Slow wave-spindle coupling during sleep predicts language learning and associated oscillatory activity

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Manuscript details

Number of pages:	41
Number of figures:	8
Abstract word count:	174
Introduction word count:	1,756
Discussion word count:	2,677
Data available at:	TBC
Code available at:	TBC

Funding: Preparation of this work was supported by Australian Commonwealth Government funding under the Research Training Program (RTP; number 212190) and Maurice de Rohan International Scholarship awarded to ZC. IB-S is supported by an Australian Research Council Future Fellowship (FT160100437). AWC and LZ-W are supported by Australian Government RTP scholarships. RTK is supported by an NIH RO1NS21135, while RFH is supported by a Feodor-Lynen Fellowship by the Alexander-von-Humboldt Foundation. This work was also supported by a UK ESRC grant (ES/N009924/1) awarded to Lisa Henderson and Gareth Gaskell.

Acknowledgements: We thank the research assistants at the Cognitive and Systems Neuroscience Research Hub. Particular thanks to Isabella Sharrad, Erica Wilkinson, Nicole June and Angela Osborn for help with data collection. Thank you also to the participants.

Conflict of interest

The authors declare no competing financial interests.

ABSTRACT

Language is one of the most defining human capabilities, involving the coordination of brain networks that generalise the meaning of linguistic units of varying complexity. On a neural level, neocortical slow waves and thalamic spindles during sleep facilitate the reactivation of newly encoded memory traces, manifesting in distinct oscillatory activity during retrieval. However, it is currently unknown if the effect of sleep on memory extends to the generalisation of the mechanisms that subserve sentence comprehension. We address this question by analysing electroencephalogram data recorded from 36 participants during an artificial language learning task and an 8hr nocturnal sleep period. We found that a period of sleep was associated with increased alpha/beta synchronisation and improved behavioural performance. Cross-frequency coupling analyses also revealed that spindle-slow wave coupling predicted the consolidation of varying word order permutations, which was associated with distinct patterns of task-related oscillatory activity during sentence processing. Taken together, this study presents converging behavioural and neurophysiological evidence for a role of sleep in the consolidation of higher order language learning and associated oscillatory neuronal activity.

Keywords: Sleep and memory; language learning; modified miniature language; sentence processing; neuronal oscillations

SIGNIFICANCE STATEMENT

The endogenous temporal coordination of neural oscillations supports information processing during both wake and sleep states. Here we demonstrate that spindle-slow wave coupling during non-rapid eye movement sleep predicts the consolidation of complex grammatical rules and modulates task-related oscillatory dynamics previously implicated in sentence processing. We show that increases in alpha/beta synchronisation predict enhanced sensitivity to grammatical violations after a period of sleep and strong spindle-slow wave coupling modulates subsequent task-related theta activity to influence behaviour. Our findings reveal a complex interaction between both wake- and sleep-related oscillatory dynamics during the early stages of language learning beyond the single word level.

1. INTRODUCTION

The human brain is highly adept at extracting regularities from its environment. This process of statistical learning is pivotal in generating knowledge of our surroundings and in deriving predictions that are critical for perceptual, cognitive and motor computations (Durrant, Cairney, & Lewis, 2016; Toth et al., 2017). Probabilistic contingencies are encountered at multiple spatiotemporal scales as exemplified by differences in the complexity of generalisations (e.g., concrete vs. abstract categories), but also in the way discrete units of information are combined (e.g., local associations vs. networks built on local associations; Fiser & Aslin, 2002; Perruchet & Pacton, 2006). For example, knowledge of an object's function is distinct from learning the complex (motor) sequence required to execute that function (e.g., hitting a nail with a hammer). From this perspective, sensory input that follows conditional regularities not only relies on mechanisms of associative memory, but also complex, hierarchical dependencies built at least in part on local statistical information.

Statistical learning requires adequate consolidation and generalisation over time, a process known to be supported by sleep (Albouy, King, Maquet, & Doyon, 2013; Durrant et al., 2016; Durrant, Taylor, Cairney, & Lewis, 2011; Lewis, Knoblich, & Poe, 2018; Lutz, Wolf, Hubner, Born, & Rauss, 2018). Behaviourally, sleep strengthens predictive sequence coding (Lutz et al., 2018), including the acquisition and prediction of auditory statistical regularities (Durrant, Cairney, & Lewis, 2013; Durrant et al., 2016). Physiologically, slow oscillations (SOs; < 1.0 Hz) and sleep spindles (~ 12-16 Hz) – prevalent during non-rapid eye-movement (NREM) sleep – replay newly encoded memory traces within the hippocampo-cortical network (Rasch & Born, 2013; Staresina et al., 2015). Moreover, the precise temporal coordination between spindles and SOs facilitates overnight memory retention (Helfrich, Mander, Jagust, Knight, & Walker, 2018; Helfrich et al, Nat Comm 2019), allowing for the integration and abstraction of information in different memory systems (Born & Wilhelm, 2012; Lewis & Durrant, 2011; Rasch, 2017).

Language is a prime example of a complex domain in which statistical regularities occur at multiple scales (e.g., phonemes, words, sentences; Bornkessel-Schlesewsky, Schlesewsky, Small, & Rauschecker, 2015; Friederici, 2005). It is likely that the learning and abstraction of language-related rules would benefit from sleep-related memory consolidation. Indeed, periods of sleep have been shown to enhance novel-word learning (Bakker, Takashima, van Hell, Janzen, & McQueen, 2015; James, Gaskell, Weighall, & Henderson, 2017; Mirković & Gaskell, 2016) as well as the generalisation of simple grammatical rules (Batterink, Oudiette, Reber, & Paller, 2014). In addition to improving behavioural performance, effects of sleep on learning manifest in distinct oscillatory brain activity (for review: Schreiner & Rasch, 2016) and event-related potentials (ERPs). For example, increased theta power (~4–7 Hz) has been reported during the recognition of newly learned words compared to unlearned words after a delay period containing sleep (Bakker et al., 2015; Schreiner, Goldi, & Rasch, 2015), while the interaction between NREM and rapid eye movement sleep (REM) modulates the amplitude of language-related ERPs (N400, late positivity) during the processing of novel grammatical rules (Batterink et al., 2014). By demonstrating sleep-related consolidation effects for linguistic stimuli of varying complexity, these findings have begun to establish a link between sleep-

related memory consolidation of various aspects of language (Rasch, 2017). However, there is limited empirical evidence to date supporting a link between oscillatory-based models of hippocampo-cortical memory consolidation and sentences-level learning.

The communicative power of language relies on the complex combinatory operations structuring small linguistic units (e.g., *neuro-scien-tist*) into larger, more complex representations (e.g., *an excit-ed neuro-scien-tist publish-ed a comment-ary*; Flick et al., 2018). While existing M/EEG studies have helped characterise the spatiotemporal correlates of complex combinatory operations in typical sentence processing, the neural correlates underlying the initial encoding, (sleep-related) consolidation and generalisation of sentence-level combinatorics is not defined. Neural oscillations provide a promising method for investigating the effect of sleep on the consolidation of sentence-level information given their prominence in cognitive computations during both wake and sleep states (e.g., Buzsáki, 1996; Canolty & Knight, 2010; Helfrich et al., 2019), including their relationship to memory encoding, consolidation and retrieval (Hasselmo, & Stern, 2014; Osipova et al., 2006; Tort, Komorowski, Manns, Koell, & Eichenbaum, 2009).

Several models have attempted to explain the role of frequency-band activity during sentence-level processing (Cross et al., 2018; Lewis & Bastiaansen, 2015; Molinaro, Monsalve, & Lizarazu, 2015). Lewis and Bastiaansen (2015) proposed that frequency activity in the beta (~ 13 – 30 Hz) and gamma (> 30 Hz) bands reflect distinct aspects of hierarchical predictive coding, with increases in beta power reflecting the propagation of top-down predictions during sentence comprehension (Lam, Schoffelen, Udden, Hulten, & Hagoort, 2016; Wang et al., 2012). Gamma activity, by contrast, is posited to reflect the forward propagation of precision-weighted prediction errors. This proposal has been corroborated by a number of studies: semantically congruent and predictable words elicit greater gamma power (Mamashli, Khan, Obleser, Friederici, & Maess, 2019; Wang, Hagoort, & Jensen, 2018), while linear beta power increases have been observed during presentation of grammatically correct sentences (Bastiaansen & Hagoort, 2015; Lam et al., 2016; Wang et al., 2012). However, formation of linguistic hierarchical predictive models during initial learning remains understudied using electrophysiology (see Weber, Christiansen, Petersson, Indefrey, & Hagoort, 2016, for a discussion on the BOLD signal correlates of repetition effects during language learning). In line with theories of predictive coding (e.g., Friston, 2010; Friston & Buzsaki, 2016), beta and gamma power may increase linearly as a function of learning efficiency, reflecting the accumulation of generative model evidence based on repeated exposure to the regularities of the linguistic input (Cross, Kohler, Schlesewsky, Gaskell, & Bornkessel-Schlesewsky, 2018). As such, sentences containing violations (e.g., ungrammatical word orders) may elicit greater beta and gamma desynchronization (i.e., a reduction in power), reflecting internal model updates based on mismatches with the actual sensory input. Further, given the role of sleep in supporting memory (Rasch & Born, 2013), prediction strength (i.e., more accurate model predictions) may be enhanced after sleep, manifesting in increases in beta and gamma frequency band power relative to an equivalent period of wake.

Other oscillatory frequency bands are also associated with linguistic learning. For instance, low frequency activity (i.e., < 13 Hz) is implicated in language learning and sentence

processing, such that alpha desynchronization (~ 8 – 12 Hz) predicts the encoding of sentences into working memory and performance on a subsequent cued recall task (Vassileiou, Meyer, Beese, & Friederici, 2018). Similar research (Kepinska, Pereda, Caspers, & Schiller, 2017) has demonstrated increased alpha synchronization during the learning of an artificial language in individuals with high language learning aptitudes, possibly reflecting more efficient and less effortful processing demands due to accelerated learning (Cross et al., 2018; Kepinska et al., 2017). These findings are in line with the general memory literature and the inhibition-timing hypothesis (Klimesch, Sauseng, & Hanslmayr, 2007): alpha oscillations modulate the activation of task-relevant cortical regions (Ichihara-Takeda et al., 2015; Jiang, van Gerven, & Jensen, 2015; Mathewson et al., 2011), possibly facilitating the flow of information through thalamo-cortical networks. As such, alpha oscillations may modulate the encoding of complex sentence-level input, but how such activity changes as a function of sleep-associated consolidation remains unclear. If sleep strengthens predictive sequence coding and memory for statistical regularities, and increased alpha power reflects more efficient information processing during sentence processing, then alpha power should increase after a period of sleep and coincide with enhanced behavioural outcomes.

Theta activity (~ 4 – 7 Hz) has also been observed during sentence-level processing. Hippocampal theta oscillations have been shown to increase for constrained (e.g., *she locked the door with the [key]*) relative to unconstrained contexts (Piai et al., 2016; e.g., *she walked in here with the …*), while increased frontal theta power has been reported for embedded-antecedent retrieval (Meyer, Grigutsch, Schmuck, Gaston, & Friederici, 2015). We have posited that theta oscillations support sentence processing by binding long distance dependencies (Cross et al., 2018), a potentially domain-general function reflecting the binding of neocortically distributed memory traces to form successively more complex representations (Backus, Schoffelen, Szebenyi, Hanslmayr, & Doeller, 2016; Crivelli-Decker, Hsieh, Clarke, & Ranganath, 2018; Herweg et al., 2016). Indeed, increases in theta-band coherence has been observed during the learning of rules that governed the combination of trisyllabic sequences in an artificial language (de Diego-Balaguer, Fuentemilla, & Rodriguez-Fornells, 2011). From this perspective, theta oscillations may serve as a neurophysiological marker of general memory processes during language-related computations, which may be strengthened during sleep via reactivation of stimulus-relevant memory traces (for a detailed discussion of the mechanisms subserving this relationship, see Cross et al., 2018).

Taken together, these lines of evidence suggest that during sentence processing, alpha oscillations coordinate information processing in neural networks that govern attention and perception (Klimesch et al., 2007; Klimesch, 2012), while theta oscillations may index the binding of information to form coherent sentential representations (Cross et al., 2018; de Diego-Balaguer et al., 2011; Piai et al., 2016). Finally, beta oscillations have been argued to support a hierarchically organised predictive coding architecture during language comprehension (Lewis & Bastiaansen, 2015; Lewis et al., 2015). However, while the oscillatory correlates of fluent sentence processing are beginning to be well-characterised, the mechanisms underlying the long-term consolidation of sentence-level regularities, including during sleep-associated consolidation, remain unclear.

To address this gap, we recorded electroencephalography (EEG) during an 8-hour nocturnal sleep period and sentence judgement tasks of a miniature language that participants

implicitly learned in the laboratory. We used non-linear directional cross-frequency coupling analyses in combination with phase-dependent correlation measures to quantify the temporal relationship between SOs and spindles during NREM sleep (for a similar approach, see Helfrich et al., 2018; Staresina et al., 2015). We also quantified spectral activity in the theta, alpha and beta bands using complex Morlet wavelets during sentence judgement tasks. These estimates were used to independently predict behavioural performance and were analysed in combination with spindle-SO coupling metrics to determine whether task-related EEG is modulated by mechanisms of sleep-based memory consolidation. Based on previous experimental results and current theory, we hypothesised that task-related theta, alpha and beta activity and NREM spindle-SO coupling would interact in their effect on language learning and sentence processing. Specifically, we predicted that:

(1) Behavioural sensitivity to grammatical violations would be improved after sleep compared to an equivalent period of wake;
(2) Improved behavioural performance would be associated with higher task-related beta and alpha power, and that this effect would be accentuated after sleep compared to wake;
(3) Greater memory-related processing, as indexed by task-related theta power, would be associated with more accurate grammaticality judgements, and;
(4) Differences in performance relative to Condition (Sleep vs Wake) and task-evoked oscillatory activity would be modulated by NREM spindle-SO coupling.

2. MATERIALS AND METHODS

2.1. Participants

Power analyses were conducted using G*Power 3 (Faul, Erdfelder, Lang, & Buchner, 2007). To detect a moderate-to-large effect size, with η^2 =.80 and α=.05, the recommended sample size was 18, based on a study examining the effect of sleep on the consolidation of novel words in native English speakers (η2 = .20; Kurdziel & Spencer, 2016). We thus recruited 36 right-handed participants who were healthy, monolingual, native English-speakers (16 male) ranging from 18 – 40 years old (mean = 25.4, SD = 7.0). Participants were randomly assigned to either a Sleep (*n* = 18) or Wake condition. All participants reported normal or corrected-to-normal vision, no history of psychiatric disorder, substance dependence, or intellectual impairment, and were not taking medication that influenced sleep or neuropsychological measures. All participants provided informed consent and received a $120 honorarium. One participant from the Sleep condition was removed from the analysis due to technical issues during the experimental tasks and sleep period, resulting in a total sample size of 35 (mean age = 25.4, SD = 7.10; 16 male; Sleep *n* = 17). Ethics approval was granted by the University of South Australia's Human Research Ethics committee (I.D: 0000032556).

2.2. Screening and control measures

The Flinders Handedness Survey (FLANDERS; Nicholls, Thomas, Loetscher, & Grimshaw, 2013) was used to screen handedness, while the Pittsburgh Sleep Quality Index (PSQI; Buysse, Reynolds, Monk, Berman, & Kupfer, 1988) screened for sleep quality. PSQI

scores ranged from 1-5 (M = 2.9, SD = 1.33), indicating good sleep quality. Prospective participants with scores > 5 were unable to participate. As an additional control, the Stanford Sleepiness Scale (SSS) was administered at the beginning and end of the experiment to measure self-perceived sleepiness. A visual statistical learning task (for a detailed description, see Siegelman, Bogaerts, & Frost, 2016) was also administered, as statistical learning ability has been shown to predict individual differences in language learning ability (Daltrozzo et al., 2017).

2.3. Electroencephalography

The electroencephalogram (EEG) was recorded during experimental tasks and sleep durations using a 32-channel BrainCap with sintered Ag/AgCI electrodes (Brain Products, GmbH, Gilching, Germany) mounted according to the extended International 10-20 system. The reference was located at FCz, with EEG signals re-referenced to linked mastoids offline. The ground electrode was located at AFz. The electrooculogram (EOG) was recorded via electrodes located at the outer canthus of each eye (horizontal EOG) and above and below participants' left eye (vertical EOG). Sub-mental electromyography (EMG) was added to facilitate accurate scoring of sleep periods. The EEG was amplified using a BrainAmp DC amplifier (Brain Products GmbH, Gilching, Germany) using an initial band-pass filter of DC – 250 Hz with a sampling rate of 1000 Hz. Electrode impedances were kept below 10kΩ.

2.4. Vocabulary and structure of Mini Pinyin

Stimuli consisted of sentences from an MML modelled on Mandarin Chinese, named Mini Pinyin (Cross, Zou-Williams, Wilkinson, Schlesewsky, Bornkessel-Schlesewsky, 2020). Mini Pinyin contains 32 transitive verbs, 25 nouns, 2 coverbs, and 4 classifiers. The nouns included 10 human entities, 10 animals and 5 objects (e.g., *apple*). Each category of noun was associated with a specific classifier, which always preceded each of the two noun phrases in a sentence. As described in Table 1, *ge* specifies a human noun, *zhi* for animals, and *xi* and *da* for small and large objects, respectively. Overall, 576 unique sentences (288 grammatical, 288 ungrammatical) were created and divided into two equivalent sets (see Cross et al., 2020 for a complete description of the stimuli).

Here we focussed on a subset of sentence conditions to investigate the mechanisms underlying the learning of thematic role assignment strategies, which fundamentally differs between the languages of the world (for review, see Bates, Devescovi, & Wulfeck, 2001). Languages like English and Dutch primarily rely on word order, while languages like German and Turkish rely more on cues such as case marking and animacy (Bornkessel & Schlesewsky, 2006; Bornkessel-Schlesewsky et al., 2015; MacWhinney, Bates, & Kliegl, 1984). From this perspective, Mini Pinyin enables a comparison between sentences with differing word orders (see Table 1). The subset contained 144 sentence stimuli. The remaining sentences were considered fillers.

As is apparent in Table 1, sentences that do not contain the coverb *ba* (i.e., Actor-Verb-Undergoer, AVU; Undergoer-Verb-Actor, UVA) yield a flexible word order, such that understanding *who is doing what to whom* is not dependent on the ordering of the noun phrases.

Instead, determining *who is doing what to whom* is facilitated by animacy cues. For instance, in the UVA condition, *the bear* is interpreted as the Actor *despite* the first noun phrase being *the apple*, since it is implausible for an apple to eat a bear. Therefore, both AVU and UVA are grammatical constructions. By contrast, sentences such as A*ba*UV yield a fixed word order, such that the inclusion of *ba* strictly renders the first noun phrase as the Actor. Note that the positioning of the verb is critical in sentences with and without a coverb. With the inclusion of a coverb, the verb must be placed at the end of the sentence, while the verb must be positioned between the noun phrases in constructions without a coverb.

Table 1. Example of grammatical and ungrammatical sentence constructions. Abbreviations: A – Actor; U – Undergoer; V – Verb; ba – coverb.

Word Order	**Grammatical**		**Ungrammatical**	
	Condition	Example	Condition	Example
Flexible	AVU	Zhi xiong chile xi pingguo. '(animal) bear eats (small object) apple.'	AUV	Zhi xiong xi pingguo chile. '(animal) bear (small object) apple eats.'
Flexible	UVA	Xi pingguo chile zhi xiong. '(small object) apple eats (animal) bear.'	UAV	Xi pingguo zhi xiong chile. '(small object) apple (animal) bear eats.'
Fixed	AbaUV	Zhi xiong ba xi pingguo chile '(animal) bear ba (small object) eats.'	UbaAV	Xi pingguo ba zhi xiong chile '(small object) apple ba (animal) bear eats.'
Fixed			AbaVU	Zhi xiong ba chile xi pingguo. '(animal) bear ba eats (small object) apple.'

2.5. Experimental protocol

Participants received a paired picture-word vocabulary booklet containing the 25 nouns and were asked to maintain a minimum of 7hrs sleep per night. Participants were required to learn the 25 nouns to ensure that they had a basic vocabulary of the nouns in order to successfully learn the 32 transitive verbs. They were asked to record periods of vocabulary

learning in an activity log. After approximately one week, participants returned to complete the main experimental session.

2.6. Vocabulary test

Participants completed a vocabulary test by translating the nouns from Mini Pinyin into English using a keyboard, as illustrated in Figure 1C. Each trial began with a 600ms fixation cross, followed by the visual presentation of the noun for up to 20 s. Prospective participants who scored < 90% were unable to complete the main experimental EEG session.

2.7. Sentence learning

Sentence and picture stimuli were presented using OpenSesame (Mathot, Schreij, & Theeuwes, 2012). During sentence learning, pictures were used to depict events occurring between two entities. While participants were aware that they would complete sentence judgement tasks at a later point, no explicit description of grammatical rules was provided during the learning task, since explicit instructions may differentially impact memory processes (Batterink, Reber, & Paller, 2015; Batterink & Neville, 2013; Weber et al., 2016). Further, participants implicitly trained on an artificial language show more native-like neural signatures of language processing, suggesting closer approximation to natural language learning (Friederici, Steinhauer, & Pfeifer, 2002; Morgan-Short, Steinhauer, Sanz, & Ullman, 2012).

Each picture corresponded to multiple sentence variations, similar to grammatical conditions in Table 1. Picture-sentence pairs were presented to participants as correct language input. Participants were presented with a fixation cross for 2000ms, followed by the picture illustrating the event between two entities for 4000ms. A sentence describing the event in the picture was then presented on a word-by-word basis. Each word was presented for 700ms followed by a 200ms ISI. This pattern continued for the 128 sentence-picture combinations (96 of which are reported in the current analysis) until the end of the task, which took approximately 40 minutes. During this task, participants were required to learn the structure of the sentences and the meaning of the verbs, classifiers and the coverb *ba*. Stimuli were pseudo-randomised, such that no stimuli of the same construction followed each other. Following the sentence learning session, participants completed the baseline sentence judgement task.

2.8. Baseline and delayed judgement tasks

The baseline sentence judgement task taken ~0 hr after learning provided a baseline to control for level of encoding, while the delayed judgement task took place ~12hrs after the learning session. During both judgement tasks, 288 novel sentences without pictures (156 of which are reported here) were presented word-by-word with a presentation time of 600ms and an ISI of 200ms. Participants received feedback on whether their response was correct or incorrect during the baseline but not the delayed judgement task. This was to ensure that participants were able to continue learning the language without explicit instruction. Figures 1A and 1B illustrate the sequence of events in the sentence learning and baseline judgement tasks, respectively.

Participants were instructed to read all sentences attentively and to judge their grammaticality (yes/no) via a button-press. As a cue for judgment, a question mark appeared in the centre of the monitor for 4000ms after the offset of the last word. Two lists of sentence stimuli were created, which were counterbalanced across participants. Half of the sentences were grammatical, with each of the grammatical constructions shown an equal number of times. The other half of the sentences were ungrammatical constructions. Stimuli were pseudo-randomised, such that no stimuli of the same construction followed each other.

2.9. Main experimental procedure

For the wake condition, participants completed the vocabulary test and EEG setup at ~08:00hr. The learning task was administered at ~09:00hr, followed by the baseline judgement task. Participants then completed the statistical learning task and were free to leave the laboratory to go about their usual daily activities, before returning for EEG setup and the delayed judgement task at ~21:00hr the same day.

Participants in the sleep condition arrived at ~20:00hr to complete the vocabulary test and EEG setup before completing the learning task at ~21:00hr, followed by the baseline judgement task. Participants were then given an 8hr sleep opportunity from 23:00hr – 07:00hr. Polysomnography was continuously recorded and later scored. After waking, participants were disconnected from the head box and given a ~1hr break to alleviate sleep inertia before completing the delayed judgement task and the statistical learning task. During this time, participants sat in a quiet room and consumed a small meal. Resting-state EEG recordings were obtained during quiet sitting with eyes open and eyes closed for two minutes, respectively. See Figure 1D for a schematic of the experimental protocol.

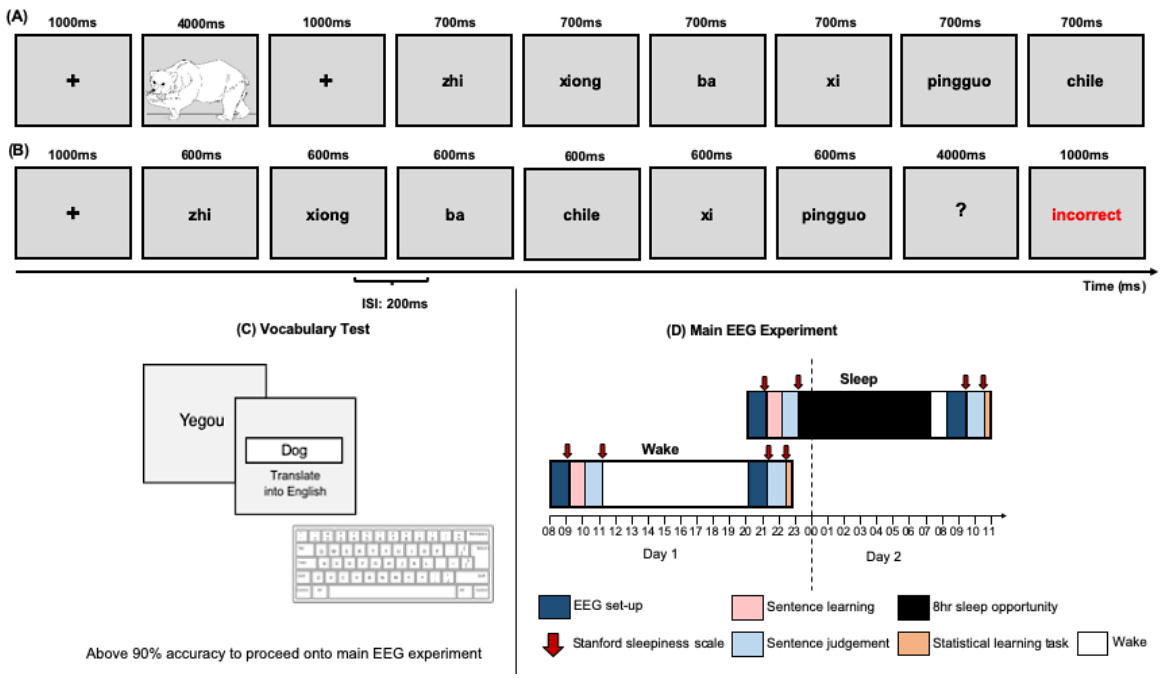

Figure 1. (A) Schematic representation of the sentence learning task. **(B)** Schematic representation of the baseline sentence judgement task. **(C)** Schematic diagram of the

vocabulary test. **(D)** Experimental protocol representing the time course of the conditions (sleep, wake) and testing sessions (sentence learning, baseline and delayed testing).

3. DATA ANALYSIS

3.1. Behavioural analysis

Three measures of behavioural performance were calculated. For behavioural models, grammaticality ratings were calculated on a trial-by-trial basis, determined by whether participants correctly identified grammatical and ungrammatical sentences. For EEG models, proportion of correct responses and difference scores (proportion correct at delayed minus proportion correct at baseline) for each sentence condition were calculated for each participant. Performance on the statistical learning task was quantified as percentage of correct responses.

3.2. EEG recording and pre-processing

Task-related EEG analyses were performed using MNE-Python (Gramfort et al., 2013). EEG data were re-referenced offline to the average of both mastoids and filtered with a digital phase-true finite impulse response band-pass filter from 0.1 – 40 Hz to remove slow signal drifts. Data segments from -0.5 – 6.5s relative to the onset of each sentence and -0.2 – 0.6s relative to the onset of each word were extracted and corrected for ocular artefacts using Independent Component Analysis (`fastica`). Bad electrodes were visually inspected based on the number of epochs dropped, and electrodes containing more than 20% of excluded epochs were interpolated with surrounding electrodes.

3.2.1. Task-related time frequency analysis.

We conducted time-frequency analyses by convolving the signal with a set of complex Morlet wavelets using the MNE function `tfr_morlet`. Frequencies ranging between 3.5 and 30 Hz were analysed using wavelet cycles that were adjusted for each individually defined frequency band of interest. The mother wavelet for each frequency band was defined as the peak frequency value divided by four (i.e., 10 Hz / 4 = 2.5 Hz; 25 Hz / 4 = 6.25 Hz). Relative power change values in the post-stimulus interval were computed as a relative change from a baseline interval spanning -1s to the onset of each sentence. Relative power changes were then extracted on a trial-by-trial basis within the following frequency ranges: theta (~ 4 – 7 Hz), alpha (~ 8 – 12 Hz) and beta (~ 13 – 30 Hz). 500ms was added to the beginning and end of each epoch to avoid edge artefacts.

To determine the individualised ranges used to define each frequency band, individual alpha frequency (IAF) was estimated from each participant's pre- and post-experiment resting-state EEG recording. IAFs were estimated from an occipital-parietal cluster (P3/P4/O1/O2/P7/P8/Pz/Iz) using `philistine.mne.savgol_iaf` (see Corcoran, Alday, Schlesewsky, & Bornkessel-Schlesewsky, 2018; see also Cross et al., 2018) implemented in MNE. IAF-adjusted frequency bandwidths were calculated using the golden mean algorithm (Klimesch, 2012).

3.2.2. Estimating broadband spectral power.

As differences in task-evoked spectral power between sleep and wake conditions at delayed testing may reflect sleep-related changes in global neural synchrony (Freeman & Zhai,

2009; Voytek et al., 2015), it is important to distinguish such broadband spectral dynamics from narrowband changes in (putative) oscillatory components. To this end, we used the irregular-resampling auto-spectral analysis toolbox (IRASA v1.0; Wen & Liu, 2015) to estimate the $1/f$ power-law exponent characteristic of background spectral activity.

IRASA aims to isolate the aperiodic or random fractal component of neural time series data via a process that involves resampling the signal at multiple non-integer factors h and their reciprocals $1/h$. Because this resampling procedure systematically shifts narrowband peaks away from their original location along the frequency spectrum, averaging the spectral densities of the resampled series attenuates peak components, while preserving the $1/f$ distribution of the fractal component. The (negative) exponent summarising the slope of aperiodic spectral activity can then be calculated by fitting a linear regression to the estimated fractal component in log-log space. For a full mathematical description of IRASA, see Wen and Liu (2016).

Trial data from each analysed electrode were epoched using a 2 s sliding window (50% overlap) and submitted to the toolbox function `amri_sig_fractal.m`. Data were detrended and anti-alias filtered as per default function settings; the output frequency range was set to 1–40 Hz. Following Muthukumaraswamy and Liley (2018), an extended set of resampling factors was selected (h = 1.1 to 2.9 in steps of 0.05, $h \neq 2$) in order to mitigate incomplete component separation on account of fractal-oscillatory interactions. A power-law function was subsequently fit to each fractal estimate within the frequency range 2.5 – 30 Hz (`amri_sig_plawfit.m`). These functions were averaged across epochs for each trial, and the inverse slope of this function taken as the $1/f$ exponent.

3.2.3. Sleep parameters and sleep EEG analyses.

Sleep data were scored by two sleep technicians (Z.R.C and S.C.) according to standardised criteria (Berry et al., 2012) within Compumedics Profusion 3 software (Melbourne, Australia). The EEG was viewed with a high-pass filter of 0.3 Hz and a low-pass filter of 35 Hz. The following sleep parameters were calculated: time in bed, total sleep time, sleep onset latency, REM onset latency, sleep efficiency, wake after sleep onset, total arousal index, and time (minutes) and percent of time spent in each sleep stage (N1, N2, N3 and R). Spindle density, spindle-SO coupling strength and spindle-SO phase-dependent correlation measures were extracted using MATLAB 2017b (The MathWorks, Natick, USA) and Fieldtrip (Oostenveld, Fries, Maris, & Schoffelen, 2011) based on published algorithms (Helfrich et al., 2018; Molle, Bergmann, Marshall, & Born, 2011; Staresina et al., 2015).

Briefly, the EEG data were re-referenced to linked mastoids and filtered from 0.1 – 40 Hz using a Butterworth filter. Data were then epoched into 30 s bins and epochs containing artifacts were manually rejected. A 50 Hz notch filter was applied to remove line noise prior to demeaning the signal. Bad electrodes were interpolated with neighbouring channels. For SOs, continuous EEG data were filtered from 0.16 – 1.25 Hz to detect zero crossing events that were between 0.8 – 2 s in length, and that met a 75-microvolt criterion. These artifact-free epochs were then extracted in segments of 5s (± 2.5s of SO trough) from the raw EEG signal. For sleep spindles, the signal was filtered between 12 – 16 Hz, while the amplitude was calculated by applying a Hilbert transform which was then smoothed with a 200ms moving

average. Amplitude threshold was set at 75% (amplitude criterion) and events were only included if they were longer than 0.5 – 3s (time criterion). Artifact-free events were then defined as 5s (± 2.5s) peak-locked sleep-spindle epochs.

To determine whether the precise temporal relationship between spindles and SOs influences the consolidation of complex grammatical rules, we calculated an event-locked cross-frequency coupling metric (for a detailed description of this method, see Helfrich et al., 2018). In brief, we first filtered the normalized SO trough-locked data into the SO component (0.1 – 1.25 Hz) and extracted the instantaneous phase angle after applying a Hilbert transform. Then we filtered the same trials between 12 – 16 Hz and extracted the instantaneous amplitude from the Hilbert transform. For every participant at channel C4 (selection based on Helfrich et al., 2018 and Mikutta et al., 2019) and epoch, we detected the maximal sleep spindle amplitude and corresponding SO phase angle. The mean circular direction (phase) and resultant vector length (coupling strength) across all NREM events were determined using the `CircStat` toolbox in MATLAB (Berens, 2009).

3.3. Statistical analysis

Data were entered into *R* version 3.5.1 (R Core Team, 2017) and analysed using (generalised) linear mixed effects models fit by maximum likelihood. Model structures included Condition (Sleep, Wake), Session (Baseline, Delayed), Sentence Type (fixed word order, flexible word order), Grammaticality (grammatical, ungrammatical), event-related spectral power (ERSP) of the time-frequency ranges of interest (theta, alpha, beta), Statistical Learning Ability, Coupling Strength, and the $1/f$ Exponent as fixed effects. Intercepts were grouped by participant and item, while participants' self-perceived sleepiness (indexed using the standard sleepiness scale) was modelled as a random effect on the slope of participant. Performance on the sentence judgement task was specified as the dependent variable.

Akaike Information Criterion (AIC; Akaike, 1974), Bayesian Information Criterion (BIC; Schwarz, 1978) and log-likelihood were used to assess model fit, while Type II Wald $\chi 2$-tests from the `car` package (Fox, 2011) were used to provide *p*-value estimates. A beta regression was used to assess the relationship between Statistical Learning Ability and behavioural performance on the sentence judgement tasks, while effects were plotted using the package `effects` (Fox et al., 2019) and `ggplot2` (Wickham, 2016). Categorical factors were sum-to-zero contrast coded, meaning that factor level estimates were compared to the grand-mean (Schad et al., 2020). Further, an 83% confidence interval (CI) threshold was used given that this approach is more conservative than the traditional 95% CI threshold and corresponds to the 5% significance level with non-overlapping estimates (Austin & Hux, 2002; MacGregor-Fors & Payton, 2013).

Finally, rather than adding sagittality and laterality as fixed effects of topographical distribution, we selected a priori regions of interest (ROI) based on the published literature. This approach was adopted (1) reduce computational complexity from additional parameters; (2) reduce the probability of encountering a Type I or Type II error; and (3) avoid model nonconvergence due to over-parameterization. Previous studies adopted cluster-based permutation methods, as well as more traditional statistical analysis approaches to isolate ROIs

for the canonical frequency bands during artificial language learning (e.g., de Diego-Balaguer et al., 2011; Kepinska, Pereda, et al., 2017) and native sentence processing (e.g., Lewis, Lemhfer, Schoffelen, & Schriefers, 2016; Meyer et al., 2015). For the alpha band, we selected a posterior cluster of electrodes (P3/P4/O1/O2/Pz/Iz), given the prominence of alpha power over occipital-parietal electrodes, particularly during visual language experiments (Kepinska, Pereda, et al., 2017; Kielar, Meltzer, Moreno, Alain, & Bialystok, 2014; Lam et al., 2016). For beta, we selected an anterior-central and anterior-left electrode cluster (FC1/FC2/Fz/F4/FC6/F8), which has been reported as a significant ROI for beta activity during higher-order language tasks (i.e., Bastiaansen & Hagoort, 2015; de Diego-Balaguer et al., 2011; Kepinska, Pereda, et al., 2017). Finally, a central-left electrode cluster (T7/CP5/C3/CP1/Cz/CP2) was chosen for the theta band based on studies reporting sleep-related memory effects (Koster, Finger, Kater, Schenk, & Gruber, 2016), as well as memory-related computations during language processing (Kielar et al., 2014; Meyer et al., 2015).

4. RESULTS

4.1. Behavioural results

Participants showed a moderate degree of accuracy on the judgement tasks (mean accuracy rates: > 60%, see Table 2).

Table 2. Mean percentage accuracy of grammaticality ratings by Condition (sleep, wake), Session (baseline, delayed), Grammaticality (grammatical, ungrammatical) and Sentence Type (fixed, flexible). Standard deviations are given in parentheses.

Sentence Type	**Sleep**		**Wake**	
	Baseline	Delayed	Baseline	Delayed
Grammatical				
Fixed	67.81 (12.88)	71.56 (22.19)	67.59 (20.63)	67.70 (26.80)
Flexible	65.19 (18.41)	58.33 (32.95)	63.19 (23.11)	62.61 (25.95)
Ungrammatical				
Fixed	48.36 (13.61)	50.65 (21.32)	52.00 (15.32)	52.35 (18.53)
Flexible	59.06 (22.78)	66.42 (23.82)	69.67 (24.37)	69.73 (27.43)
Total	**60.11 (18.59)**	**61.74 (26.17)**	**63.11 (21.80)**	**63.10 (25.33)**

Statistical analysis revealed non-significant main effects of Condition (Sleep versus Wake; $\chi2(1) = .26$, $p = .60$) and Session (Baseline versus Delayed; $\chi2(1) = .01$, $p = .89$) on behavioural performance. There was a significant main effect of Grammaticality, such that the probability of a correct response was higher for grammatical sentences ($\chi2(1) = 58.96$, $p < .001$). The main effect of Type was also significant, with the probability of a correct response being significantly greater for flexible word order sentences ($\chi2(1) = 6.51$, $p = .01$). All two-, three- and four-way interactions were resolved using the `effects` package (Fox, 2003; see Figure 2 and Table 3 for a summary of interaction effects).

Table 3. Type II Wald χ^2 tests for interaction terms examining the relationship between Grammaticality, Type, Condition and Session on the probability of a correct response.

Parameters	***χ2***	***df***	***p***
Grammaticality x Type	141.52	1	**<.001**
Grammaticality x Condition	6.65	1	**.009**
Type x Condition	10.10	1	**.001**
Grammaticality x Session	4.30	1	**.03**
Type x Session	0.25	1	.61
Condition x Session	1.21	1	.27
Grammaticality x Type x Session	2.03	1	.15
Grammaticality x Type x Condition	1.60	1	.20
Grammaticality x Condition x Session	1.05	1	.30
Type x Condition x Session	9.74	1	**.001**
Grammaticality x Type x Condition x Session	10.59	1	**.001**

Most importantly, the Type x Condition x Session and Grammaticality x Type x Condition x Session interactions were significant. As illustrated in Figure 2A, the likelihood of a correct response for ungrammatical sentences with a flexible word order was higher at Baseline testing for the Wake condition, while the likelihood of a correct response was higher for grammatical fixed word order sentences at Delayed testing for the Sleep condition.

To compensate for any differences in baseline performance, Figure 2B illustrates the data in terms of change in performance between Baseline and Delayed testing. Here, both the high-level interactions can be understood. For the fixed-order sentences (left-hand side) there is a general improvement in performance after sleep and a general worsening of performance after wake. This is consistent with a consolidation benefit of sleep for fixed-order aspects of the novel grammar. For the flexible-order sentences (right-hand side), the general pattern is for a small benefit of wake on performance, but no overall change across sleep. However, the 4-way interaction suggests that the pattern of performance for the Sleep condition is more complex: for ungrammatical sentences there is an apparent improvement in performance, but this is mirrored by a roughly equal decrement in performance for the grammatical sentences. This aspect of the data was not predicted, but perhaps makes sense in terms of a criterion shift. The three-way interaction shows that sleep benefits generalisation for fixed but not flexible word order sentences. Given this selective improvement in grammatical knowledge across sleep, the participants may have become more confident in their knowledge of the fixed order sentences, and hence less inclined to endorse flexible order sentences, leading to more correct rejections of ungrammatical sentences, but also more incorrect endorsements of the grammatical sentences.

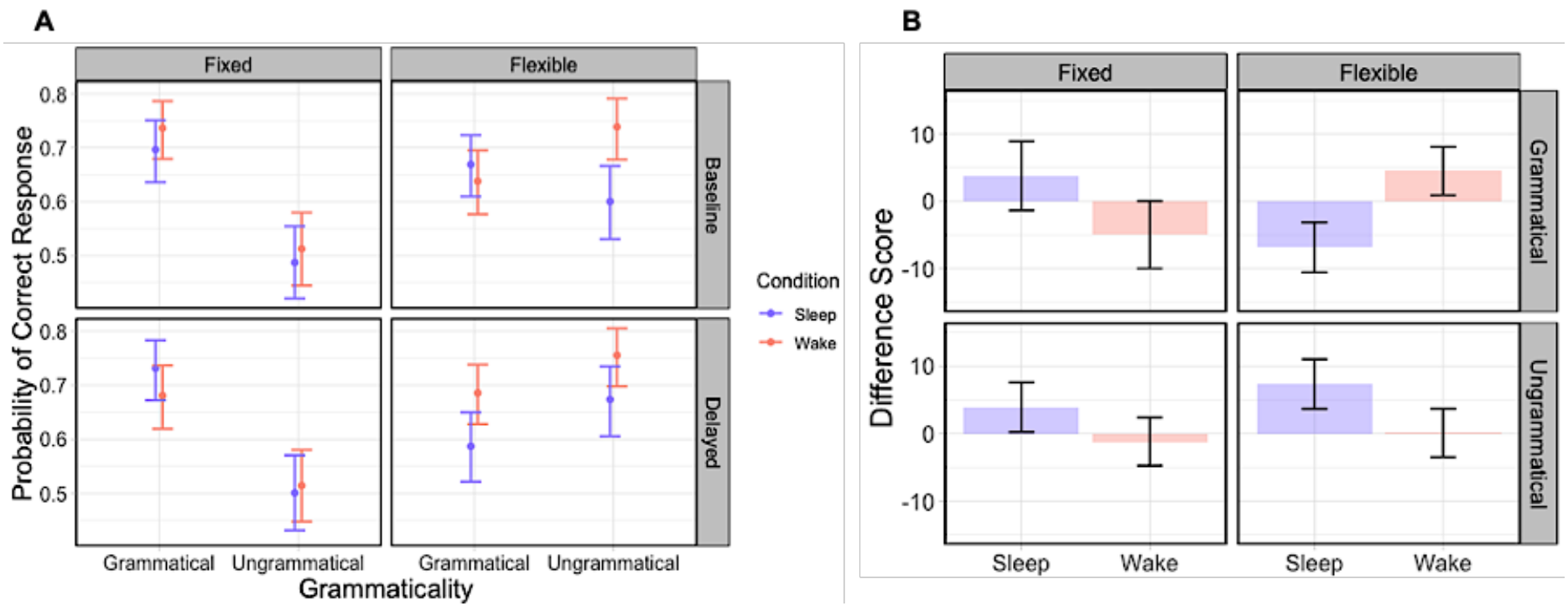

Figure 2. (A) Modelled relationship between the probability of correct response (y-axis), Grammaticality (x-axis), Sentence Type (left facet = fixed, right facet = flexible), Session (top = Baseline, bottom = Delayed) and Condition (purple = Sleep, orange = Wake). **(B)** Difference scores (percentage correct at Delayed – Baseline; positive values indicate improvements) between the Sleep and Wake conditions on grammatical and ungrammatical fixed word order sentences, and grammatical and ungrammatical flexible word order sentences.

4.2. Neurophysiological results

4.2.1. Sleep-related changes in broadband spectral activity.

To address whether changes in frequency-band activity reflect task-related changes in underlying neural populations or non-oscillatory activity (Dave, Brothers, & Swaab, 2018), we examined whether the $1/f$ exponent predicted changes in task-evoked oscillatory power from Baseline to Delayed sessions between the Sleep and Wake conditions. This analysis was performed to distinguish task-related oscillatory activity from broadband neural activity (i.e., changes in $1/f$ slope) induced by a period of sleep relative to wake (Miskovic, MacDonald, Rhodes, & Cote, 2019; Wen & Liu, 2016). Figure 3 shows the three-way interaction effects for the three models, as well as a decomposition of the fractal versus the oscillatory components in the task-related EEG. The theta model did not show a significant Condition x Session x $1/f$ interaction ($\chi2(1) = 2.99$, $p = .08$); however, there were significant Condition x $1/f$ ($\chi2(1) = 23.00$, $p < .001$) and Session x $1/f$ interactions ($\chi2(1) = 7.15$, $p = .007$). Similarly, for the alpha model, there was no Condition x Session x $1/f$ interaction ($\chi2(1) = 0.14$, $p = .71$), while both Condition x $1/f$ ($\chi2(1) = 32.47$, $p < .001$) and Session x $1/f$ were significant ($\chi2(1) = 14.65$, $p < .001$). By contrast, the beta model showed a significant Condition x Session x $1/f$ interaction ($\chi2(1) = 25.37$, $p <.001$), suggesting that differences in task-evoked EEG power in the ~13 – 30 Hz range may reflect alterations in underlying spiking activity attributed to a period of sleep versus wake (Freeman & Zhai, 2009; Voytek et al., 2015) instead of memory-related changes in the organisation of underlying neuronal assemblies. Further, the two-way interactions between Condition and Session on the $1/f$ exponent in the theta and alpha bands suggests potential time-of-day effects. To control for these differences, we included the $1/f$ exponent as a covariate in all statistical models examining differences between the Sleep and Wake conditions. This approach reduces the amount of variance in the residual error term, increases statistical power, and has been adopted as an alternative baselining approach in ERP research (Alday, 2019).

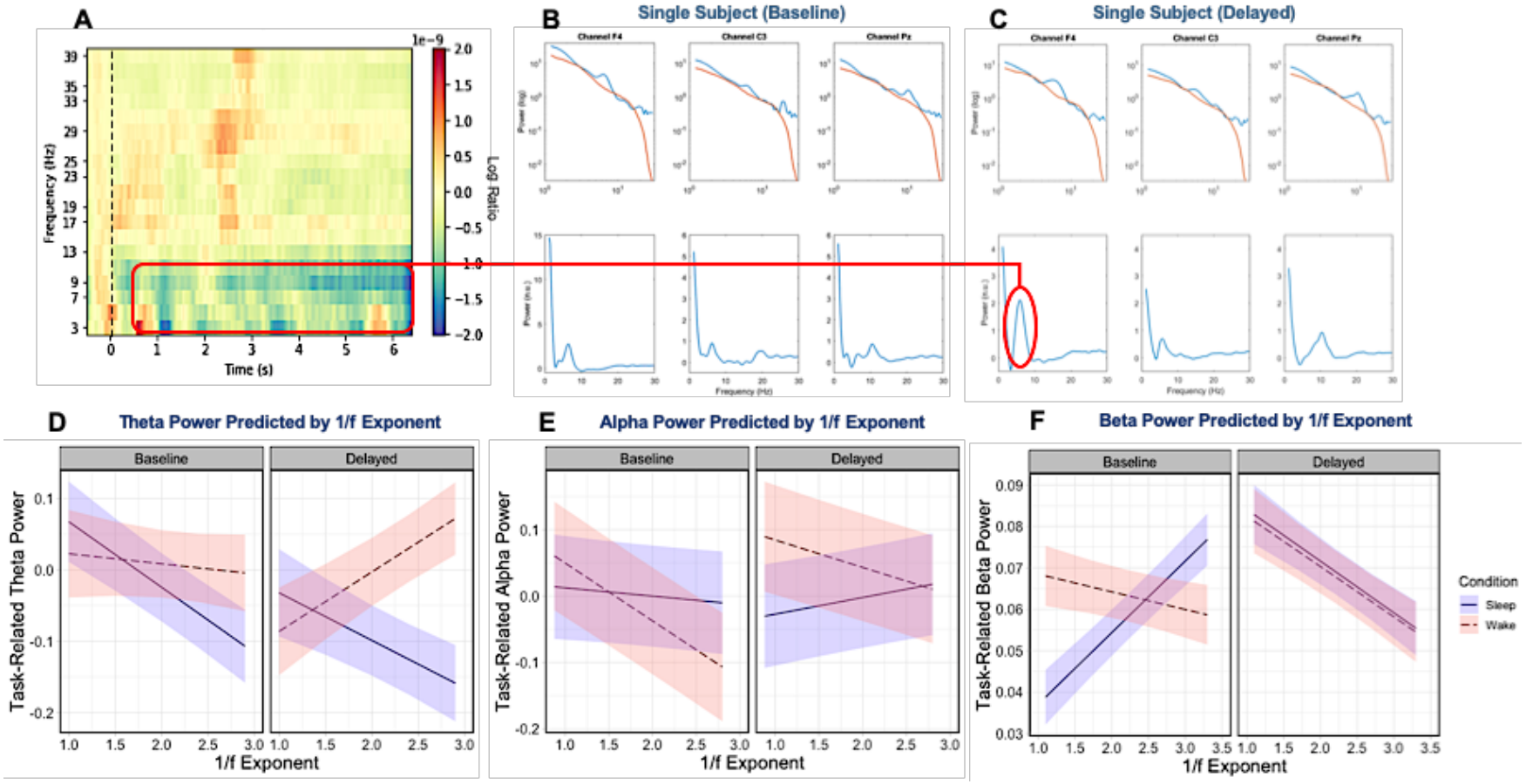

Figure 3. (A) ERSP plot of changes in spectral power for a single participant at electrode F4 for the AbaUV condition at Delayed testing. The dashed line represents stimulus onset. Figures **(B)** and **(C)** illustrate extracted power spectral density (PSD) estimates of fractal and oscillatory dynamics for the same participant for electrodes F4, C3 and Pz across Baseline and Delayed testing, respectively. All panels are PSD estimates for the AbaUV sentence condition. The bottom row reflects the difference wave between the Total (blue) and Fractal (red) PSD estimates that are illustrated in the top row of each panel. Figures **(D)**, **(E)** and **(F)** illustrate the modelled effects between task-related power (y-axis), the $1/f$ exponent (x-axis) and testing session (Baseline, Delayed) for theta, alpha and beta activity (left to right), respectively. The Sleep condition is the pink solid line, while the Wake condition is the dashed blue line. The shaded areas illustrate the 83% confidence interval.

4.2.2. Neuronal oscillations and incremental sentence processing.

We then examined task-evoked power in the theta, alpha and beta bands at Baseline and Delayed testing during the sentence judgement tasks between the Sleep and Wake conditions, as illustrated in Figure 4. The first model focussed on oscillatory activity in the theta band. Our analysis revealed a significant Power x Session x Condition interaction ($\chi2(1) = 5.18$, $p = .02$): while an increase in task-evoked theta power predicted a decrease in the proportion of correct responses at Baseline testing for both conditions, the slope was steeper for the Sleep condition. Further, at Delayed testing, the effect of theta on behaviour diminished for both the Sleep and Wake conditions; however, the effect was more inverted for the Sleep condition. This suggests that greater theta desynchronization shortly after learning is associated with more accurate sentence processing, while an increase in theta synchronisation after a delay period of sleep relative to an equivalent period of wake correlates with enhanced sensitivity to grammatical violations.

Next, we tested whether task-evoked alpha power was modulated by a period of sleep compared to an equivalent period of wake. We observed a main effect of Power ($\chi2(1) = 20.89$, $p < .001$) and Session ($\chi2(1) = 30.09$, $p < .001$) and a Power x Session x Condition interaction ($\chi2(1) = 34.66$, $p < .001$): increased alpha power predicted a decrease in the proportion of correct responses at Baseline for both conditions, while an increase in alpha power predicted a higher proportion of correct responses at Delayed testing for the Sleep condition but not the Wake condition.

Finally, we assessed the relationship between task-evoked beta power, sleep and performance on the judgement tasks. A main effect of Power ($\chi2(1) = 16.05$, $p < .001$) and Session ($\chi2(1) = 23.57$, $p < .001$) showed that the proportion of correct responses was predicted by modulations in beta power and time (Baseline to Delayed testing). There was also a Power x Session x Condition interaction ($\chi2(1) = 4.62$, $p = .03$): while a decrease in beta power at Baseline testing predicted an increase in the proportion of correct responses for both conditions, an increase in beta power at Delayed testing predicted an increase in the proportion of correct responses for the Sleep condition, while the reverse was observed for the Wake condition (for full model summaries, see the Supplementary Materials).

Taken together, our analyses demonstrate that sleep relative to an equivalent period of wake results in a shift in the relationship between alpha/beta power and performance: directly after learning, greater alpha/beta desynchronization predicted a higher proportion of correct responses, while greater alpha/beta synchronisation predicted behaviour after a delay period containing sleep. This effect was similar but less pronounced for theta activity, indicating a delay period after learning rather than sleep *per se* may influence the effect of task-evoked low frequency activity on sentence processing.

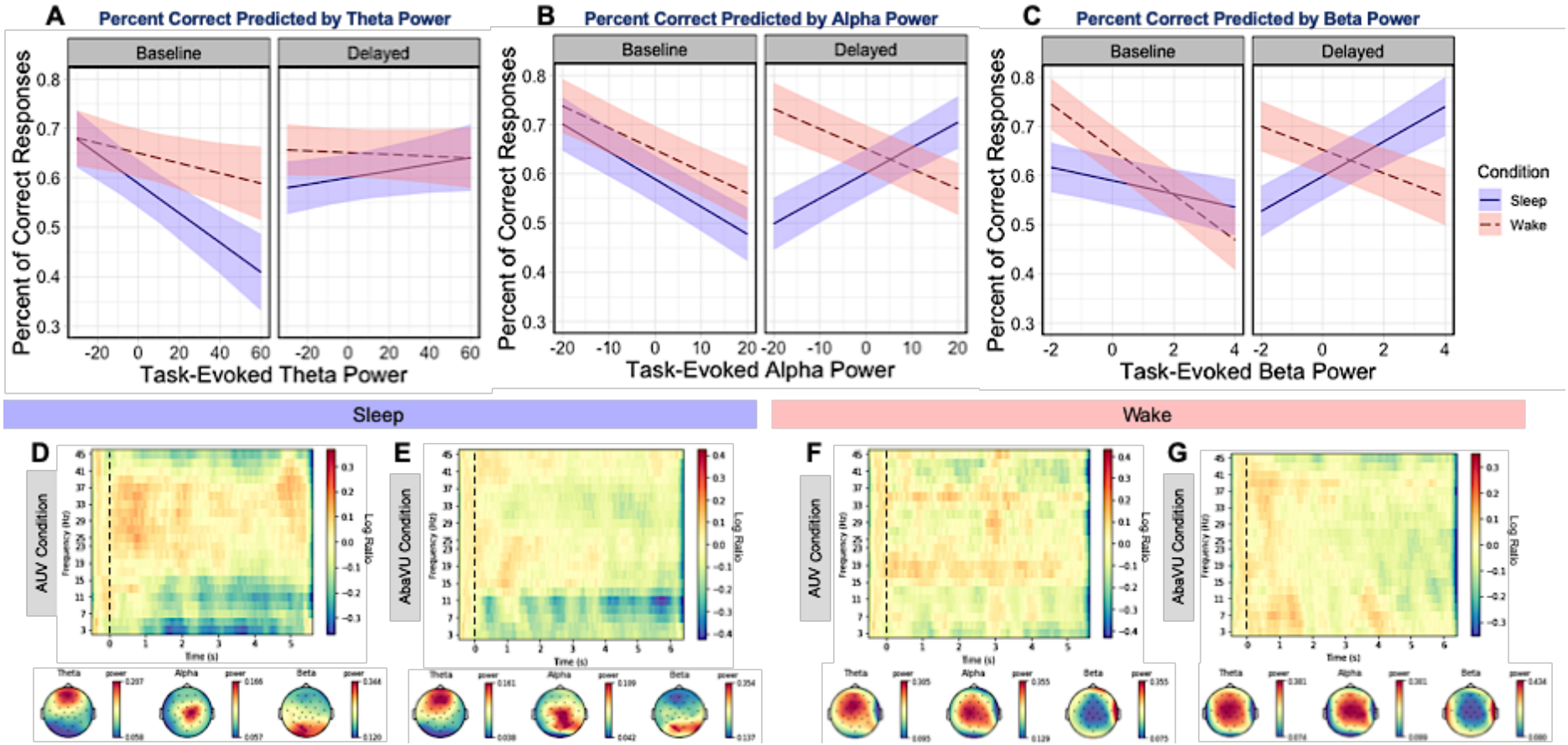

Figure 4. Relationship between task-evoked oscillatory activity and percent of correct responses between conditions at Baseline and Delayed testing for the **(A)** theta, **(B)** alpha and **(C)** beta bands. The bottom half of the figure illustrates ERSP plots for the Sleep and Wake conditions at Delayed testing for sentence violation conditions with flexible (**D**, **F**) and fixed (**E**, **G**) word orders. Topographical plots for the three frequency bands are provided under each ERSP plot. All ERSP plots are derived from electrode Cz.

4.2.3. Associations between NREM neurophysiology and memory retention

Given that we observed clear differences between the Sleep and Wake conditions on the relationship between frequency-band power and behavioural performance, the next step was to examine whether the significant four-way interaction in section 4.1. "Behavioural Results" can be explained by correlates of sleep-related memory consolidation. Based on recent research (e.g., Helfrich et al., 2018; Holz et al., 2012; Mikutta et al., 2019), we focussed on two cardinal markers of sleep-related memory consolidation: (1) the coupling strength between maximal spindle amplitude and the phase of the slow oscillation, and (2) spindle onset relative to the phase of the SO. While Phase did not significantly predict changes in behavioural performance across sleep (Phase x Type x Grammatically: $\chi2(1) = .13$, $p = .71$), there was a significant Coupling x Type x Grammatically interaction on behavioural difference scores ($\chi2(1) = 4.97$, $p = .02$); see Figure 5A and 5B for the preferred spindle onset to SO phase and phase of SO of maximal spindle amplitude, respectively).

As is illustrated in Figure 5C, there was no effect of spindle-SO coupling on performance for ungrammatical fixed and flexible word order sentences; however, stronger spindle-SO coupling predicted improvements in performance for grammatical flexible word order sentences and losses for grammatical fixed word order sentences, respectively. These results suggest that the rules governing flexible word order sentences benefit from stronger sleep-based consolidation and may be prioritized over the rules governing fixed word order sentences. Figure 7 illustrates single participant variability in peak spindle activity and a full-night multi-taper spectrogram.

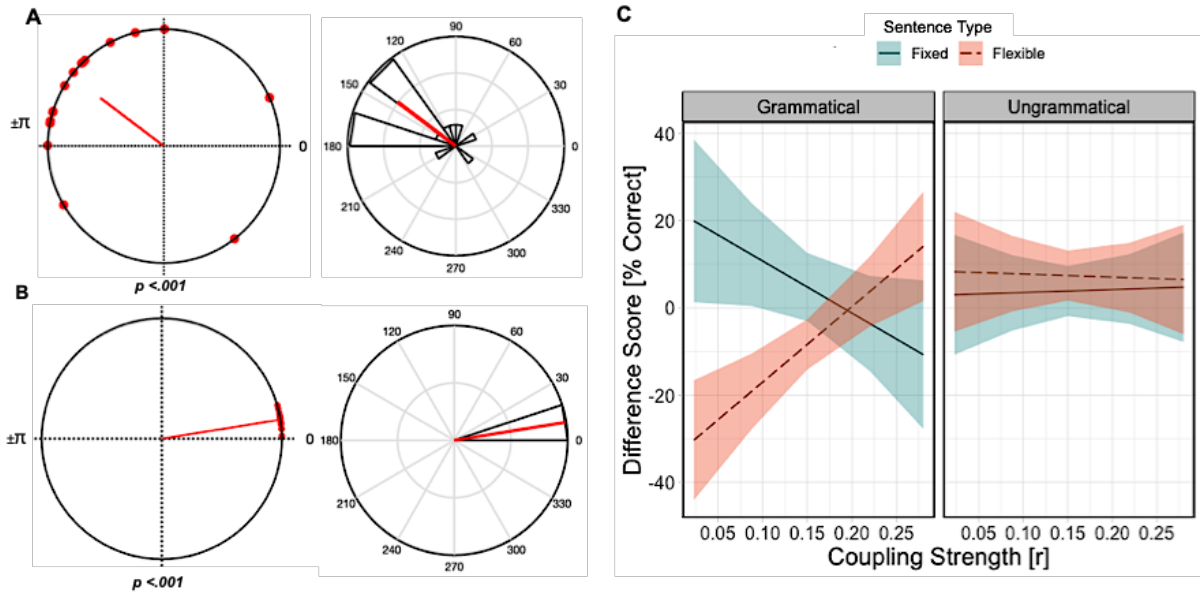

Figure 5. (A) Preferred phase of SO to spindle onset. **(B)** Maximal spindle amplitude to SO phase. **(C)** Modelled effects between spindle-SO coupling (x-axis; left = weaker coupling, right = stronger coupling) Sentence Type (solid blue = fixed word order sentences, dashed orange = flexible word order sentences) and Grammaticality (left = grammatical, right = ungrammatical) on difference scores (y-axis; positive values indicate an improvement in performance from Baseline to Delayed testing). The red circles on plots A and B represent individual participants, while the solid red lines represent the mean vector length of the circular distributions.

4.2.4. Spindle-SO coupling modulates task-evoked oscillatory activity and behavioural sensitivity to grammatical violations.

Next, we addressed whether NREM neurophysiology modulates task-evoked oscillatory activity during sentence processing, and whether this interaction predicts sensitivity to grammatical violations. Given that we observed a significant effect of spindle-SO coupling on difference scores for grammatical fixed and flexible word order sentences, we implemented a linear mixed-effects analysis for the theta, alpha and beta bands, with coupling strength, task-evoked power and the $1/f$ exponent as fixed effects, focussing on grammatical fixed and flexible sentence types. The dependent variable was difference scores in percent of correct responses between Baseline and Delayed testing.

We observed significant Coupling Strength x Power x Sentence Type interactions for all three bands (Theta: $\chi2(1) = 72.37$, $p < .001$; Alpha: $\chi2(1) = 84.31$, $p < .001$; Beta: $\chi2(1) = 86.35$, $p < .001$). These interactions were resolved in Figure 6, which illustrates a clear and differential influence of spindle-SO coupling strength on task-evoked oscillatory activity and sensitivity to fixed and flexible sentences. As is shown in Figure 6, task-evoked theta and alpha activity interact similarly with spindle-SO coupling strength to influence the detection of fixed and flexible word order sentences. Specifically, when spindle-SO coupling strength is weak, greater theta/alpha desynchronization predicts higher performance for fixed word order sentences, but a decrease in performance for flexible word order sentences. This relationship diminishes with strong spindle-SO coupling. By contrast, when spindle-SO coupling is weak, greater task-evoked beta synchronisation predicts the detection of fixed word order sentences, while the inverse is observed with strong spindle-SO coupling. There was no effect of spindle-SO coupling and beta power on performance for flexible word order sentences.

Together, these results demonstrate that low-frequency task-related activity (i.e., < 12 Hz) differentially influence the processing of different word order permutations when spindle-SO coupling is weak, while high task-related frequency activity (i.e., > 13 Hz) and weak spindle-SO coupling facilitates successful sentence processing for fixed but not flexible word order sentences.

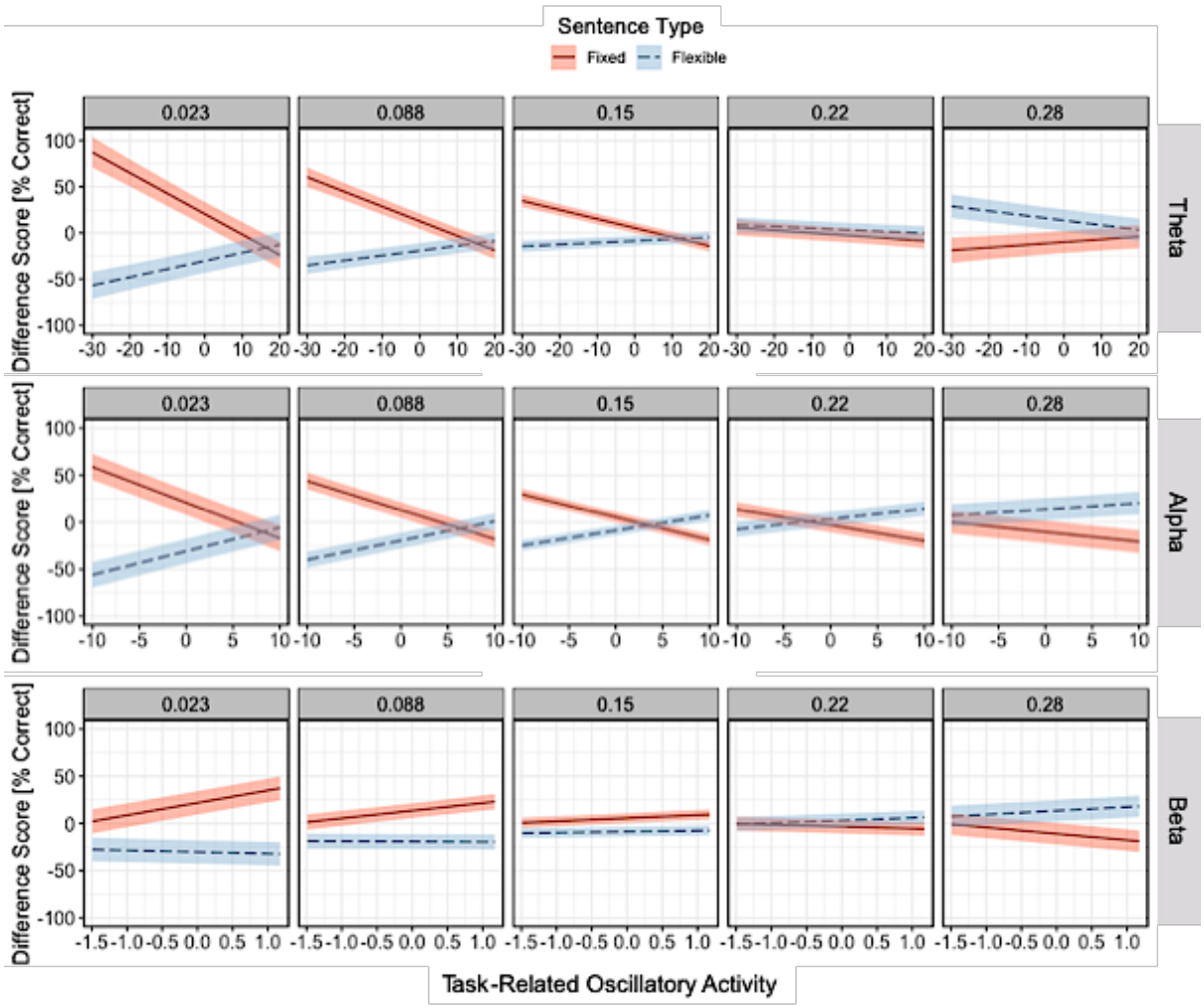

Figure 6. Modelled effects of (a) task-evoked power in each frequency band (top = theta, middle = alpha, bottom = beta) and (b) spindle-SO coupling strength on differences in proportion of correct responses between Baseline and Delayed testing (y-axis; positive scores indicate an improvement in performance). Task-evoked theta, alpha and beta power are represented on the x-axis (left = greater desynchronization, right = greater synchronization), while coupling strength is faceted from low (left) to high (right). The lines represent Sentence Type: the orange solid lines represent fixed word order sentences, while the blue dashed line represents flexible word order sentences.

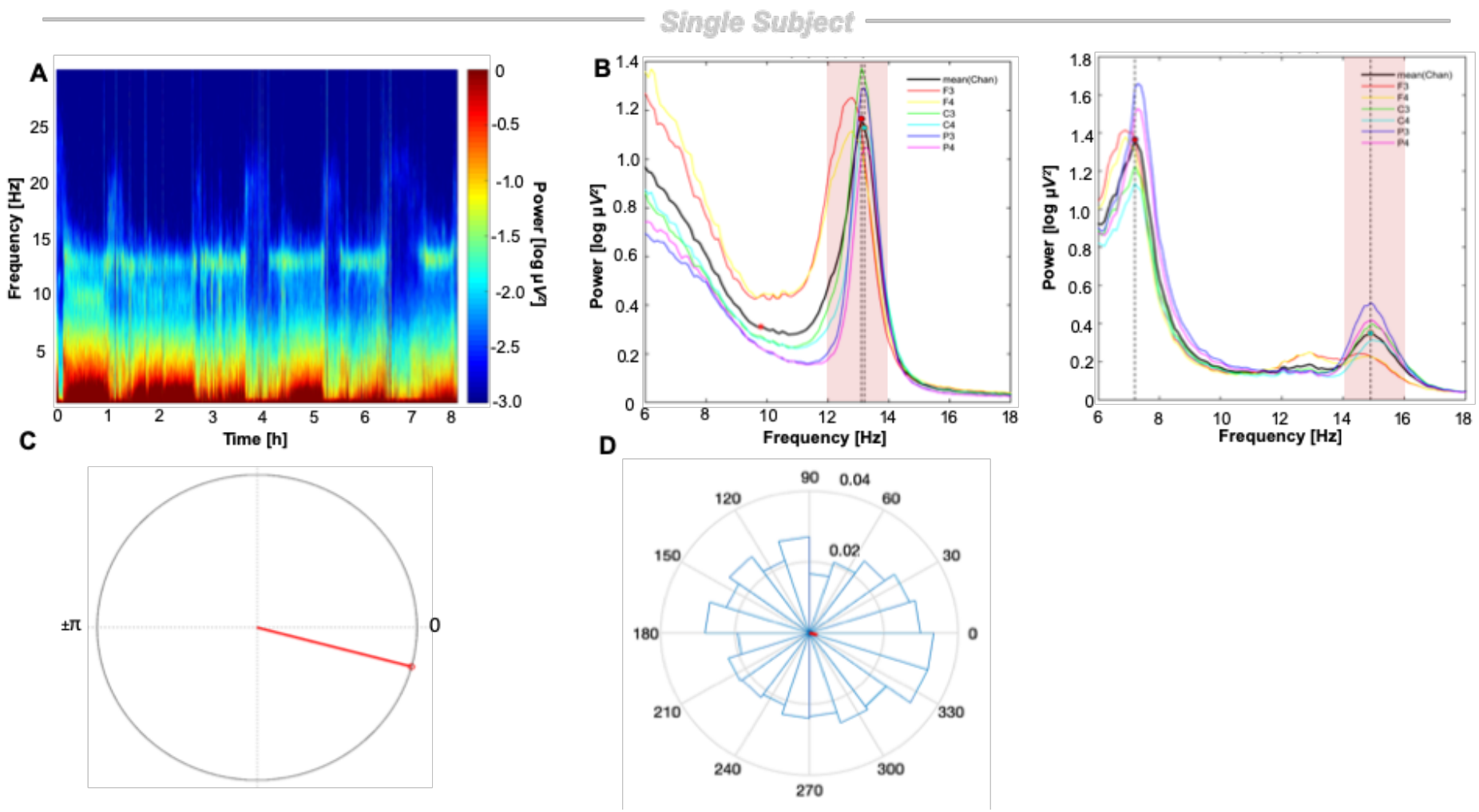

Figure 7. Sleep EEG analyses during NREM sleep for a single participant. **(A)** Hypnogram and full-night multi-taper spectrogram. **(B)** Power spectrum density plot illustrating differences in peak spindle frequency between two participants across six electrodes. **(C)** and **(D)** circular histogram of maximal amplitude of detected spindle events relative to the SO phase. All plots are derived from electrode C4.

4.2.5. Statistical learning ability modulates task-evoked beta power.

As an exploratory analysis, we examined the relationship between statistical learning ability, task-evoked beta power and accuracy on the judgement tasks. This analysis was conducted to test the idea that statistical learning ability is a domain-general mechanism underlying language learning (Daltrozzo et al., 2017; Siegelman et al., 2016), and that language-related predictions during sentence processing are reflected in beta activity (Cross et al., 2018; Lewis et al., 2015). In accord with prior literature, a beta regression indicated that statistical learning ability positively predicted proportion of correct responses ($\chi2(1) = 12.38$, $\beta = .01$, pseudo $R^2 = .29$, $p < .001$). Our main analysis revealed a significant interaction between statistical learning ability and task-related beta power ($\chi2(1) = 30.08$, $p < .001$). As illustrated in Figure 8B, proportion of correct responses at low levels of beta power tended to increase as a function of statistical learning ability. This association diminished as beta power increased.

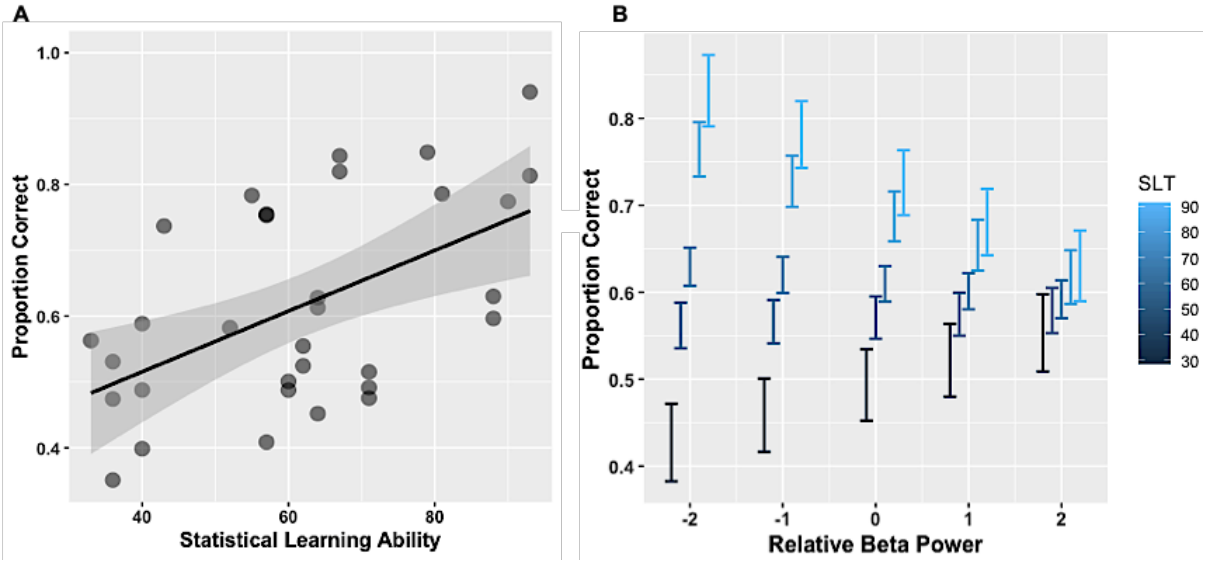

Figure 8. (A) Relationship between statistical learning ability (x-axis) and proportion of correct responses (y-axis). **(B)** Modelled effects between statistical learning ability, task-evoked beta power and proportion of correct responses on the sentence judgement tasks. Statistical learning ability is represented in the dark to light blue gradient (low-high), while beta power is represented on the x-axis (left = greater desynchronization, right = greater synchronization). Proportion of correct responses is represented on the y-axis.

5. DISCUSSION

The coordination between SOs and sleep spindles has been hypothesised to provide an optimal temporal receptive window for hippocampal-cortical communication during sleep-related memory consolidation (Helfrich et al., 2019; Staresina et al., 2015). Here, we show that the interaction between these cardinal markers of NREM sleep extends to the consolidation and generalisation of complex sentence-level regularities. Behaviourally, we demonstrated that a period of sleep compared to an equivalent period of wake benefits the consolidation of fixed relative to flexible word order rules, and that this effect is modulated by the strength of spindle-SO coupling. Our results further reveal that spindle-SO coupling is likely to (1) be associated with changes in task-evoked oscillatory activity in the theta, alpha, and beta bands during sentence processing; (2) that this effect is not explained by sleep-induced changes in the $1/f$

distribution of broadband neural activity; and (3) that it may result in qualitatively distinct topographical distributions in frequency-band activity relative to an equivalent period of wake, possibly reflecting alterations in underlying memory-related neuronal populations. Moreover, we demonstrated that beta power during sentence processing correlates with individual differences in statistical learning ability, and that this effect interacts with performance on our language task. This observation suggests that beta activity may play a more domain-general role during language learning and sentence processing.

5.1. Beyond single word learning: a role for sleep in consolidating word order rules

Using a complex modified miniature language paradigm, we demonstrated that a period of sleep facilitates the extraction of fixed relative to flexible word order rules. Importantly, the key distinction between these word order permutations is that successful interpretation of fixed word order sentences relates to the linear position of the noun phrases and verb (i.e., the first noun phrase is invariably the Actor and is verb-final). By contrast, successful interpretation of flexible word order sentences depends more heavily on the animacy of the nouns. As such, fixed word order sentences, requiring a more linear order-based interpretation, are more compatible with an English word-order-based processing strategy (Bornkessel & Schlesewsky, 2006; Bornkessel-Schlesewsky et al., 2015; MacWhinney, Bates, & Kliegl, 1984). However, while the Sleep condition was more sensitive to fixed than flexible word order rules (Figure 2B), stronger spindle-SO coupling predicted improved performance for flexible word order sentences and predicted a deterioration in performance for fixed word order sentences. While this might contradict the effect reported in Figure 2B, we believe that these findings support the Complementary Learning Systems model (McClelland, McNaughton, & O'Reilly, 1995; Norman, 2010), in that generalization of non-canonical word order rules may have relied more heavily on the hippocampal system and thus benefited more from sleep-associated consolidation. This is in contrast to the fixed word order rules which may have been more systematic with existing grammatical knowledge and thus required less sleep-associated consolidation and generalization and thus were more rapidly integrated with existing neocortical memory systems (Dingemanse, Blasi, Lupyan, Christiansen, & Monaghan, 2015; Gilboa & Marlatte, 2017; Mirković & Gaskell, 2016; Tse et al., 2007). This prioritization of novel, non-canonical word order rules may have also had a knock-on effect on the consolidation of the fixed word order rules, resulting in the inverse relationship observed between spindle-SO coupling, fixed word order sentences and behavioural performance.

Taken together, higher order language learning appears to depend on existing knowledge, with mechanisms of sleep-related memory consolidation generalizing novel linguistic information over grammatical rules that are compatible with prior knowledge. Next, we discuss how the neurobiological processes underpinning the beneficial effect of spindle-SO coupling on memory consolidation extends to higher order language learning.

5.2. Spindle-SO coupling as a neurobiological marker of sleep-associated memory consolidation and higher-order language learning

Recent work has demonstrated that the coupling between SOs and spindles predicts successful overnight memory consolidation (Helfrich et al., 2018; Mikutta et al., 2019;

Muehlroth et al., 2019; Niknazar, Krishnan, Bazhenov, & Mednick, 2015). However, these studies often utilised old-new paradigms with single words (Helfrich et al., 2018; Mikutta et al., 2019) or word-image pairs (Muehlroth et al., 2019), leaving the functional relevance of these NREM oscillations for the generalisation of more complex linguistic information unknown. Moreover, such sleep-related memory effects are typically reported at the behavioural level, overlooking the critical influence that these effects may have on task-evoked neural activity.

Adding to this body of literature, we have demonstrated that the generalisation of non-canonical grammatical rules is facilitated by the strength of NREM spindle-SO coupling. Mechanistically, during SWS, the cortex is highly synchronised during the up state of the SO, allowing effective interregional communication, particularly between the prefrontal cortex and hippocampal complex. It is during this SO up state that spindles induce an influx of Ca^{2+} into excitatory neurons, enabling synaptic plasticity and the generalisation and stabilisation of memory traces (Niknazar et al., 2015). From this perspective, the interaction between these cardinal markers of sleep-related memory processing appear to extend beyond the consolidation of single words and images and to the generalisation of sentence-level regularities.

In the following, we discuss how spindle-SO coupling, as a marker of sleep-associated memory consolidation, modulates task-related aperiodic and oscillatory activity, as well as the mechanisms such changes might reflect during sentence processing.

5.3. Task-evoked theta power reflects sleep-induced changes in $1/f$ activity

The role of narrowband (oscillatory) neural activity has been studied extensively in relation to memory formation (Backus et al., 2016; Johnson & Knight, 2015; Klimesch, Freunberger, & Sauseng, 2010; Osipova et al., 2006) and language processing (for review, see Meyer, 2017). However, the majority of this evidence overlooks broadband changes in spectral activity (c.f. Sheehan, Sreekumar, Inati, & Zaghloul, 2018), including changes in the dominant $1/f$ distribution of power after a period of sleep. Recent evidence suggests that broadband neural activity may be functionally and behaviourally relevant, including for language (Dave et al., 2018) and memory processing (Sheehan et al., 2018). Sheehan et al. (2018) found that human intracranial EEG (iEEG) theta power during a memory task is dynamically related to the $1/f$ slope, while Ouyang and colleagues (2019) revealed that $1/f$ activity explains cognitive processing speed above that of alpha activity. Here, we demonstrated that $1/f$ activity after a period of sleep covaries with low-frequency task-related activity during sentence processing, such that a decrease in task-related theta power was predicted by a steeper $1/f$ slope after an 8hr sleep opportunity relative to an equivalent period of wake.

Sleep-related effects on memory retrieval have been reported in the theta band (Bakker et al., 2015; Schreiner et al., 2015), with greater theta power interpreted as reflecting strengthened memory traces induced by sleep-dependent consolidation. However, these studies did not control for changes in $1/f$ activity. Based on recent observations, low frequency power changes recorded via scalp EEG may also reflect a dynamic global shift in the

exitatory/inhibitory ratio of memory-related cortical networks (Muthukumaraswamy & Liley, 2018; Peterson, Rosen, Campbell, Belger, & Voytek, 2018; Voytek et al., 2015). As such, our finding that greater task-evoked theta desynchronisation at Delayed testing was predicted by $1/f$ activity demonstrates, at least in part, that $1/f$ and oscillatory activity dynamically contribute to information processing and memory retrieval (Fellner et al., 2019; Sheehan et al., 2018) during sentence processing.

We also observed that spindle-SO coupling interacted with task-evoked theta power to predict behavioural performance after controlling for variation in the $1/f$ slope. Specifically, when spindle-SO coupling strength was low, higher performance for fixed word order sentences was predicted by a decrease in theta power, while the inverse was observed for flexible word order sentences, and this effect diminished when spindle-SO coupling was high. In line with systems consolidation theory (Born & Wilhelm, 2012), NREM oscillatory activity contributes to the consolidation of newly encoded memory representations, which may manifest in stronger theta power during retrieval, indicating a stronger memory trace (Schreiner et al., 2015). Our findings do not directly match this prediction given we did not observe a significant association between increased theta power and grammaticality judgements at Delayed testing in the Sleep condition. However, our results do reveal that when spindle-SO coupling is high, the relationship between task-evoked theta activity and behavioural performance diminishes. This suggests that NREM oscillatory activity not only strengthens newly encoded memory traces, but also offers an explanation regarding the relationship between $1/f$ activity and task-evoked theta activity. Specifically, NREM oscillatory activity facilitates the downscaling of synaptic weight accumulated during wakefulness (Tononi & Cirelli, 2014), and in doing so, modifies the signal-to-noise ratio during memory retrieval. Theta and $1/f$ activity may therefore reflect separable aspects of memory processing, as demonstrated by Sheehan et al. (2018), with sleep-associated changes in synaptic weight manifesting in more pronounced $1/f$ activity and a marked decrease in task-evoked (theta) oscillatory activity.

5.4. Alpha oscillations reflect sleep-related effects on attention and perception

At Delayed testing, an increase in alpha power predicted an increase in correct responses for the Sleep condition, while the reverse was observed for the Wake condition. It is argued that one function of alpha synchronisation is to prevent competing memory traces from being concurrently activated during memory retrieval (Hanslmayr, Staudigl, & Fellner, 2012). Increased alpha power during memory processing has also been argued to reflect goal-directed inhibition and disengagement of task-irrelevant brain regions (Kepinska, Pereda, et al., 2017; Park et al., 2014). From this perspective, those who slept may have had greater access to more fine-tuned and integrated memory representations, while those in the Wake condition required more effortful processing (as reflected in decreased alpha power) in order to efficiently bind individual words to form a coherent sentential percept. This interpretation is in line with Kepinska et al. (2017), who reported that greater alpha power predicted enhanced behavioural performance on a language learning task for individuals with a greater language learning aptitude. As such, similar to those with a higher aptitude who have the ability to learn complex

language-related regularities, sleep-based consolidation mechanisms may serve a functional role in fine-tuning networks involved in processing a newly learned language (Cross et al., 2018), requiring less attentional resources post-sleep to process incoming task-relevant stimuli. An increase in alpha dysynchronisation may therefore reflect more effortful processing by suppressing the input of irrelevant cortical regions to efficiently retrieve encoded memory traces to interpret incoming linguistic information.

This interpretation is also in line with principles of predictive coding: recent work has demonstrated that sleep results in increased prediction accuracy for sequence knowledge (Lutz et al., 2018), and has been used to explain sleep-based consolidation effects of linguistic stimuli (Rauss & Born, 2017). Predictive-coding accounts (e.g., Friston, 2010; Hobson & Friston, 2012; Rauss & Born, 2017) conceive the brain as a prediction engine that infers the causes of its sensory states by modelling the statistical regularities of its environment. Further, given that sleep optimises cortical memory representations through a process of active consolidation and generalisation, the relationship between an increase in alpha power post-sleep and enhanced behavioural responses might reflect the propagation of top-down predictions during sentence processing, an interpretation supported by recent computational work (Alamia & VanRullen, 2019).

It is also important to note the differences between the current study and studies examining event-related changes in alpha activity in response to more general aspects of memory. Previous research has reported increased alpha desynchronization during memory retrieval (Fellner et al., 2019; Hanslmayr, Staresina, & Bowman, 2016; Hanslmayr et al., 2012). These studies often employ episodic memory tasks of word-scene (Minarik, Berger, & Sauseng, 2018) and word-word pairs (Martín-Buro, Wimber, Henson, & Staresina, 2019), likely requiring different processing demands than incremental sentence processing of a newly learned language. Analogous to this research, we found that a decrease in alpha power predicted greater behavioural gains in the Wake condition. As such, the correlation between increased alpha power on behavioural performance may manifest as a result of overnight consolidation processes, rather than a 10-minute delay period from learning to retrieval (e.g., Minarik et al., 2018). Functionally, this relationship between increased alpha power and enhanced behavioural performance may reflect a thalamo-cortical gating mechanism, preferentially processing memory representations that have undergone sleep-based consolidation.

5.5. Beta power indexes statistical learning ability and predictive coding during sentence processing

Current models of beta oscillations and sentence processing (Lewis, Schoffelen, Schriefers, & Bastiaansen, 2016; Lewis et al., 2015, 2015) predict that during sentence comprehension, an increase in beta power reflects the maintenance of model predictions, while a decrease in beta power reflects prediction error signals. Based on emerging evidence for the role of sleep in forming hierarchical predictive models (Friston, 2010; Hobson & Friston, 2012; Lutz et al., 2018; Rauss & Born, 2017), we predicted that sleep-based memory consolidation, linked to reductions in synaptic weight (Tononi & Cirelli, 2014), would accentuate beta power

during sentence processing relative to an equivalent period of wake, with this increase predicting greater sensitivity to grammatical violations (Cross et al., 2018). Results from the current study support this hypothesis: an increase in post-sleep beta power during sentence processing predicted an increase in the proportion of correct responses, while the reverse was observed after an equivalent period of wake.

These results provide empirical support for the proposal that oscillatory beta activity reflects top-down predictions (Fontolan, Morillon, Liegeois-Chauvel, & Giraud, 2014; Lewis & Bastiaansen, 2015; Lewis et al., 2015), and that these predictive codes are strengthened during sleep. We also demonstrated that statistical learning ability interacts with beta power on behavioural performance: as statistical learning ability increased and beta activity decreased, proportion of correct responses increased (Figure 7). This suggests that individuals with a greater sensitivity to statistical regularities are also more efficient at integrating new linguistic input into current sentence-level representations. This is in line with idea that an unpredicted change in the (linguistic) sensory input results in a decrease in beta power, or that beta power increases in a direction-specific manner in response to incoming linguistic information with high levels of certainty (Lewis & Bastiaansen, 2015; Lewis et al., 2015).

5.6. Limitations and future directions

One major limitation of the current study is the lack of an adaptation night and further control conditions, making it difficult to disentangle circadian effects on sleep and memory (e.g., Tucker et al., 2017). While our experimental design is analogous to previous work, future studies should include groups in AM-PM (12h Wake), PM-AM (12h Sleep), PM-PM (24h Sleep early) and AM-AM (24h Sleep late), as recommended by Nemeth, Gerbier and Janacsek (2019). We did, however, model participants' sleepiness levels in our statistical analyses, which partially controlled for potential time-of-day effects. Further, the evidence presented here is correlational and neuroanatomical inferences are unable to be drawn based on scalp-recorded EEG. However, this is the first study to relate sleep-based memory consolidation mechanisms to sentence-level oscillatory activity, and as such, has set the foundation for future work using techniques with greater spatial-temporal resolution. For example, electrocorticography and stereoelectroencephalography would allow for a better characterization of task-evoked cortical dynamics and spindle-SO coupling between cortical regions and the hippocampal complex, respectively (Helfrich et al., 2019, 2018). This approach could be further complemented by demonstrating a selective reinstatement of memory traces during spindle-SO coupling using representational similarity analysis (Zhang, Fell, & Axmacher, 2018). Specifically, identifying stimulus-specific representations during the encoding of sentence-level regularities and tracking the replay of stimulus activity related to spindle-SO events would further demonstrate the critical role of sleep-based oscillatory mechanisms on higher-order language learning.

5.7. Conclusion

In summary, our results demonstrate that the temporal coupling between NREM SOs and spindles subserves the consolidation of complex sentence-level regularities. In particular, we demonstrated that spindle-SO coupling promotes the consolidation of non-canonical word

order rules, and also modulates task-evoked oscillatory activity previously implicated in language learning (Diego-Balaguer et al., 2011; Kepinska et al., 2017) and sentence processing (Meyer, 2017). Our results also show that changes in task-evoked low frequency activity (i.e., < 7 Hz) may be susceptible to sleep-related changes in the $1/f$ slope, providing an alternative interpretation for theta-related sleep-dependent consolidation effects (Schreiner et al., 2015). As such, these findings add to models of sleep-based memory consolidation (e.g., Born & Wilhelm, 2012; Lewis & Durrant, 2011) and help characterise how effects of sleep-related oscillatory dynamics on memory manifest in oscillatory activity during complex language-related combinatorial operations.

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