**Sentence Examples**
Bǎ Plausible (Actor-first)	zhi junma bặ xi pingguo chile. (animal) horse bặ (small object) apple eat. *"The horse eats the small apple."*
Bǎ Implausible (Actor-first)	xi pingguo bặ zhi junma chile. (small object) apple bặ (animal) horse eat. *"The small apple eats the horse."*
Bèi Plausible (Undergoer-first)	da shubao bèi ge yisheng dale. (large object) bag bèi (human) doctor hit. *"The doctor hits the large bag."*
Bèi Implausible (Undergoer-first)	ge yisheng bèi da shubao dale. (human) doctor bèi (large object) bag hit. *"The large bag hits the doctor."*

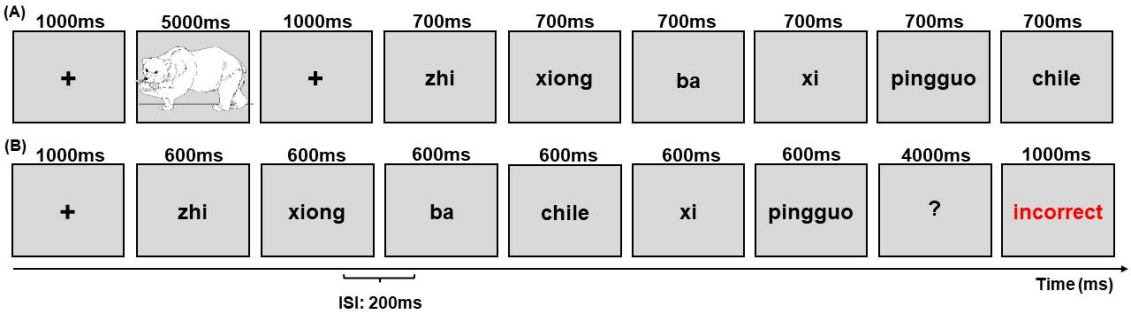
2.3 Procedure

Each participant received a picture-word pair booklet containing each of the 25 nouns approximately one week before testing to gain a basic vocabulary before the experimental tasks. Eligible participants visited the Cognitive Neuroscience Laboratory at the University of South Australia to undergo testing. Before continuing onto the main testing phase, participants were required to score above 90% on a vocabulary test designed to test their knowledge of the 25 nouns. All 36 participants included in this analysis scored above 90%.

The main testing session consisted of a sentence learning task, a baseline sentence judgement task, and a delayed judgement task (approximately 12 hours after the learning and baseline tasks). All sentence and picture stimuli were presented via OpenSesame (Mathôt et al., 2012). The learning task used pictures to depict events involving two entities and was designed for the participants to learn the meaning of the verbs, coverbs, classifiers, and overall sentence structure. Each trial began with a 1000ms fixation cross, followed by pictures depicting the event. Subsequently, a sentence describing the event pictured was presented on a word-by-word basis, with each word presented for 700ms. The inter-stimulus interval (ISI) was 200ms. This trial structure was used for a total of 128 pseudorandomised picture-sentence combinations.

Following the learning task, participants completed the baseline and delayed judgement tasks. Both judgment tasks consisted of 288 pseudorandomised novel sentences (without pictures) presented word-by-word, with each word being presented for 600ms each with an ISI of 200ms. Participants were required to judge the grammaticality of each sentence (cued by a question mark presented on screen for 4000ms) by pressing a button. During the baseline judgment task, participants also received feedback as to whether their response was correct. They did not receive feedback in the delayed judgement task. Two stimuli lists were used to counterbalance the order of stimuli presentation across participants. Half of the sentences were grammatical constructions, and the other half were ungrammatical constructions. See Figure 1 for a schematic of both the learning and baseline judgement tasks.

Figure 1. Schematic Representation of Trials Within the **(A)** Learning and **(B)** Baseline Judgement Tasks (adapted from Cross et al., 2021)

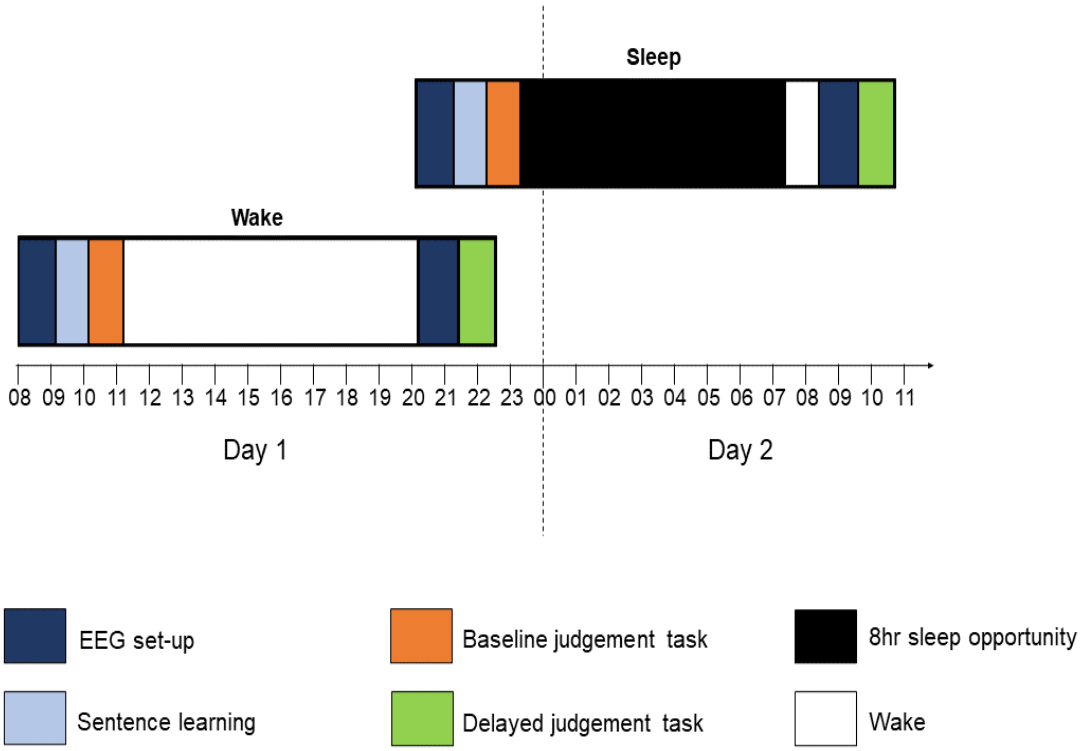


Note: The sentence presented in the top row (A) demonstrates a trial within the learning phase, in which the event picture is presented followed by the sentence explaining said event. The bottom row (B) depicts a trial from the baseline judgment task, in which the sentence is presented for judgement, followed by a prompt for a judgement. After this, feedback was presented as to whether the judgement was correct or incorrect. In both A and B translates specifically to *"Animal bear bǎ small apple to eat"* or *"The bear ate the apple"*.

Participants in the wake condition completed the learning and baseline judgment tasks at approximately 09:00hr before leaving the laboratory to undergo their normal daily routine.

Participants returned at approximately 21:00hr the same day to complete the delayed judgment task. Participants in the sleep condition completed the learning and baseline judgment tasks at approximately 21:00hr after EEG set up. Following this, participants were given an 8-hour sleep opportunity between 23:00hr – 07:00hr, in which polysomnography was continuously recorded. When woken, participants were given approximately 1 hour to overcome sleep inertia before completing the delayed judgement task. For a schematic of the experimental protocol refer to Figure 2.

Figure 2. Schematic Representation of Experimental Protocol (adapted from Cross et al. 2021)



Note: This figure shows the stepwise procedure for the sleep condition (above) and the wake condition (below). The x-axis shows the time of day in hours as the experiment progressed, starting with 8am on the left and ending with 11am (the following day) on the right. For the wake condition (below), participants began at approximately 08:00hr (am), underwent setup and initial testing followed by a period of wake and subsequent testing. For the sleep condition (above), participants began at approximately 21:00hr (pm), underwent setup and initial testing followed by a period of sleep and subsequent testing. The coloured legend indicates the task being completed at the approximate time and the dotted line at 0 represents 00.00hrs (midnight) where testing crossed into the following day.

2.4 Data Analysis

All statistical analyses were performed in *R* (R Core Team, 2017). Mixed-effects regression models were fitted using maximum likelihood via the *lme4* (Bates et al., 2015). Other packages included in mixed-model analysis and output reporting included the *car* (Fox & Weisberg, 2019), *Rmisc* (Hope, 2013), *effects* (Fox & Weisberg, 2019), *Hmisc* (Harrell Jr, 2019), *apaTables* (Stanley & Spence, 2018) and *performance* (Lüdecke et al., 2021). Data was arranged using *tidyverse* (Wickham et al., 2019), *reshape2* (Wickham, 2007), *plyr* (Wickham, 2011), *sjmisc* (Lüdecke,

2018a), and packages involved in plotting included *lattice* (Sarkar, 2008), *sjPlot* (Lüdecke, 2018b), *ggpubr* (Kassambara, 2020), *RColorBrewer* (Neuwirth, 2014). All effects were plotted using the *ggplot2* package (Wickham et al., 2021) and *ggeffects* (Lüdecke et al., 2020). Rayleigh's test for non-uniformity was run using *CircStats* (Lund & Agostinelli, 2012). Analysis scripts can be found at the following Open Science Framework repository: https://tinyurl.com/turbidus.

Behavioural analysis

Performance on both the baseline and delayed tasks were quantified using d-prime (Lockhart & Murdock, 1970; Wixted, 2014). d-prime is a measure of discriminability and is defined as the difference between the z-transformed scores of hit rate (HR) and false alarm rate (FA; i.e., d-prime = z[HR] – z[FA]). For example, calculating d-prime for bă verb position violations consisted of isolating bă verb position violation sentences and scoring the sentences based on the criteria described in Table 2. Following this, a formula of z(HR(bă grammatical) – z(FA(bă ungrammatical)) was applied, and this was repeated analogously for each sentence type. d-prime calculations for the baseline testing session were added into the behavioural linear mixed-effects model for comparison to delayed scores. Baseline scores were also added into subsequent sleep neurophysiology models to control for baseline performance when predicting delayed memory outcomes. Positive d-prime scores indicate good memory performance, whereas negative scores indicate poor memory performance. d-prime scores of 0 reflect chance performance.

Table 2. Description of How Responses Were Scored to Calculate D-Prime for the Delayed Testing Phase for Measurement of Memory Performance.

Scoring	Description
Hit	A grammatical sentence is correctly identified as grammatical.
Miss	A grammatical sentence is incorrectly identified as ungrammatical.
Correct rejection	An ungrammatical sentence is correctly identified as ungrammatical.
False alarm	An ungrammatical sentence is incorrectly identified as grammatical.

2.4.1 Sleep EEG analysis

Sleep EEG was pre-processed according to the specifications detailed in (Cross et al., 2021). Briefly, sleep EEG was scored according to standardised criteria (Berry et al., 2012) by two sleep technicians using Compumedics Profusion 3 software (Melbourne, Australia). A high-pass filter of 0.3 Hz and a low-pass filter of 35 Hz were applied for viewing. For the analysis, the EEG was filtered from 0.1 – 40 Hz and re-referenced to linked mastoids. Artifact rejection was performed automatically, in which a covariance-based artifact rejection method was used with hypnograms (Barachant, 2015; Barthélemy et al., 2019). Additionally, the EEG was down-sampled from 1000 Hz to 100 Hz to reduce computational processing time.

Phase-amplitude coupling (PAC) events were detected using published algorithms (Dvorak & Fenton, 2014; Helfrich et al., 2019; Staresina et al., 2015) via the YASA toolbox implemented in MNE Python (Vallat, 2020). An event-locked method was utilized, in which the SOs were detected initially, and spindle events that occur within the detected SOs were subsequently identified. The PAC strength between SOs and spindles was calculated using the Mean Vector Length (MVL) method (Canolty et al., 2006). MVL is calculated by combining the amplitude of the frequency for amplitude (i.e. spindle) with the phase of the frequency for phase (i.e. SO), in which the combined signals become complex vectors (Canolty et al., 2006; Hülsemann et al., 2019; Munia & Aviyente, 2019). The average length of these vectors can be delineated, whereby the vector length represents the magnitude (or strength) of the coupling event (Hülsemann et al., 2019).

For the REM theta analysis, power spectral density (PSD) estimates were calculated on consecutive 30s epochs with a 4-second sliding window. Intervals were tapered by a single Hanning window before applying a fast Fourier transformation that resulted in interval power spectra with a frequency resolution of 0.25 Hz. Power spectra were then averaged across all blocks (Welch’s method) and normalised by the effective noise bandwidth to obtain PSD estimates for relative theta power (4 – 8 Hz) during REM epochs for each channel.

2.4.2 Individual alpha frequency calculation

Individual alpha frequency (IAF) estimates for each subject were calculated from eyes-closed resting-state EEG recordings according to the method detailed by

Corcoran et al. (2018), via the *philistine* package (Alday, 2019). Resting-state recordings were taken at the beginning of the learning task and after the judgment task for 2 minutes (eyes open and eyes closed). Estimates were taken using the peak alpha frequency (PAF) method, in which the most prominent peak in the alpha bandwidth was delineated. The PAF for each participant was estimated from occipital and parietal channels (P3/P4/P7/P8/Pz/O1/O1/Oz) as this is where the alpha rhythm is most prominent during resting-state eyes closed periods (Babu Henry Samuel et al., 2018; Capotosto et al., 2017). For a detailed description of the IAF estimation procedure, please see Corcoran et al. (2018).

2.4.3 Statistical analysis

Data were analysed using linear mixed-effects models via the *lme4* package (Bates et al., 2015). For all models, Participant ID was specified as a random effect on the intercept (Brown, 2020) and significance of effects were examined using Type II Wald tests from the *car* package (Fox & Weisberg, 2018).

Model predictors (fixed effects) included Condition (sleep, wake), Coverb (bǎ, bèi), Violation Type (noun phrase order, verb position), Session (baseline, delayed), PAC events (quantified as MVL), IAF, and Baseline d-prime scores. d-prime scores from the delayed testing session were specified as the outcome variable. Categorical variables were sum-to-zero contrast coded, with coefficients reflecting deviation from the grand mean (Schad et al., 2020). The first model was run exploring the effect of Condition (sleep vs. wake), Sentence Type (coverb and violation type), Session (baseline, delayed), and IAF on memory performance. A second model was run to investigate the effect of PAC, sentence type, and IAF on memory performance to explore neurophysiological factors in detail.

Two additional exploratory models were run to investigate the role of REM sleep and associated theta power on memory performance. Predictors of the initial model included IAF, Coverb, Violation Type, Baseline d-prime scores, REM Theta power (scaled) and topographical components, saggitality (anterior, central, posterior) and laterality (left, midline, right), to explore oscillatory influences during REM on delayed d-prime scores. An additional model was run with predictors of IAF, Coverb, Violation Type, Baseline d-prime Scores and Percentage of Time in REM Sleep (scaled), to investigate how REM sleep influences delayed d-prime scores.

3 RESULTS

3.1 Descriptive Statistics

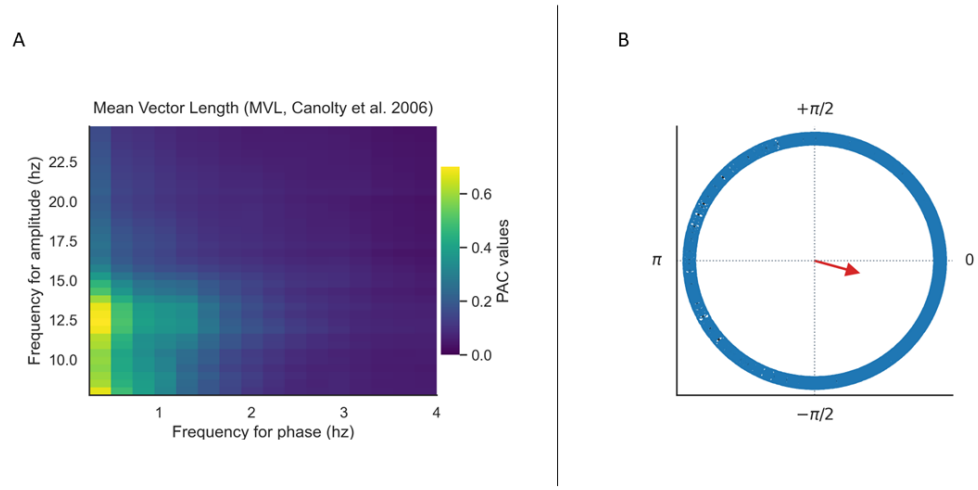
Overall, the average d-prime score across conditions was .60 (*SD* = .85) at the baseline testing session and .87 (*SD* = 1.40) at the delayed testing session (refer to Table 3 for d-prime scores per sentence type). Sleep variables including total sleep time, sleep onset latency, wake after sleep onset, and the total amount of time spent in each sleep stage are reported in Table 4, while Figure 4 shows a comodulogram and circular histogram from a single participant to illustrate the estimated PAC metrics.

Table 3. Mean D-Prime Scores (and Standard Deviations) for Baseline and Delayed Testing Sessions in the Sleep and Wake Groups for Each Sentence Type.

Violation Type	**Sleep**		**Wake**	
	Baseline	Delayed	Baseline	Delayed
Bǎ				
Noun Order	.26 (.55)	.40 (1.10)	.16 (.52)	.15 (.86)
Verb Position	.86 (.78)	1.37 (1.22)	1.40 (.91)	1.20 (1.43)
Bèi				
Noun Order	.29 (.66)	.49 (1.15)	-.01 (.68)	.07 (1.03)
Verb Position	.98 (1.04)	1.25 (1.77)	1.09 (.09)	1.2 (1.54)

Note: Standard deviation is in parentheses.

Figure 3. Examples of Phase-Amplitude Coupling Metrics from a Single Participant at Channel Cz for Visualisation Purposes



Note: A. Comodulogram illustrating the phase-amplitude coupling between the SO and the spindle. Here, the warmer colours (i.e., yellow) depicts where the coupling is strongest. As shown, this is occurring at approximately 0.5 Hz for the frequency for phase (the SO, x-axis) and approximately 12.5 Hz for the frequency for amplitude (the spindle, y-axis). **B.** Circular histogram of the preferred phase of SO to maximal spindle amplitude. Here, each instance of phase-amplitude coupling is instantiated along a circular distribution, allowing the ability to see the most common angle of the SO phase whenever the spindle amplitude is maximal (between -π/2 and 0, closer to 0).

Table 4. Descriptive Statistics (Means, Standard Deviations, and Ranges) for Sleep Parameters Measured During the 8-Hour Sleep Opportunity Between Baseline and Delayed Testing.

Sleep Stage	Mean Minutes (SD)	% of TST (SD)
N1	38.06 (29.93)	10.05 (8.34)
N2	196.29 (47.01)	49.52 (10.52)
SWS	104.24 (42.93)	25.85 (9.75)
REM	61.29 (40.01)	14.58 (8.70)
Sleep Parameter	**Mean Minutes (SD)**	**Range**
TST	399.88 (68.06)	203.5 – 472.5
SOL	15.24 (12.42)	1 – 42.5
WASO	52.65 (56.47)	0 - 225
EEG Parameter	**Mean (SD)**	
Mean Vector Length (MVL)	.23 (.01)	.21 - .27
REM Theta Power	.20 (.04)	.02 - .33

Note: SD = standard deviation; TST = total sleep time; SOL = sleep onset latency; WASO = wake after sleep onset; N1 = stage 1; N2 = stage 2; SWS = slow wave sleep; REM = rapid eye movement sleep; MVL = PAC metric used to quantify the strength of coupling between SOs and spindles.

3.2 Behavioural Analysis

The results reported in the following summarise the effects most pertinent to the current behavioural hypotheses, drawing on mixed model output summaries (for *β* values) and Type II Wald Chi-square test for chi-square and *p* values. Full model and Wald test summaries can be found in the supplementary material.

Mixed model analyses revealed a significant interaction between Condition, IAF and Violation Type predicting d-prime at delayed testing, as shown in Figure 4A (refer to Table 5 for statistic values of significant interactions). Notably, both the sleep and wake conditions showed a similar level of performance for noun order violations. In contrast, for verb positioning violations, the wake condition showed a negative relationship between IAF and post-wake memory performance, such that as

IAF increased, memory performance decreased. For the sleep condition, no relationship was observed between IAF and post-sleep memory performance. These results suggest IAF had a greater effect on delayed memory outcome for those in the wake condition, compared to those who slept, and this effect was greatest for the verb positioning rule.

Figure 4A illustrates that IAF differentially influenced memory performance at delayed testing depending both on condition and sentence type. Further, sleep influenced memory performance, thus encouraging further examination of the effects of specific sleep physiology (i.e., PAC strength between SOs and spindles) on memory outcomes, which we report below.

Table 5. Statistical Values for Significant Effects Within the Behavioural Model Examined via Type II Wald Chi-Square Tests

Parameters	χ^2	***df***	***β***	***p***
IAF	4.90	1	-.33	.027
Violation Type	95.00	1	-1.47	<.001
Condition x Session	4.51	1	-.12	.034
Session x IAF	11.08	1	.17	<.001
Condition x Violation Type x IAF	3.89	1	0.10	.048

Note: χ^2 = chi-square ratio, *df* = degrees of freedom, *β* = beta value, *p* = statistical significance.

3.3 Sleep Analysis

The results reported in the following summarise the effects most pertinent to the current hypotheses related to SWS neurophysiology, drawing on mixed model output summaries (for β values) and Type II Wald Chi-square tests for *p* values. Full model and Wald test summaries can be found in the supplementary material.

Mixed-effects modelling showed a significant interaction between PAC, Coverb and Violation Type, suggesting that coupling strength modulated performance at delayed testing, modulated by Coverb and Violation Type (refer to Table 6 for statistical values). As shown in Figure 4B, PAC did not influence performance for noun order violations of either coverb. However, for verb position violations, as coupling strength increased, differences in performance can be seen depending on

coverb. Specifically, as coupling strength increased, performance for Undergoer-first constructions decreased and performance for Actor-first constructions increased.

Significant three-way interactions were also observed for IAF x Coverb x Violation Type, IAF x Coverb x Baseline d', and IAF x Violation Type x Baseline d', indicating that IAF influences post-sleep memory performance, as modulated by grammatical rule type and pre-sleep performance.

Table 6. Statistical Values for Significant Interaction Effects Within Neurophysiological Model Examined via Type II Wald Chi-Square Tests

Parameters	χ^2	***df***	***β***	***p***
Violation Type	5.83	1	-2.50	.016
Baseline d'	37.30	1	-1.70	<.001
PAC x Coverb	9.99	1	-.30	.001
IAF x Coverb	13.16	1	.46	<.001
IAF x Violation Type	6.71	1	.25	.009
Coverb x Violation Type	7.60	1	2.00	.006
IAF x Baseline d'	10.60	1	.27	.001
PAC x Coverb x Type	5.91	1	1.30	.015
IAF x Coverb x Type	10.83	1	-.23	<.001
IAF x Coverb x Baseline d'	9.42	1	-.57	.002
IAF x Violation Type x Baseline d'	4.018	1	-.28	.045

Note: χ^2 = chi-square ratio, *df* = degrees of freedom, *β* = beta value, *p* = statistical significance.

3.4 Exploratory Analysis

The results reported in the following summarise the effects most pertinent to exploratory investigation into REM sleep neurophysiology, drawing on mixed model output summaries (for β values) and Type II Wald Chi-square tests for *p* values. Full model and Wald test summaries can be found in the supplementary material. As literature suggests an effect of REM sleep on the consolidation of memory, two exploratory models were run, with an initial model to investigate the effect of theta power during REM and a subsequent model exploring the effect of percentage of time spent in REM on memory.

The initial mixed-model analysis revealed significant four-way REM Theta Power x IAF x Baseline d' x Saggitality interaction, as shown in Figure 4C (refer to Table 7 for statistical values). Here, the largest differences between IAF values can be seen for higher pre-sleep performance scores and most prominently at posterior regions. There is also a notable relationship between post-sleep performance and theta power during REM for high IAF individuals, such that as theta power increases, memory performance also increases. This pattern indicates both IAF and theta power modulate memory performance at delayed testing, and thus, rule extraction.

Table 7. Statistical Values for Significant Interaction Effects Within the Exploratory Model (REM Theta Power) Examined via Type II Wald Chi-Square Tests

Parameters	χ^2	***df***	***β***	***p***
Coverb	9.84	1	-2.40	.002
Violation Type	21.93	1	-1.80	<.001
Baseline d'	185.85	1	-4.30	<.001
REM Theta x Coverb	8.30	1	3.25	.004
IAF x Coverb	31.75	1	.26	<.001
IAF x Type	33.87	1	.16	<.001
Coverb x Type	53.21	1	.32	<.001
IAF x Baseline d'	110.88	1	.55	<.001
Coverb x Baseline d'	28.30	1	3.00	<.001
Violation Type x Baseline d'	4.53	1	1.80	.033
IAF x Coverb x Type	18.72	1	-.05	<.001
REM Theta x IAF x Baseline d'	9.36	1	.22	.002
IAF x Coverb x Baseline d'	22.10	1	-.36	<.001
IAF x Type x Baseline d'	7.55	1	-.17	.006
REM Theta x IAF x Coverb x Saggitality	7.73	1	.16, -.33	.021
REM Theta x IAF x Baseline d' x Saggitality	6.66	1	04, -.33	.036

Note: χ^2 = chi-square ratio, *df* = degrees of freedom, *β* = beta value, *p* = statistical significance.

Subsequent mixed-model analyses exploring percentage of time spent in REM sleep revealed a significant REM x Coverb x Type interaction (χ^2 (1) = 7.41, β = -.69, p = .006), with the resolved interaction being shown in Figure 4D (refer to Table 8 for statistical values). Interestingly, percentage of time spent in REM also shows no visible effect on noun order violations. However, for verb positioning violations, there

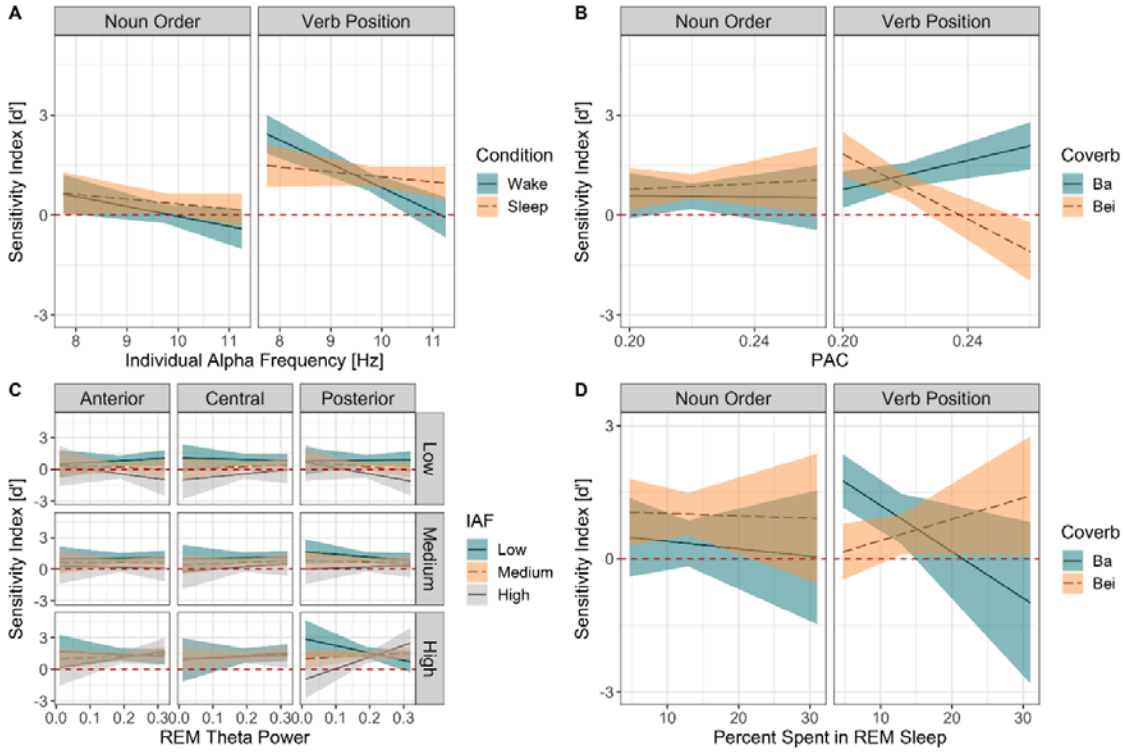
is a positive relationship between percentage of REM and post-sleep memory performance for Undergoer-first (bèi) constructions. In contrast, a negative relationship is seen for Actor-first (bǎ) constructions, indicating that processes during REM sleep are benefitting one rule type, whilst being detrimental for another.

Table 8. Statistical Values for Significant Interaction Effects Within the Exploratory Model (Percentage of Time in REM) Examined via Type II Wald Chi-Square Tests

Parameters	χ^2	***df***	***β***	***p***
Violation Type	4.43	1	-1.20	.035
Baseline d’	38.20	1	2.00	<.001
IAF x Coverb	17.75	1	.73	<.001
Coverb x Type	8.08	1	3.01	.004
IAF x Baseline d’	5.45	1	-0.06	.020
IAF x Coverb x Type	12.57	1	-.32	<.001
REM x Coverb x Type	7.41	1	-.69	.006
REM x Coverb x Baseline d’	4.33	1	3.72	.037
IAF x Coverb x Baseline d’	10.66	1	-.86	.001

Note: χ^2 = chi-square ratio, *df* = degrees of freedom, *β* = beta value, *p* = statistical significance.

Figure 4. Plotted interactions from the behavioural model (A), sleep model (B), and exploratory models examining REM Theta Power (C) and percentage of time in REM sleep (D)



Note: All interactions are predicting performance scores at delayed testing (on the y-axis) quantified using d-prime (fitted model values). For all plots, the shaded areas of colour represent 83% confidence intervals and the red dashed line intercepting the y-axis at 0 represents chance performance (d' = 0). **(A)** Condition x IAF x Violation Type interaction. IAF values are depicted on the x-axis, beginning with lower IAF values. Additionally, plot is faceted by Violation Type on the top axis, split into 2 facets, with the left facet showing the relationship between PAC and delayed d-prime for noun order violations and the right facet showing this relationship for verb position violations **(B)** PAC x Coverb x Type interaction. PAC values are shown on the x-axis, from lower coupling values (left) to higher coupling values (right), with higher coupling values indicating better coupling strength between slow-oscillations (SOs) and spindles. Violation Type is shown on the top axis, split into 2 facets, with noun order violations on the left and verb positioning violations on the right. **(C)** REM Theta Power x IAF x Saggitality x Baseline d' interaction. REM Theta Power is shown on the x-axis, from lower power values (left) to higher power values (right), with higher power values reflecting higher power spectral density values. Saggitality is shown on the top axis, split into 3 facets, moving from anterior (left) to central (middle) and posterior (right), depicting topographical positioning. Performance scores at baseline testing are shown along the right axis, from lower values (top) to higher values (bottom), with higher values indicating better performance at baseline. **(D)** Percentage of REM x Coverb x Violation Type interaction. Percentage of time spent in REM sleep is shown along the x-axis, from lower values (left) to higher values (right), with higher values depicting higher percentage of time spent in REM. Violation Type is shown on the top axis, split into 2 facets, with noun order violations on the left and verb positioning violations on the right.

4 DISCUSSION

Slow oscillation-spindle coupling during SWS, and REM sleep have been independently linked to memory consolidation (Diekelmann & Born, 2010; Doppelmayr et al., 2005; Hutchison & Rathore, 2015; Klimesch, 1997, 1999; Klinzing et al., 2019; Latchoumane et al., 2017; Lewis & Durrant, 2011; Sopp et al., 2017). Here, we provide evidence for the interaction of these factors within a rule-based context in language processing. Behaviourally, results indicate a negative relationship between individual alpha frequency (IAF) and post-wake memory performance in the wake condition, such that as IAF increased, memory performance decreased for verb positioning rules. Regarding sleep neurophysiology, results indicate an interaction between phase-amplitude coupling (PAC) and sentence type (violation type and coverb). Specifically, higher PAC was associated with increased acceptability judgement performance for Actor-first (bǎ) sentences and decreased performance for Undergoer-first (bèi) sentences within verb position violations. Our exploratory analyses of post-sleep memory performance further revealed a significant interaction between REM theta power, IAF, saggitality (anterior, midline and posterior regions) and pre-sleep performance. For high pre-sleep performers with a high IAF, as REM theta power increased, so did post-sleep memory performance, with this effect being most prominent in posterior regions. Additionally, proportion of REM sleep interacted with coverb and violation type, such that greater time spent in REM sleep was associated with decreased post-sleep performance on Actor-first constructions and increased performance for Undergoer-first constructions. Overall, results indicate that sleep neurophysiology and IAF influence consolidation and subsequent performance at both behavioural and neural levels and that patterns of memory performance differ across distinct rule types.

4.1 The influence of IAF and sleep on memory performance at the behavioural level

Our results partially supported the hypothesis (H^1) that behavioural performance should be enhanced post-sleep relative to post-wake. Specifically, in the post-wake condition, as IAF increased, memory performance decreased. As such, this result divergences from previous work showing that high resting alpha is associated with better performance on an array of tasks, including those assessing

memory (Doppelmayr et al., 2005; Klimesch, 1997, 1999). However, more recent results (e.g., Ociepka et al., 2022) in which high IAF was not associated with greater intelligence, indicate that perhaps the association between high IAF and greater performance on a variety of tasks is not as explicit as once believed. In fact, in another reanalysis of Cross et al., (2021) examining a different linguistic manipulation, Nalaye et al., (2022) found a similar negative relationship between IAF and performance on the Mini Pinyin grammaticality judgement task, with lower-IAF individuals performing better. In combination with our results, it appears that high IAF is not beneficial in every context. Interestingly, Ociepka et al., (2022) found that IAF was positively correlated with processing speed which is consistent with existing literature linking IAF to the speed and amount of information that obtained during each processing cycle (Samaha & Postle, 2015; Surwillo, 1963). Specifically, Samaha and Postle (2015) suggest that a higher IAF indicates faster cycles of information processing and a finer temporal resolution of incoming sensory information. Thus, in the current study, speed of information processing may have affected hippocampal-neocortical information transfer that occurs during sleep-dependent consolidation by influencing the speed and amount of information within each information processing cycle. This result suggests that higher-IAF individuals perform worse when unable to access offline, sleep-dependent memory consolidation.

Previous literature describes memory consolidation as a process of repeatedly reactivating memory traces to transfer information from the hippocampus to the neocortex (Yassa & Reagh, 2013). Low IAF (slower cycles) may thus be beneficial during wake (Howard et al., 2017), helping to protect against interference effects, with low IAF individuals preserving the initially encoded traces with less interference than high IAF individuals in the wake group. Interference refers to a phenomenon where new information, or in this case, new memory traces, interferes with the recall of previous information or stored memories (Baddeley & Dale, 1966; Bunting et al., 2004; Logie et al., 1990; May et al., 1999; Radvansky & Copeland, 2006). However, for those with high IAF and thus, faster cycles of information processing, this may have led to higher levels of interference and a detrimental effect on post-wake memory performance. Interestingly, those in the sleep condition appear to perform at a similar level regardless of IAF. This effect could be related to sleep

neurophysiology, such that the mechanisms of sleep-dependent consolidation are modulating post-sleep memory performance over and above IAF.

Our proposed role of IAF in information processing may also help to explain why testing session (baseline vs. delayed) is critical when observing effects of IAF. It may be that the temporal receptive windows associated with IAF influence both the process of consolidation as well as initial encoding (Khader et al., 2010; Klimesch et al., 1996; Klimesch et al., 1997). If memory consolidation occurs via repeated reactivation of encoded memory traces, the process of offline consolidation can only be as strong as the initial memory traces (Collette et al., 2014; Klinzing et al., 2019; Marshall & Born, 2007; Wagner & Born, 2008; Yassa & Reagh, 2013). As such, the rules that are being extracted rely on the quality of the traces related to such rules. However, this analysis did not specifically look at the process of encoding which limits the understanding of what may be occurring during this time (for an in depth analysis of the encoding phase, see Cross et al., 2022). Despite this, analyses reported here provide further evidence for an effect of IAF on memory consolidation, consistent with previous literature (Doppelmayr et al., 2005; Klimesch, 1997, 1999; Klimesch et al., 1994, 1999; Richard Clark et al., 2004; Vogt et al., 1998).

4.2 Neural mechanisms underlying sleep-based consolidation of rules

Both the behavioural and sleep analyses provide evidence for H^2, which hypothesised that IAF and PAC would individually predict post-sleep memory performance. Both models indicated that IAF influenced post-sleep memory performance. Further, in the sleep model, results showed an interaction between PAC, coverb, and violation type, such that as PAC increased, post-sleep memory performance for Actor-first sentences increased, while it decreased for Undergoer-first constructions. Interestingly, this only occurred for verb position violations.

Slow oscillation-spindle PAC is suggested to reflect hippocampal-neocortical information transfer during NREM sleep (Diekelmann & Born, 2010; Klinzing et al., 2019; Lewis & Durrant, 2011), and as such, increased PAC associated with post-sleep performance suggests NREM sleep-based consolidation processes have occurred for rule-based information. This result is broadly consistent with previous literature linking NREM sleep neurophysiology to memory consolidation (Diekelmann

et al., 2010; Diekelmann & Born, 2010; Lewis & Durrant, 2011; Nieuwenhuis et al., 2013; Stickgold & Walker, 2013; Tononi & Cirelli, 2006). In particular, literature suggests that sleep facilitates rule extraction for both linguistic rules and non-linguistic rules (e.g., statistical) when looking at total SWS duration (Batterink et al., 2014; Djonlagic et al., 2009; Durrant et al., 2011; Nieuwenhuis et al., 2013). However, our results link PAC mechanisms (e.g., SO-spindle coupling), and the associated hippocampal-neocortical information transfer believed to occur within these mechanisms, to memory performance in a rule-based context.

Interestingly, PAC only influenced one rule type (verb position) and rule complexity may play a role in this pattern. Performance on noun order violations overall was poor, suggesting this rule type was highly complex and difficult to learn. As such, if these violations were initially encoded poorly, the role for PAC would be limited as the encoded memory traces were too weak to be consolidated into long-term memory (Collette et al., 2014; Klinzing et al., 2019). Literature suggests certain factors during encoding can affect subsequent consolidation of memory such as information saliency (Klinzing et al., 2019) or oscillatory activity during encoding (Cohen et al., 2015). These factors during encoding may have decreased the quality of memory traces for noun order violations, leading to less requirement for PAC. However, this interpretation is speculative and requires further examination of the encoding phase (see Cross et al., 2022) to permit better understanding of how encoding processes affects subsequent rule extraction.

SO-spindle PAC demonstrated an effect on verb position violations. Specifically, for Actor-first (bǎ) sentences, increased PAC moderately improved memory performance. This may be due to native English speakers being most familiar with sentences in which the Actor occurs before the Undergoer (MacWhinney et al., 1984), which is also the case for bǎ sentences. Better regularity extraction may have been influenced by such familiarity, leading to an effect of PAC for Actor-first sentences. Interestingly, PAC negatively affected performance for Undergoer-first (bèi) sentences. This may have been due to the non-schema conforming nature of these constructions, in which they differ considerably from native English. According to the iOTA model of sleep-based memory consolidation, non-schema conforming information is often downscaled to preferentially encode

information analogous to existing knowledge (Lewis et al., 2018; Lewis & Durrant, 2011). Additionally, theories of memory consolidation, such as Complementary Learning Systems theory (McClelland et al., 1995), suggest that information similar to that of previous knowledge tends to be encoded and consolidated easier (Tse et al., 2011) and quicker (Tse et al., 2007), due to associative schemas. As such, the associative schema here is likely the grammatical elements of English, allowing the similar information (Actor-first sentences) to be more easily consolidated. Thus, this may explain how NREM mechanisms in our findings had the greatest effect on information closest to existing knowledge (i.e., Actor-first constructions) and had little to no effect on information dissimilar to existing knowledge (i.e., Undergoer-first constrictions).

Alternatively, literature exploring thalamo-cortical sleep spindles and their coupling to hippocampal ripples has found that spindle-ripple coupling promotes memory replay over and above SO-spindle coupling (Latchoumane et al., 2017). Specifically, Latchoumane et al. (2017) indicates that thalamic spindles aid in regulation of hippocampal ripple timing. From this, it is suggested that spindle-ripple coupling is the primary mechanism driving repeated reactivation and thus, memory consolidation. It should be noted that this perspective still implicates SO-spindle coupling for the effective hippocampal-neocortical transmission. Thus, spindle-ripple coupling may drive memory reactivation, while SO-spindle coupling drives memory transmission (Klinzing et al., 2019). This may explain why the effect of SO-spindle coupling was not as large in the current analyses, indicating the need for further exploration of spindle-ripple coupling (Klinzing et al., 2019; Latchoumane et al., 2017).

Finally, H^3, which assumed that IAF and PAC would interact to predict memory performance, was not supported as the results of the sleep model did not show any significant interactions between IAF and PAC. This suggests that IAF and PAC predict post-sleep memory performance independently, implying that the underlying neural mechanisms that are influencing memory performance may be distinct. As mentioned above, exploring broader oscillatory activity (e.g. spindle ripple coupling Bakker et al., 2015; Latchoumane et al., 2017; Prat et al., 2016; Weiss &

Rappelsberger, 2000) will build a better understanding of how neural mechanisms may interact or independently affect rule extraction.

4.3 The role of REM sleep in memory consolidation and rule extraction

An exploratory analysis was included to investigate the effect of REM sleep neurophysiology on rule extraction. Our initial model exploring the effect of REM theta power revealed a significant interaction between REM theta power, IAF, saggitality and pre-sleep memory performance, such theta activity at posterior regions modulated differences in performance relative to IAF and pre-sleep performance. Specifically, memory performance increased as REM theta power increased for higher-IAF individuals who performed well at baseline testing.

Previous literature primarily explored the role of theta activity in emotional memory consolidation (Boyce et al., 2016; Cross et al., 2020a; Hutchison & Rathore, 2015; Kim et al., 2020; Nishida et al., 2009; Schäfer et al., 2020), however the role of REM theta activity within non-emotional memory contexts is still largely unexplored. Our results indicate differences in post-sleep memory performance relative to REM theta activity in posterior regions, contrasting with existing literature linking REM theta with central regions (Fogel et al., 2007) and anterior regions (Simor et al., 2016). Posterior theta has been described as the human correlate of the ponto-geniculo-occipital (PGO) wave (Frauscher et al (2018), which has been previously attributed to memory consolidation and neuronal plasticity in experimental animal research (Datta, 2000; Datta et al., 2004). If so, the posterior theta activity reported here may reflect changes in neuronal plasticity (Grosmark et al., 2012; Hobson & Friston, 2012) and the consolidation of rule-based information; however, this interpretation is tentative and requires further investigation. Additionally, the relationship between REM theta and post-sleep memory outcomes appears to differ depending on IAF. Our results revealed a positive relationship between REM theta and post-sleep memory for higher-IAF and a negative relationship for lower-IAF individuals. Cross et al. (2020a) also found a complex relationship between IAF and theta power during REM sleep. Higher IAF may have allowed for increased reactivations of memory during sleep, or allowed the brain to preferentially encode salient information (Cross et al., 2020a; Heib et al., 2015).

When looking more broadly at the proportion of time spent in REM sleep, results revealed an interaction between REM sleep percentage, coverb and violation type. Specifically, higher proportions of REM sleep positively affected performance for Undergoer-first constructions (bèi) and led to decreased performance for Actor-first constructions (bǎ), contrasting the pattern seen within NREM sleep mechanisms. This result partially contrasts the results of Matorina & Poppenk, (2019), in which it was discovered that higher proportions of REM sleep led to a decrease in performance on a statistical learning task. Matorina & Poppenk, (2019) proposed that REM sleep may in fact be working against processes of extracting regularities, as it is more useful for a process called schema reconstruction, which disbands and reintegrates current and existing information into abstract schemas, allowing for more creativity and abstract thought (Landmann et al., 2014). Further evidence for this comes from the iOTA model, in which REM sleep is proposed as the ideal setting for forming novel and abstract representations. Thus, NREM is likely most beneficial for associative memory processes, while REM sleep may facilitate the construction of abstract schemas (Lewis et al., 2018). The findings presented here provide support for this hypothesis, as demonstrated by the favourable effect of NREM sleep on Actor-first constructions and REM sleep for Undergoer-first constructions. Overall, despite tentative interpretation, our results provide preliminary evidence for REM theta and IAF in rule-based contexts and demonstrate support for REM in non-schema conforming memory consolidation, providing a foundation for future research to further identify the underlying mechanisms.

4.4 Conclusions

Here, we presented a novel exploration into rule extraction and consolidation, demonstrating differential effects of individual processing capabilities. Contrary to previous understanding of individual electrophysiological differences, we indicate a beneficial influence of lower IAF on memory within a rule-based context, proposing that higher-IAF and lower-IAF individuals draw on different information processing strategies as opposed to simply showing differing performance outcomes. Further, we demonstrated differential effects of SO-spindle coupling for specific grammatical elements, favouring the consolidation of those analogous to existing grammatical knowledge. Additionally, we demonstrated support for the role of REM sleep in consolidating non-schema conforming information, through creativity and abstract

schema reconstruction. Finally, we provided preliminary evidence for a relationship between REM sleep and IAF within rule extraction, a previously limited area of research. Future research should focus on further delineating the relationship between REM theta activity and individual processing capabilities in rule-based consolidation, which would further our understanding of the complex relationship between individual differences, sleep neurophysiology and memory consolidation.

5 REFERENCES

Ackermann, S., & Rasch, B. (2014). Differential effects of non-REM and REM sleep on memory consolidation? *Current Neurology and Neuroscience Reports*, *14*(2), 430.

Alday, P. M. (2019). *Philistine documentation*. https://philistine.readthedocs.io/_/downloads/en/latest/pdf/

Babu Henry Samuel, I., Wang, C., Hu, Z., & Ding, M. (2018). The frequency of alpha oscillations: Task-dependent modulation and its functional significance. *NeuroImage*, *183*, 897–906. https://doi.org/10.1016/j.neuroimage.2018.08.063

Baddeley, A. D., & Dale, H. (1966). The effect of semantic similarity on retroactive interference in long-and short-term memory. *Journal of Verbal Learning and Verbal Behavior*, *5*(5), 417–420.

Bakker, I., Takashima, A., van Hell, J. G., Janzen, G., & McQueen, J. M. (2015). Changes in Theta and Beta Oscillations as Signatures of Novel Word Consolidation. *Journal of Cognitive Neuroscience*, *27*(7), 1286–1297. https://doi.org/10.1162/jocn_a_00801

Barachant, A. (2015). *PyRiemann: Biosignals classification with Riemannian Geometry—PyRiemann 0.2.6 documentation*. https://pyriemann.readthedocs.io/en/latest/index.html

Barthélemy, Q., Mayaud, L., Ojeda, D., & Congedo, M. (2019). The Riemannian Potato Field: A Tool for Online Signal Quality Index of EEG. *IEEE Transactions on Neural Systems and Rehabilitation Engineering*, *27*(2), 244–255. https://doi.org/10.1109/TNSRE.2019.2893113

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/doi:10.18637/jss.v067.i01

Batterink, L. J., Oudiette, D., Reber, P. J., & Paller, K. A. (2014). Sleep facilitates learning a new linguistic rule. *Neuropsychologia*, *65*, 169–179.

Bergmann, T. O., & Born, J. (2018). Phase-Amplitude Coupling: A General Mechanism for Memory Processing and Synaptic Plasticity? *Neuron*, *97*(1), 10–13. https://doi.org/10.1016/j.neuron.2017.12.023

Berry, R. B., Budhiraja, R., Gottlieb, D. J., Gozal, D., Iber, C., Kapur, V. K., Marcus, C. L., Mehra, R., Parthasarathy, S., & Quan, S. F. (2012). Rules for scoring respiratory events in sleep: Update of the 2007 AASM manual for the scoring of sleep and associated events. *Journal of Clinical Sleep Medicine*, *8*(05), 597–619.

Bornkessel, I. D., Fiebach, C. J., Friederici, A. D., & Schlesewsky, M. (2004). "Capacity" reconsidered: Interindividual differences in language comprehension and individual alpha frequency. *Experimental Psychology*, *51*(4), 279–289.

Boyce, R., Glasgow, S. D., Williams, S., & Adamantidis, A. (2016). Causal evidence for the role of REM sleep theta rhythm in contextual memory consolidation. *Science (New York, N.Y.)*, *352*(6287), 812–816. https://doi.org/10.1126/science.aad5252

Brown, V. A. (2020). *An approachable introduction to linear mixed effects modeling with implementation in R*. https://doi.org/10.31234/osf.io/9vghm

Bunting, M. F., Conway, A. R. A., & Heitz, R. P. (2004). Individual differences in the fan effect and working memory capacity. *Journal of Memory and Language*, *51*(4), 604–622. https://doi.org/10.1016/j.jml.2004.07.007

Canolty, R. T., Edwards, E., Dalal, S. S., Soltani, M., Nagarajan, S. S., Kirsch, H. E., Berger, M. S., Barbaro, N. M., & Knight, R. T. (2006). High Gamma Power Is Phase-Locked to Theta Oscillations in Human Neocortex. *Science*, *313*(5793), 1626–1628. https://doi.org/10.1126/science.1128115

Canolty, R. T., & Knight, R. T. (2010). The functional role of cross-frequency coupling. *Trends in Cognitive Sciences*, *14*(11), 506–515.

Capotosto, P., Baldassarre, A., Sestieri, C., Spadone, S., Romani, G. L., & Corbetta, M. (2017). Task and Regions Specific Top-Down Modulation of Alpha Rhythms in Parietal Cortex. *Cerebral Cortex*, *27*(10), 4815–4822. https://doi.org/10.1093/cercor/bhw278

Chatburn, A., Lushington, K., & Kohler, M. J. (2021). Consolidation and generalisation across sleep depend on individual EEG factors and sleep spindle density. *Neurobiology of Learning and Memory*, *179*, 107384. https://doi.org/10.1016/j.nlm.2021.107384

Cohen, N., Pell, L., Edelson, M. G., Ben-Yakov, A., Pine, A., & Dudai, Y. (2015). Peri-encoding predictors of memory encoding and consolidation. *Neuroscience & Biobehavioral Reviews*, *50*, 128–142. https://doi.org/10.1016/j.neubiorev.2014.11.002

Collette, F., Grandjean, J., Lorant, C., & Bastin, C. (2014). The Role of Memory Traces Quality in Directed Forgetting: A Comparison of Young and Older Participants. *Psychologica Belgica*, *54*(4), 310–327. https://doi.org/10.5334/pb.au

Cross, Z. R., Corcoran, A. W., Schlesewsky, M., Kohler, M. J., & Bornkessel-Schlesewsky, I. (2022). Oscillatory and Aperiodic Neural Activity Jointly Predict Language Learning. *Journal of Cognitive Neuroscience*, 1–20. https://doi.org/10.1162/jocn_a_01878

Cross, Z. R., Helfrich, R. F., Corcoran, A. W., Kohler, M. J., Coussens, S., Zou-Williams, L., Schlesewsky, M., Gaskell, M. G., Knight, R. T., & Bornkessel-Schlesewsky, I. (2021). *Spindle-slow oscillation coupling during sleep predicts sequence-based language learning* (p. 2020.02.13.948539). bioRxiv. https://doi.org/10.1101/2020.02.13.948539

Cross, Z. R., Santamaria, A., Corcoran, A. W., Chatburn, A., Alday, P. M., Coussens, S., & Kohler, M. J. (2020a). Individual alpha frequency modulates sleep-related emotional memory consolidation. *Neuropsychologia*, *148*, 107660.

Cross, Z. R., Zou-Williams, L., Wilkinson, E., Schlesewsky, M., & Bornkessel-Schlesewsky, I. (2020b). *Mini Pinyin: A modified miniature language for studying language learning and incremental sentence processing* [Preprint]. PsyArXiv. https://doi.org/10.31234/osf.io/b9erz

Datta, S. (2000). Avoidance Task Training Potentiates Phasic Pontine-Wave Density in the Rat: A Mechanism for Sleep-Dependent Plasticity. *Journal of Neuroscience*, *20*(22), 8607–8613. https://doi.org/10.1523/JNEUROSCI.20-22-08607.2000

Datta, S., Mavanji, V., Ulloor, J., & Patterson, E. H. (2004). Activation of Phasic Pontine-Wave Generator Prevents Rapid Eye Movement Sleep Deprivation-Induced Learning Impairment in the Rat: A Mechanism for Sleep-Dependent Plasticity. *Journal of Neuroscience*, *24*(6), 1416–1427. https://doi.org/10.1523/JNEUROSCI.4111-03.2004

Diekelmann, S., & Born, J. (2010). The memory function of sleep. *Nature Reviews Neuroscience*, *11*(2), 114–126.

Diekelmann, S., Born, J., & Wagner, U. (2010). Sleep enhances false memories depending on general memory performance. *Behavioural Brain Research*, *208*(2), 425–429. https://doi.org/10.1016/j.bbr.2009.12.021

Djonlagic, I., Rosenfeld, A., Shohamy, D., Myers, C., Gluck, M., & Stickgold, R. (2009). Sleep enhances category learning. *Learning & Memory*, *16*(12), 751–755.

Doppelmayr, M., Klimesch, W., Hödlmoser, K., Sauseng, P., & Gruber, W. (2005). Intelligence related upper alpha desynchronization in a semantic memory task. *Brain Research Bulletin*, *66*(2), 171–177.

Durrant, S. J., Cairney, S. A., & Lewis, P. A. (2013). Overnight consolidation aids the transfer of statistical knowledge from the medial temporal lobe to the striatum. *Cerebral Cortex*, *23*(10), 2467–2478.

Durrant, S. J., Taylor, C., Cairney, S., & Lewis, P. A. (2011). Sleep-dependent consolidation of statistical learning. *Neuropsychologia*, *49*(5), 1322–1331.

Dvorak, D., & Fenton, A. A. (2014). Toward a proper estimation of phase–amplitude coupling in neural oscillations. *Journal of Neuroscience Methods*, *225*, 42–56.

Fenn, K. M., & Hambrick, D. Z. (2012). Individual differences in working memory capacity predict sleep-dependent memory consolidation. *Journal of Experimental Psychology. General*, *141*(3), 404–410. https://doi.org/10.1037/a0025268

Fogel, S. M., Smith, C. T., & Cote, K. A. (2007). Dissociable learning-dependent changes in REM and non-REM sleep in declarative and procedural memory systems. *Behavioural Brain Research*, *180*(1), 48–61. https://doi.org/10.1016/j.bbr.2007.02.037

Fox, J., & Weisberg, S. (2018). *An R companion to applied regression*. Sage publications.

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*, 154.

Frank, M. C., & Gibson, E. (2011). Overcoming Memory Limitations in Rule Learning. *Language Learning and Development*, *7*(2), 130–148. https://doi.org/10.1080/15475441.2010.512522

Frauscher, B., Joshi, S., von Ellenrieder, N., Nguyen, D. K., Dubeau, F., & Gotman, J. (2018). Sharply contoured theta waves are the human correlate of ponto-geniculo-occipital waves in the primary visual cortex. *Clinical Neurophysiology*, *129*(8), 1526–1533. https://doi.org/10.1016/j.clinph.2018.04.605

Furman, A. J., Meeker, T. J., Rietschel, J. C., Yoo, S., Muthulingam, J., Prokhorenko, M., Keaser, M. L., Goodman, R. N., Mazaheri, A., & Seminowicz, D. A. (2018). Cerebral peak alpha frequency predicts individual differences in pain sensitivity. *NeuroImage*, *167*, 203–210. https://doi.org/10.1016/j.neuroimage.2017.11.042

García-Lázaro, H. G., Ramirez-Carmona, R., Lara-Romero, R., & Roldan-Valadez, E. (2012). Neuroanatomy of episodic and semantic memory in humans: A brief review of neuroimaging studies. *Neurology India*, *60*(6), 613–617. https://doi.org/10.4103/0028-3886.105196

Girardeau, G., & Zugaro, M. (2011). Hippocampal ripples and memory consolidation. *Current Opinion in Neurobiology*, *21*(3), 452–459. https://doi.org/10.1016/j.conb.2011.02.005

Gómez, R. L., Bootzin, R. R., & Nadel, L. (2006). Naps promote abstraction in language-learning infants. *Psychological Science*, *17*(8), 670–674. https://doi.org/10.1111/j.1467-9280.2006.01764.x

Grandy, T. H., Werkle-Bergner, M., Chicherio, C., Lövdén, M., Schmiedek, F., & Lindenberger, U. (2013). Individual alpha peak frequency is related to latent factors of general cognitive abilities. *NeuroImage*, *79*, 10–18. https://doi.org/10.1016/j.neuroimage.2013.04.059

Grosmark, A. D., Mizuseki, K., Pastalkova, E., Diba, K., & Buzsáki, G. (2012). REM Sleep Reorganizes Hippocampal Excitability. *Neuron*, *75*(6), 1001–1007. https://doi.org/10.1016/j.neuron.2012.08.015

Harrell Jr, F. E. (2019). Package 'hmisc.' *CRAN2018*, *2019*, 235–236.

Heib, D. P. J., Hoedlmoser, K., Anderer, P., Gruber, G., Zeitlhofer, J., & Schabus, M. (2015). Oscillatory Theta Activity during Memory Formation and Its Impact on Overnight Consolidation: A Missing Link? *Journal of Cognitive Neuroscience*, *27*(8), 1648–1658. https://doi.org/10.1162/jocn_a_00804

Helfrich, R. F., Lendner, J. D., Mander, B. A., Guillen, H., Paff, M., Mnatsakanyan, L., Vadera, S., Walker, M. P., Lin, J. J., & Knight, R. T. (2019). Bidirectional prefrontal-hippocampal dynamics organize information transfer during sleep in humans. *Nature Communications*, *10*(1), 1–16. https://doi.org/10.1038/s41467-019-11444-x

Helfrich, R. F., Mander, B. A., Jagust, W. J., Knight, R. T., & Walker, M. P. (2018). Old brains come uncoupled in sleep: Slow wave-spindle synchrony, brain atrophy, and forgetting. *Neuron*, *97*(1), 221-230. e4.

Hobson, J. A., & Friston, K. J. (2012). Waking and dreaming consciousness: Neurobiological and functional considerations. *Progress in Neurobiology*, *98*(1), 82–98. https://doi.org/10.1016/j.pneurobio.2012.05.003

Hope, R. M. (2013). *Rmisc: Ryan miscellaneous. R package version 1.5*. CRAN.

Howard, C. J., Arnold, C. P. A., & Belmonte, M. K. (2017). Slower resting alpha frequency is associated with superior localisation of moving targets. *Brain and Cognition*, *117*, 97–107. https://doi.org/10.1016/j.bandc.2017.06.008

Hülsemann, M. J., Naumann, E., & Rasch, B. (2019). Quantification of Phase-Amplitude Coupling in Neuronal Oscillations: Comparison of Phase-Locking Value, Mean Vector Length, Modulation Index, and Generalized-Linear-Modeling-Cross-Frequency-Coupling. *Frontiers in Neuroscience*, *13*. https://doi.org/10.3389/fnins.2019.00573

Humiston, G. B., Tucker, M. A., Summer, T., & Wamsley, E. J. (2019). Resting States and Memory Consolidation: A Preregistered Replication and Meta-Analysis. *Scientific Reports*, *9*(1), 19345. https://doi.org/10.1038/s41598-019-56033-6

Hutchison, I. C., & Rathore, S. (2015). The role of REM sleep theta activity in emotional memory. *Frontiers in Psychology*, *6*, 1439.

Jensen, O., Bonnefond, M., & VanRullen, R. (2012). An oscillatory mechanism for prioritizing salient unattended stimuli. *Trends in Cognitive Sciences*, *16*(4), 200–206.

Kassambara, A. (2020). Package 'ggpubr.' *R Package Version 0.1*, *6*.

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

Kim, S. Y., Kark, S. M., Daley, R. T., Alger, S. E., Rebouças, D., Kensinger, E. A., & Payne, J. D. (2020). Interactive effects of stress reactivity and rapid eye movement sleep theta activity on emotional memory formation. *Hippocampus*, *30*(8), 829–841.

Klimesch, W. (1997). EEG-alpha rhythms and memory processes. *International Journal of Psychophysiology*, *26*(1–3), 319–340.

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: A review and analysis. *Brain Research Reviews*, *29*(2–3), 169–195.

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Sciences*, *16*(12), 606–617.

Klimesch, W., Doppelmayr, M., Pachinger, T., & Ripper, B. (1997). Brain oscillations and human memory: EEG correlates in the upper alpha and theta band. *Neuroscience Letters*, *238*(1), 9–12. https://doi.org/10.1016/S0304-3940(97)00771-4

Klimesch, W., Doppelmayr, M., Schimke, H., & Pachinger, T. (1996). Alpha frequency, reaction time, and the speed of processing information. *Journal of Clinical Neurophysiology: Official Publication of the American Electroencephalographic Society*, *13*(6), 511–518. https://doi.org/10.1097/00004691-199611000-00006

Klimesch, W., Doppelmayr, M., Schwaiger, J., Auinger, P., & Winkler, T. (1999). Paradoxical'alpha synchronization in a memory task. *Cognitive Brain Research*, *7*(4), 493–501.

Klimesch, W., Schimke, H., Doppelmayr, M., Ripper, B., Schwaiger, J., & Pfurtscheller, G. (1996). Event-related desynchronization (ERD) and the Dm effect: Does alpha desynchronization during encoding predict later recall performance? *International Journal of Psychophysiology*, *24*(1), 47–60. https://doi.org/10.1016/S0167-8760(96)00054-2

Klimesch, W., Schimke, H., & Schwaiger, J. (1994). Episodic and semantic memory: An analysis in the EEG theta and alpha band. *Electroencephalography and Clinical Neurophysiology*, *91*(6), 428–441.

Klinzing, J. G., Niethard, N., & Born, J. (2019). Mechanisms of systems memory consolidation during sleep. *Nature Neuroscience*, *22*(10), 1598–1610. https://doi.org/10.1038/s41593-019-0467-3

Landmann, N., Kuhn, M., Piosczyk, H., Feige, B., Baglioni, C., Spiegelhalder, K., Frase, L., Riemann, D., Sterr, A., & Nissen, C. (2014). The reorganisation of memory during sleep. *Sleep Medicine Reviews*, *18*(6), 531–541. https://doi.org/10.1016/j.smrv.2014.03.005

Latchoumane, C.-F. V., Ngo, H.-V. V., Born, J., & Shin, H.-S. (2017). Thalamic Spindles Promote Memory Formation during Sleep through Triple Phase-Locking of Cortical, Thalamic, and Hippocampal Rhythms. *Neuron*, *95*(2), 424-435.e6. https://doi.org/10.1016/j.neuron.2017.06.025

Lewis, P. A., & Durrant, S. J. (2011). Overlapping memory replay during sleep builds cognitive schemata. *Trends in Cognitive Sciences*, *15*(8), 343–351. https://doi.org/10.1016/j.tics.2011.06.004

Lewis, P. A., Knoblich, G., & Poe, G. (2018). How Memory Replay in Sleep Boosts Creative Problem-Solving. *Trends in Cognitive Sciences*, *22*(6), 491–503. https://doi.org/10.1016/j.tics.2018.03.009

Lockhart, R. S., & Murdock, B. B. (1970). Memory and the theory of signal detection. *Psychological Bulletin*, *74*(2), 100.

Logie, R. H., Zucco, G. M., & Baddeley, A. D. (1990). Interference with visual short-term memory. *Acta Psychologica*, *75*(1), 55–74.

Lüdecke, D. (2018a). sjmisc: Data and variable transformation functions. *Journal of Open Source Software*, *3*(26), 754.

Lüdecke, D. (2018b). sjPlot: Data visualization for statistics in social science. *R Package Version*, *2*(1).

Lüdecke, D., Aust, F., Crawley, S., & Ben-Shachar, M. (2020). Package 'ggeffects.' *Create Tidy Data Frames of Marginal Effects for "Ggplot" from Model Outputs*, *23*.

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, *6*(60).

Lund, U., & Agostinelli, C. (2012). Circstats: Circular Statistics, from "Topics in Circular Statistics"(2001). *R Package Version*, *2*(1).

Lutz, N. D., Diekelmann, S., Hinse-Stern, P., Born, J., & Rauss, K. (2017). Sleep Supports the Slow Abstraction of Gist from Visual Perceptual Memories. *Scientific Reports*, *7*(1), 1–9. https://doi.org/10.1038/srep42950

MacWhinney, B., Bates, E., & Kliegl, R. (1984). Cue validity and sentence interpretation in English, German, and Italian. *Journal of Verbal Learning and Verbal Behavior*, *23*(2), 127–150.

Maingret, N., Girardeau, G., Todorova, R., Goutierre, M., & Zugaro, M. (2016). Hippocampo-cortical coupling mediates memory consolidation during sleep. *Nature Neuroscience*, *19*(7), 959–964. https://doi.org/10.1038/nn.4304

Maquet, P., Laureys, S., Peigneux, P., Fuchs, S., Petiau, C., Phillips, C., Aerts, J., Del Fiore, G., Degueldre, C., Meulemans, T., Luxen, A., Franck, G., Van Der Linden, M., Smith, C., & Cleeremans, A. (2000). Experience-dependent changes in cerebral activation

during human REM sleep. *Nature Neuroscience*, *3*(8), 831–836. https://doi.org/10.1038/77744

Marshall, L., & Born, J. (2007). The contribution of sleep to hippocampus-dependent memory consolidation. *Trends in Cognitive Sciences*, *11*(10), 442–450. https://doi.org/10.1016/j.tics.2007.09.001

Mathewson, K. E., Lleras, A., Beck, D. M., Fabiani, M., Ro, T., & Gratton, G. (2011). Pulsed out of awareness: EEG alpha oscillations represent a pulsed-inhibition of ongoing cortical processing. *Frontiers in Psychology*, *2*, 99.

Mathôt, S., Schreij, D., & Theeuwes, J. (2012). OpenSesame: An open-source, graphical experiment builder for the social sciences. *Behavior Research Methods*, *44*(2), 314–324.

Matorina, N., & Poppenk, J. (2019). Sleep promotes relational overlapping memories for long-term generalization. *BioRxiv*.

Matorina, N., & Poppenk, J. (2021). Memory decay distinguishes subtypes of gist. *Neurobiology of Learning and Memory*, *185*, 107519. https://doi.org/10.1016/j.nlm.2021.107519

May, C. P., Hasher, L., & Kane, M. J. (1999). The role of interference in memory span. *Memory & Cognition*, *27*(5), 759–767. https://doi.org/10.3758/BF03198529

McClelland, J. L., McNaughton, B. L., & O'Reilly, R. C. (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

Muehlroth, B. E., Sander, M. C., Fandakova, Y., Grandy, T. H., Rasch, B., Shing, Y. L., & Werkle-Bergner, M. (2019). Precise Slow Oscillation–Spindle Coupling Promotes Memory Consolidation in Younger and Older Adults. *Scientific Reports*, *9*(1), 1–15. https://doi.org/10.1038/s41598-018-36557-z

Mueller, J. L. (2006). L2 in a nutshell: The investigation of second language processing in the miniature language model. *Language Learning*, *56*, 235–270.

Munia, T. T. K., & Aviyente, S. (2019). Time-Frequency Based Phase-Amplitude Coupling Measure For Neuronal Oscillations. *Scientific Reports*, *9*(1), 12441. https://doi.org/10.1038/s41598-019-48870-2

Nalaye, H., Cross, Z. R., Schlesewsky, M., & Bornkessel-Schlesewsky, I. (2022). *Electrophysiological indices of individual differences in adult language learning* (p. 2022.06.07.495229). bioRxiv. https://doi.org/10.1101/2022.06.07.495229

Neuwirth, E. (2014). Package 'RColorBrewer.' *ColorBrewer Palettes*.

Nieuwenhuis, I. L., Folia, V., Forkstam, C., Jensen, O., & Petersson, K. M. (2013). Sleep promotes the extraction of grammatical rules. *PloS One*, *8*(6).

Nishida, M., Pearsall, J., Buckner, R. L., & Walker, M. P. (2009). REM sleep, prefrontal theta, and the consolidation of human emotional memory. *Cerebral Cortex (New York, N.Y.: 1991)*, *19*(5), 1158–1166. https://doi.org/10.1093/cercor/bhn155

Ociepka, M., Kałamała, P., & Chuderski, A. (2022). High individual alpha frequency brains run fast, but it does not make them smart. *Intelligence*, *92*, 101644. https://doi.org/10.1016/j.intell.2022.101644

Popa, D., Duvarci, S., Popescu, A. T., Léna, C., & Paré, D. (2010). Coherent amygdalocortical theta promotes fear memory consolidation during paradoxical sleep. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(14), 6516–6519. https://doi.org/10.1073/pnas.0913016107

Pothos, E. M. (2007). Theories of artificial grammar learning. *Psychological Bulletin*, *133*(2), 227.

Prat, C. S., Yamasaki, B. L., Kluender, R. A., & Stocco, A. (2016). Resting-state qEEG predicts rate of second language learning in adults. *Brain and Language*, *157–158*, 44–50. https://doi.org/10.1016/j.bandl.2016.04.007

Radvansky, G. A., & Copeland, D. E. (2006). Memory retrieval and interference: Working memory issues. *Journal of Memory and Language*, *55*(1), 33–46. https://doi.org/10.1016/j.jml.2006.02.001

Richard Clark, C., Veltmeyer, M. D., Hamilton, R. J., Simms, E., Paul, R., Hermens, D., & Gordon, E. (2004). Spontaneous alpha peak frequency predicts working memory performance across the age span. *International Journal of Psychophysiology*, *53*(1), 1–9. https://doi.org/10.1016/j.ijpsycho.2003.12.011

Samaha, J., & Postle, B. R. (2015). The Speed of Alpha-Band Oscillations Predicts the Temporal Resolution of Visual Perception. *Current Biology*, *25*(22), 2985–2990. https://doi.org/10.1016/j.cub.2015.10.007

Sarkar, D. (2008). *Lattice: Multivariate data visualization with R*. Springer Science & Business Media.

Schabus, M., Kerstin, H., Thomas, P., Anderer, P., Gruber, G., Parapatics, S., Sauter, C., Kloesch, G., Klimesch, W., Saletu, B., & Zeitlhofer, J. (2008). Interindividual sleep spindle differences and their relation to learning-related enhancements. *Brain Research*, *1191*, 127–135. https://doi.org/10.1016/j.brainres.2007.10.106

Schad, D. J., Vasishth, S., Hohenstein, S., & Kliegl, R. (2020). How to capitalize on a priori contrasts in linear (mixed) models: A tutorial. *Journal of Memory and Language*, *110*, 104038. https://doi.org/10.1016/j.jml.2019.104038

Schäfer, S. K., Wirth, B. E., Staginnus, M., Becker, N., Michael, T., & Sopp, M. R. (2020). Sleep's impact on emotional recognition memory: A meta-analysis of whole-night, nap, and REM sleep effects. *Sleep Medicine Reviews*, *51*, 101280.

Simor, P., Gombos, F., Szakadát, S., Sándor, P., & Bódizs, R. (2016). EEG spectral power in phasic and tonic REM sleep: Different patterns in young adults and children. *Journal of Sleep Research*, *25*(3), 269–277. https://doi.org/10.1111/jsr.12376

Singh, Y., Singh, J., Sharma, R., & Talwar, A. (2015). FFT transformed quantitative EEG analysis of short term memory load. *Annals of Neurosciences*, *22*(3), 176–179. PubMed. https://doi.org/10.5214/ans.0972.7531.220308

Smit, C. M., Wright, M. J., Hansell, N. K., Geffen, G. M., & Martin, N. G. (2006). Genetic variation of individual alpha frequency (IAF) and alpha power in a large adolescent twin sample. *International Journal of Psychophysiology*, *61*(2), 235–243. https://doi.org/10.1016/j.ijpsycho.2005.10.004

Sopp, M. R., Michael, T., Weeß, H.-G., & Mecklinger, A. (2017). Remembering specific features of emotional events across time: The role of REM sleep and prefrontal theta oscillations. *Cognitive, Affective, & Behavioral Neuroscience*, *17*(6), 1186–1209.

Stanley, D. J., & Spence, J. R. (2018). Reproducible Tables in Psychology Using the apaTables Package. *Advances in Methods and Practices in Psychological Science*, *1*(3), 415–431. https://doi.org/10.1177/2515245918773743

Staresina, B. P., Bergmann, T. O., Bonnefond, M., van der Meij, R., Jensen, O., Deuker, L., Elger, C. E., Axmacher, N., & Fell, J. (2015). Hierarchical nesting of slow oscillations, spindles and ripples in the human hippocampus during sleep. *Nature Neuroscience*, *18*(11), 1679–1686. https://doi.org/10.1038/nn.4119

Stark, S., Gordon, B., & Stark, C. (2008). A case study of amnesia: Exploring a paradigm for new semantic learning and generalization. *Brain Injury*, *22*(3), 283–292. https://doi.org/10.1080/02699050801953081

Stark, S. M., & Stark, C. E. (2016). Introduction to Memory. In *Neurobiology of language* (pp. 841–854). Elsevier.

Stickgold, R., & Walker, M. P. (2013). Sleep-dependent memory triage: Evolving generalization through selective processing. *Nature Neuroscience*, *16*(2), 139.

Surwillo, W. W. (1961). Frequency of the ‘alpha’rhythm, reaction time and age. *Nature*, *191*(4790), 823–824.

Surwillo, W. W. (1963). The relation of simple response time to brain-wave frequency and the effects of age. *Electroencephalography and Clinical Neurophysiology*, *15*(1), 105–114.

Tononi, G., & Cirelli, C. (2006). Sleep function and synaptic homeostasis. *Sleep Medicine Reviews*, *10*(1), 49–62.

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

Tse, D., Takeuchi, T., Kakeyama, M., Kajii, Y., Okuno, H., Tohyama, C., Bito, H., & Morris, R. G. M. (2011). Schema-Dependent Gene Activation and Memory Encoding in Neocortex. *Science*, *333*(6044), 891–895. https://doi.org/10.1126/science.1205274

Tucker, M. A., Humiston, G. B., Summer, T., & Wamsley, E. (2020). Comparing the Effects of Sleep and Rest on Memory Consolidation. *Nature and Science of Sleep*, *12*, 79–91. https://doi.org/10.2147/NSS.S223917

Vogt, F., Klimesch, W., & Doppelmayr, M. (1998). High-frequency components in the alpha band and memory performance. *Journal of Clinical Neurophysiology*, *15*(2), 167–172.

Wagner, U., & Born, J. (2008). Memory consolidation during sleep: Interactive effects of sleep stages and HPA regulation. *Stress*, *11*(1), 28–41. https://doi.org/10.1080/10253890701408822

Wamsley, E. J. (2019). Memory Consolidation during Waking Rest. *Trends in Cognitive Sciences*, *23*(3), 171–173. https://doi.org/10.1016/j.tics.2018.12.007

Wang, L., Schlesewsky, M., Philipp, M., & Bornkessel-Schlesewsky, I. (2012). The role of animacy in online argument interpretation in Mandarin Chinese. In *Case, word order and prominence* (pp. 91–119). Springer.

Weiss, S., & Rappelsberger, P. (2000). Long-range EEG synchronization during word encoding correlates with successful memory performance. *Cognitive Brain Research*, *9*(3), 299–312. https://doi.org/10.1016/S0926-6410(00)00011-2

Wickham, H. (2007). Reshaping data with the reshape package. *Journal of Statistical Software*, *21*, 1–20.

Wickham, H. (2011). The Split-Apply-Combine Strategy for Data Analysis. *Journal of Statistical Software*, *40*, 1–29. https://doi.org/10.18637/jss.v040.i01

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S.

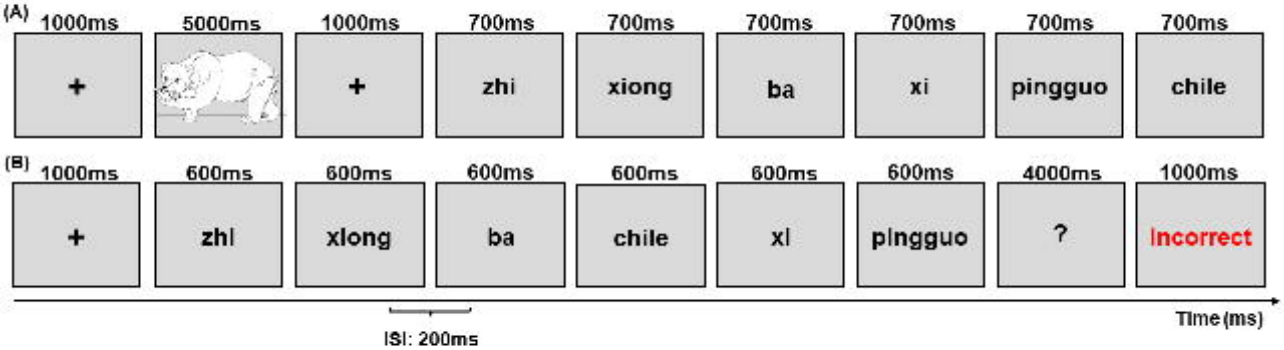
M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., … Yutani, H. (2019). Welcome to the Tidyverse. *Journal of Open Source Software*, *4*(43), 1686. https://doi.org/10.21105/joss.01686

Wickham, H., Chang, W., Henry, L., Pedersen, T. L., Takahashi, K., Wilke, C., Woo, K., Yutani, H., Dunnington, D., & RStudio. (2021). *ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics* (3.3.5) [Computer software]. https://CRAN.R-project.org/package=ggplot2

Wilhelm, I., Rose, M., Imhof, K. I., Rasch, B., Büchel, C., & Born, J. (2013). The sleeping child outplays the adult's capacity to convert implicit into explicit knowledge. *Nature Neuroscience*, *16*(4), 391–393. https://doi.org/10.1038/nn.3343

Wixted, J. T. (2014). Signal detection theory. *Wiley StatsRef: Statistics Reference Online*.

Yassa, M., & Reagh, Z. (2013). Competitive Trace Theory: A Role for the Hippocampus in Contextual Interference during Retrieval. *Frontiers in Behavioral Neuroscience*, *7*, 107. https://doi.org/10.3389/fnbeh.2013.00107


(A)
1000ms
+
5000ms
1000ms
+
700ms
zhi
700ms
xiong
700ms
ba
700ms
xi
700ms
pingguo
700ms
chile
(B)
1000ms
+
600ms
zhi
600ms
xiong
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xi
600ms
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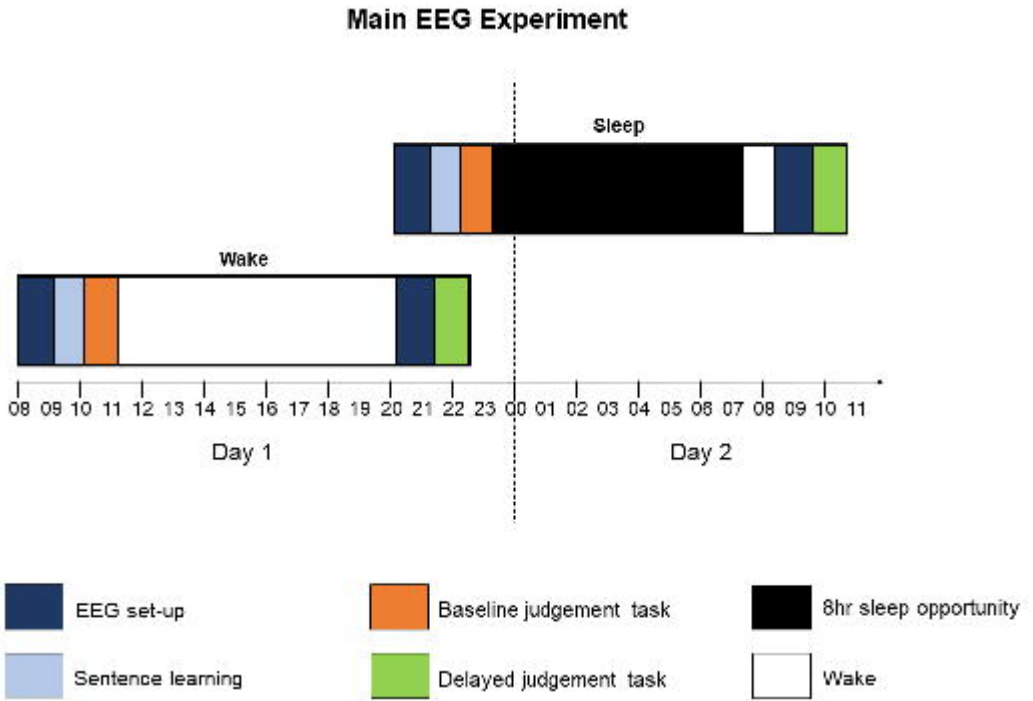
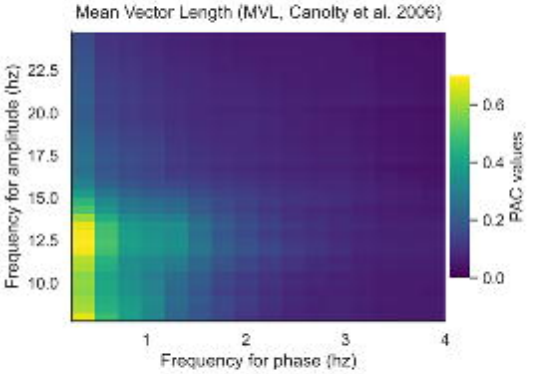
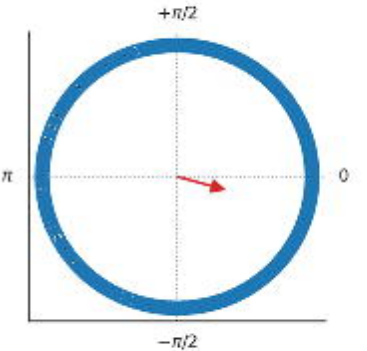
4000ms
?
1000ms
Incorrect
ISI: 200ms
Time (ms)

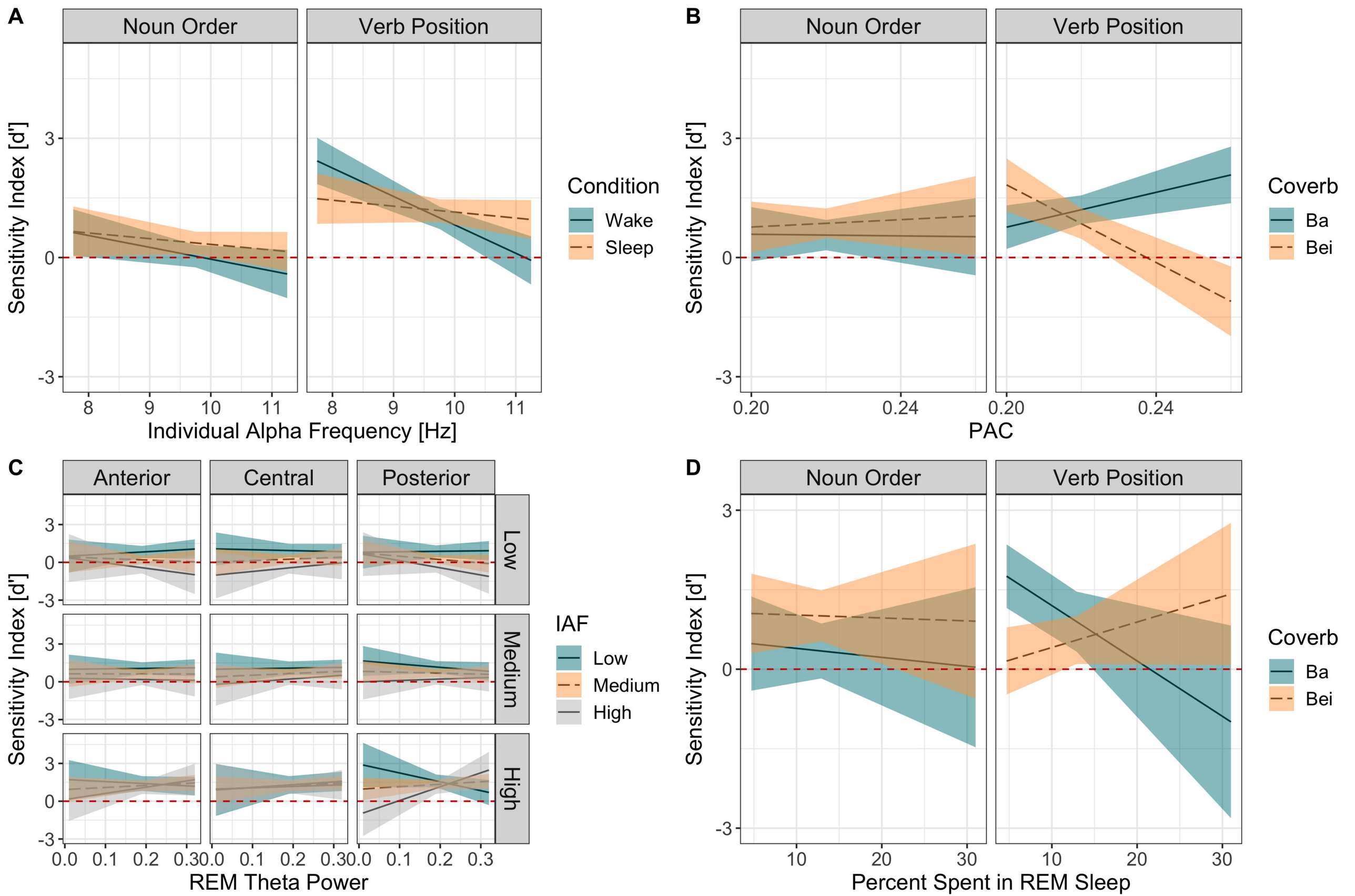

Main EEG Experiment
Sleep
Wake
08 09 10 11 12 13 14 15 16 17 18 19 20 21 22 23 00 01 02 03 04 05 06 07 08 09 10 11
Day 1
Day 2
EEG set-up
Sentence learning
Baseline judgement task
Delayed judgement task
8hr sleep opportunity
Wake

A


Mean Vector Length (MVL, Canolty et al. 2006)
Frequency for amplitude (hz)
22.5
20.0
17.5
15.0
12.5
10.0
1
2
3
4
Frequency for phase (hz)
0.6
0.4
0.2
0.0
PAC values

B


+π/2
π
0
−π/2


A
Noun Order
Verb Position
Sensitivity Index [d']
3
0
-3
8
9
10
11
Individual Alpha Frequency [Hz]
Condition
Wake
Sleep
B
Noun Order
Verb Position
Sensitivity Index [d']
0.20
0.24
PAC
Coverb
Ba
Bei
C
Anterior
Central
Posterior
Low
Medium
High
Sensitivity Index [d']
0.0
0.1
0.2
0.3
REM Theta Power
IAF
Low
Medium
High
D
Noun Order
Verb Position
Sensitivity Index [d']
10
20
30
Percent Spent in REM Sleep
Coverb
Ba
Bei