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Slow oscillation-spindle coupling predicts sequence-based language learning

Zachariah R. Cross[1,2*], Randolph F. Helfrich[3], Andrew W. Corcoran[1,4], Mark J. Kohler[5], Scott W. Coussens[1,5], Lena Zou-Williams[1], Matthias Schlesewsky[1], M. Gareth Gaskell[6], Robert T. Knight[7,8], Ina Bornkessel-Schlesewsky[1]

[1]Cognitive Neuroscience Laboratory, University of South Australia, Adelaide, Australia, 5072.
[2]Northwestern Feinberg School of Medicine, Chicago, Illinois, United States of America, 60611.
[3]Center for Neurology, Hertie-Institute for Clinical Brain Research, University of Tübingen, Germany, 72076.
[4]Monash Centre for Consciousness and Contemplative Studies, Monash University, Melbourne, Australia, 3800.
[5]Faculty of Health and Medical Sciences, The University of Adelaide, Adelaide, Australia, 5000.
[6]Department of Psychology, University of York, York, United Kingdom, YO10 5DD.
[7]Department of Psychology, UC Berkeley, Berkeley, California, USA, 94720.
[8]Helen Wills Neuroscience Institute, UC Berkeley, Berkeley, California, USA, 94720.

*Corresponding author: zachariah.cross@northwestern.edu

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Abstract

Sentence comprehension involves the rapid decoding of semantic and grammatical information, a process fundamental to communication. As with other cognitive processes, language comprehension relies partly on long-term memory. However, the electrophysiological mechanisms underpinning the initial encoding and generalisation of higher-order linguistic knowledge remains elusive, particularly from a sleep-based consolidation perspective. One candidate mechanism that may subserve the consolidation of language is the temporal coordination of slow oscillations (SO) and sleep spindles during non-rapid eye movement sleep (NREM). To examine this hypothesis, we analysed electroencephalographic (EEG) data recorded from 35 participants ($M_{age} = 25.4$, $SD = 7.10$; 16 males) during an artificial language learning task, contrasting performance between individuals who were given an 8hr nocturnal sleep period or an equivelant period of wake. We found that sleep relative to wake was associated with superior performance for rules that followed a sequence-based word order. Post-sleep sequence-based word order processing was associated with an increase in task-related theta power, an electrophysiological signature of successful memory consolidation. Frontal NREM SO-spindle coupling was also positively associated with behavioural sensitivity to sequence-based word order rules, as well as with task-related theta power. As such, theta activity during retrieval of previously learned information correlates with SO-spindle coupling, thus linking neural activity in the sleeping and waking brain. Taken together, this study presents converging behavioural and neurophysiological evidence for a role of NREM SO-spindle coupling and task-related theta activity as signatures of successful memory consolidation and retrieval in the context of higher-order language learning.

SIGNIFICANCE STATEMENT. The endogenous temporal coordination of neural oscillations supports information processing during both wake and sleep states. Here we demonstrate that slow oscillation-spindle 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 theta power predict enhanced sensitivity to grammatical violations after a period of sleep and strong slow oscillation-spindle 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.

Keywords: Sleep and memory; language learning; sentence processing; neural oscillations; cross-frequency coupling.

Introduction

The human brain is adept at extracting regularities from sensory input, a process pivotal for generating knowledge of one's physical and social environment (Santolin and Saffran 2018). Learning of such regularities plays a key role in the development of linguistic competencies, enabling the implicit acquisition of grammatical rules embedded in ambient speech (Cross et al. 2021; Isbilen, McCauley, and Christiansen 2022; Romberg and Saffran 2010, 2010). While this perspective of language learning has informed insights concerning the encoding of local dependencies, the acquisition of more complex linguistic structures remains less understood. Here, we address this gap from the perspective of sleep-based memory consolidation, a well-established mechanism governing the generalisation of knowledge from sensory experience (Brodt et al. 2023; Diekelmann, Wilhelm, and Born 2009; Xie, Earle, and Myers 2018).

A plethora of evidence (for review, see Rasch and Born 2013) demonstrates that sleep plays an active role in memory by consolidating and generalising mnemonic information. This dynamic account of the sleeping brain is captured by the Active System Consolidation hypothesis (ASC; Born and Wilhelm 2012; Klinzing, Niethard, and Born 2019). Core to ASC is that sleep facilitates repeated reactivation of encoded memory representations (Rasch and Born 2013). This reactivation is dependent on cortical glutamatergic synapses, which weaken during prolonged wakefulness (Kavanau 1997; Rasch and Born 2013). The ASC is supported by electrophysiological evidence that learned sequences are replayed during non-rapid eye-movement (NREM) sleep, potentially via sleep spindle and slow oscillatory (SO) activity. Sleep spindles are bursts of electrical activity occurring between 11 – 16 Hz, while SOs centred at 1 Hz reflect synchronized membrane potential fluctuations between hyperpolarised up-states and depolarised down-states of neocortical neurons (Crunelli and Hughes 2010; Vyazovskiy and Harris 2013). The precise coupling between SOs and spindles provides a temporal receptive window for the replay of hippocampal memory traces and their transfer to cortex for long-term storage (Bastian et al. 2022; Mikutta et al. 2019). Critically, the transfer of newly encoded information from hippocampus to cortex enables generalisation of mnemonic information, allowing cortex to gradually learn the regularities of sensory input – a process known to support language learning (Cross et al. 2018; Davis and Gaskell 2009; Rasch 2017).

Mechanisms of sleep-based memory consolidation have been associated with aspects of language learning, including novel-word learning (Bakker et al. 2015; James et al. 2017; Mirković and Gaskell 2016) as well as the generalisation of grammatical rules (Batterink et al. 2014; Nieuwenhuis et al. 2013). However, work examining the association between sleep and language often only involves behavioural measures as proxies for memory consolidation (e.g., (Mirković and Gaskell 2016; Nieuwenhuis et al. 2013), or examines structure (e.g., grammar; Nieuwenhuis et al. 2013) and meaning (i.e., semantics; Bakker et al. 2015; Batterink and Paller 2017; Batterink, Westerberg, and Paller 2017) in the language input separately (cf. Batterink et al. 2014). Neurobiological models of sleep and memory and language processing would benefit from a direct investigation of the relation between sleep and higher-order language, such as at the sentence level (Cross et al. 2018; Rasch 2017; Schreiner and Rasch 2017), in conjunction with online measures of neural activity. This would extend our understanding of the complexity of language learning beyond single words, and how the generalisation of newly acquired linguistic knowledge is supported by sleep (for review, see Cross et al. 2018) and how the brain learns environmental regularities that span multiple scales of complexity and how this information is organised across sleep and wake.

Here, we present data addressing the contribution of sleep-based memory consolidation to complex rule learning in language at the sentence level. We used the modified miniature language Mini Pinyin (Cross et al. 2021), which is modelled on Mandarin Chinese, to contrast rules that instantiate a fixed or flexible word order. Mandarin naïve Monolingual native English speakers completed a learning task where they were shown pictures of two-person events, followed by a sentence describing the event in the picture. During this task, participants learned varying word order rules without explicit instruction and then completed a baseline memory task prior to either 8hr of sleep or an equivalent period of wake (Figure 1). Participants then completed a delayed memory task to assess changes in memory of the word order rules after the 8hr delay.

We focussed on theta oscillations (~ 3 – 7 Hz), which were quantified using complex Morlet wavelets across sentence presentation during the memory tasks. Theta oscillations are implicated in relational binding and memory-based decision making (Backus et al. 2016; Buzsáki 2002; Jacobs et al. 2006). From this perspective, theta should track successful language learning and sleep-based consolidation (Cross et al. 2018). We further quantified whole-scalp NREM SO-spindle coupling. SO-spindle coupling as well as task-related theta power were used to independently predict language learning, and to determine whether task-related theta is modulated by sleep-based memory consolidation.

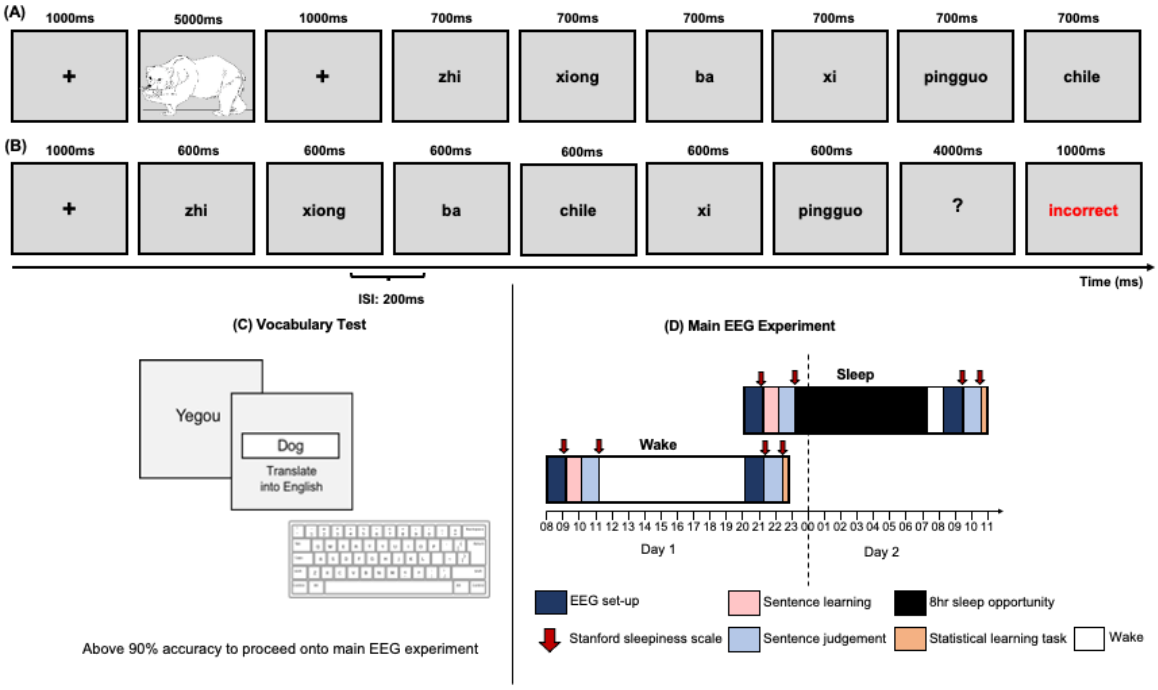


Fig 1. Illustration of stimulus presentation and experimental protocol. (A) Schematic representation of a single trial of a grammatical sentence during the sentence learning task. **(B)** Schematic representation of a single trial during the baseline sentence judgement task. This sentence is a violation of the verb-position, whereby the verb *chile* is positioned in the middle of the sentence when it should be positioned at the end of the sentence. Here, the participant incorrectly categorised this sentence as grammatical, and thus received feedback indicating that their response was incorrect. **(C)** Schematic diagram of the vocabulary test, which required participants to translate the nouns (e.g., *yegou*) into English (e.g., *dog*) using a keyboard. **(D)** Experimental protocol representing the time course of the conditions (sleep, wake) and testing sessions (sentence learning task, baseline, and delayed sentence judgement tasks). After completing the vocabulary test, participants were randomly assigned to either the sleep or wake conditions, with each participant only completing one of the two conditions. Time is represented along the x-axis, while each coloured block corresponds to a different task during the experimental protocol.

Methods

Participants

We recruited 36 right-handed participants who were healthy, monolingual, native English-speakers (16 male) aged 18 – 40 years old (M_{age} = 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 disorders, 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 (M_{age} = 25.4, SD = 7.10; 16 males; Sleep *n* = 17). Ethics approval was granted by the University of South Australia's Human Research Ethics committee (I.D: 0000032556).

Screening and control measures

The Flinders Handedness Survey (FLANDERS; Nicholls et al. 2013) was used to screen handedness, while the Pittsburgh Sleep Quality Index (PSQI; Buysse et al. 1989) screened for sleep quality. PSQI scores ranged from 1-5 (*M* = 2.9, *SD* = 1.33) out of a possible range of 0 – 21, with higher scores indicating worse 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.

Electroencephalography

The electroencephalogram (EEG) was recorded during the learning and sentence judgement tasks and sleep opportunities using a 32-channel BrainCap with sintered Ag/AgCl 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 1cm from 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.

Vocabulary and structure of Mini Pinyin

Stimuli consisted of sentences from a modified miniature language based on Mandarin Chinese (Cross et al. 2021). This language contained 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 illustrated in Figure 2B, *ge* specifies a human noun, *zhi* for animals, and *xi* and *da* for small and large objects, respectively. Overall, this stimulus set contained 576 unique sentences (288 grammatical, 288 ungrammatical) which are divided into two equivalent sets (see Cross et al. 2021 for a complete description of the stimuli; for the complete set of stimuli, visit: https://tinyurl.com/3an438h2).

We focussed on a subset of sentence conditions to investigate the mechanisms underlying the learning of different word order rules, which fundamentally differs between natural languages (for review, see Bates, Devescovi, and Wulfeck 2001). Languages like English and Dutch rely primarily on word order, while languages like German and Turkish rely more on cues such as case marking and animacy (Bornkessel and Schlesewsky 2006; Bornkessel-Schlesewsky et al. 2015; MacWhinney, Bates, and Kliegl 1984). From this perspective, Mini Pinyin enabled a comparison between sentences with differing word orders (see Figure 3A), and the influence sleep may have on the respective consolidation of fixed and flexible word order rules. The subset of stimuli in the current analysis contained 96 sentences in the sentence learning task and 144 sentences in the grammaticality judgement tasks. The remaining sentences were considered fillers. These filler sentences included sentences that violated classifier-noun pairs, and thus were not suitable for testing predictions regarding fixed and flexible word order processing (for a full description of all sentence conditions present in this language, please see Cross et al. 2021).

As is apparent in Figure 3A, 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.

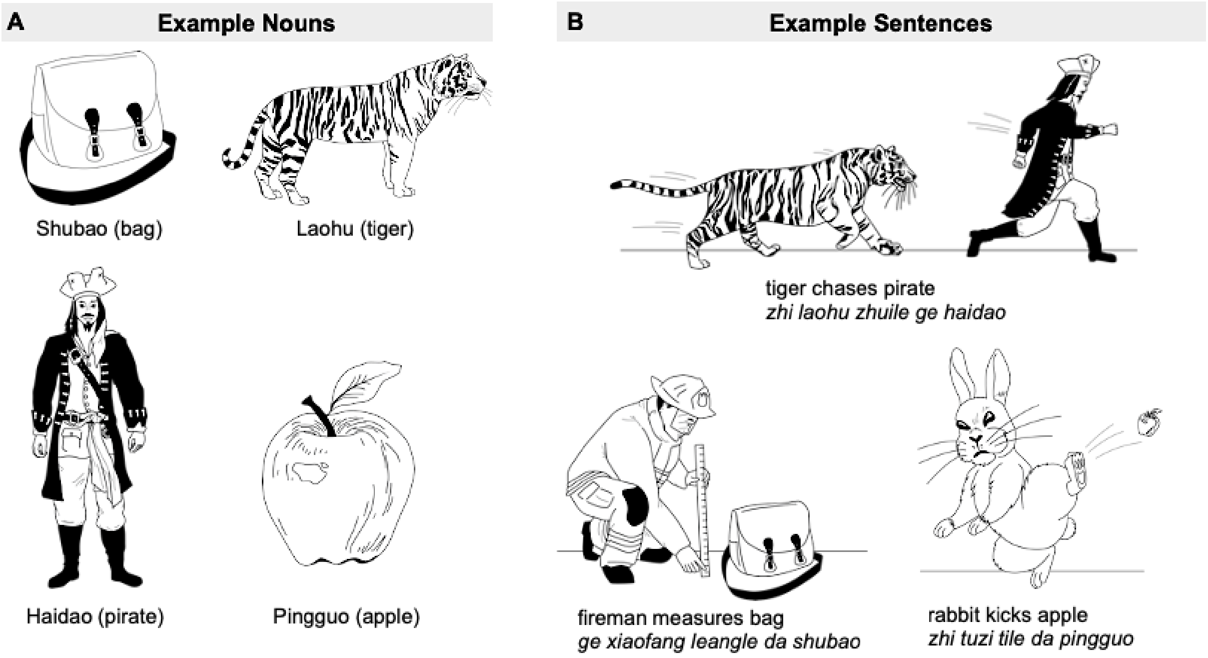
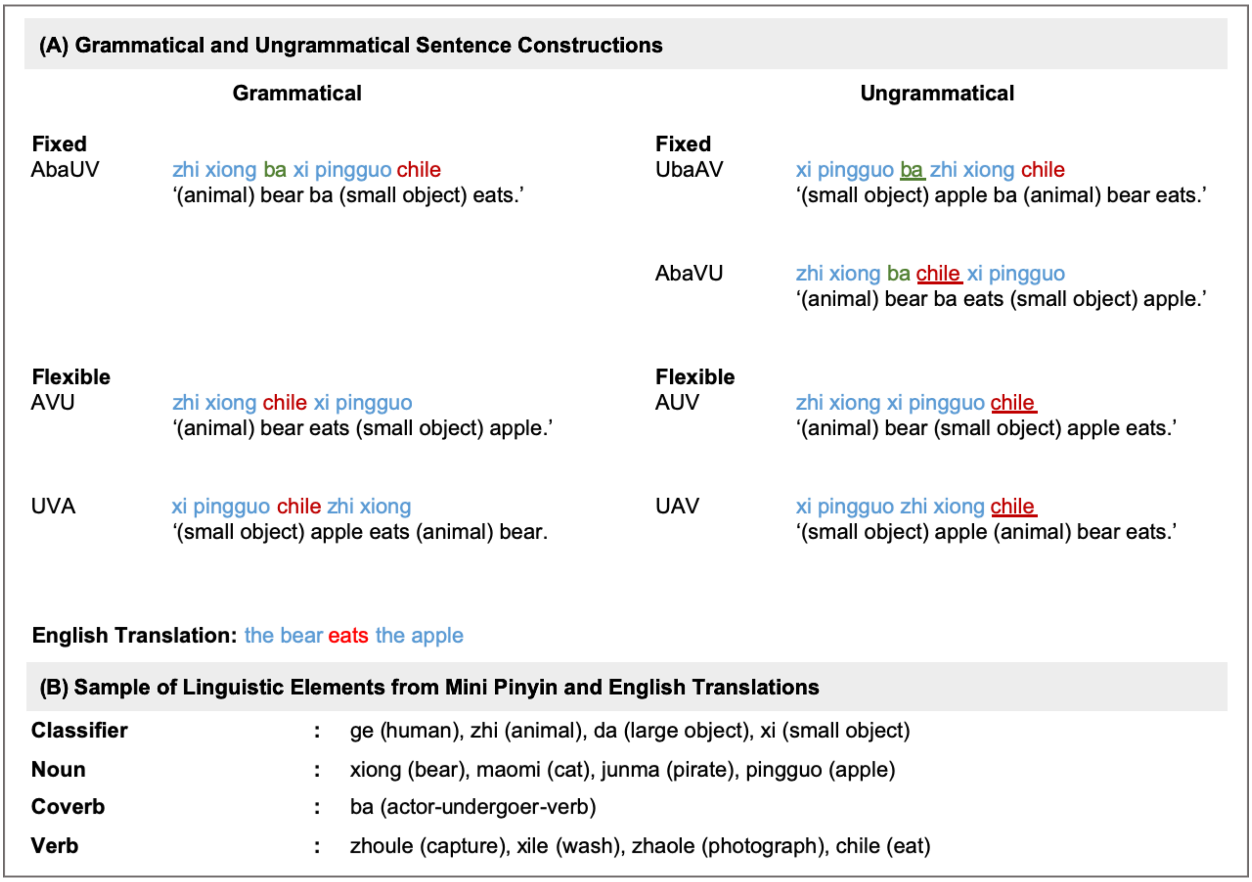


Fig 2. Example of images used in vocabulary and sentence learning phases. (A) Portion of the 25 illustrations used in the vocabulary booklet, which included human, animal, and inanimate objects (i.e., bag, apple). **(B)** Portion of the illustrations used in the sentence learning task, illustrating the interaction

between two entities. Note that the entities used in sentence learning task are the same as the illustrations used in the vocabulary booklet.



(A) Grammatical and Ungrammatical Sentence Constructions

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

English Translation: the bear eats the apple

(B) Sample of Linguistic Elements from Mini Pinyin and English Translations

Classifier	:	ge (human), zhi (animal), da (large object), xi (small object)
Noun	:	xiong (bear), maomi (cat), junma (pirate), pingguo (apple)
Coverb	:	ba (actor-undergoer-verb)
Verb	:	zhoule (capture), xile (wash), zhaole (photograph), chile (eat)

Fig 3. Exemplar word order rules and vocabulary items of Mini Pinyin. (A) Example of grammatical and ungrammatical fixed and flexible word order sentences. Classifiers and nouns are coded in blue, while verbs are red. The coverb *ba* is coded in green. For the ungrammatical sentences (right), the point of violation in the sentence is underlined. The direct English translation for each sentence construction is provided below (i.e., *the bear eats the apple*). **(B)** A sample of the linguistic elements present in Mini Pinyin and their English translation. Note that *ba* does not have a specific meaning, but when present in a sentence, instantiates a strict actor-undergoer-verb word order.

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 (see Figure 2A for a portion of nouns from the vocabulary booklet). Participants were required to learn the 25 nouns to ensure that they had a basic vocabulary of the nouns to successfully learn the 32 transitive verbs. They were asked to record periods of vocabulary learning in an activity log. Participants were instructed to study the booklet for at least fifteen minutes per day and were informed that they would need to pass a vocabulary test before commencing the main experimental protocol. After approximately one week, participants returned to complete the main experimental session, where EEG was recorded during a sentence learning task, baseline, and delayed sentence judgement tasks.

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 20s. Prospective participants who scored < 90% were unable to complete the main experimental EEG session. As such, all 36 participants included in the current paper obtained over 90% correct on the vocabulary test. The proportion of individuals who did not pass the vocabulary test was small (e.g., approximately less than 5 cases); however, the exact number was not recorded.

Sentence learning

Sentence and picture stimuli were presented using OpenSesame (Mathôt, Schreij, and Theeuwes 2012). During sentence learning, pictures were used to depict events occurring between two entities. The pictures and entities shown during the learning task were combinations of the static pictures shown in the vocabulary booklet (for an example of booklet versus sentence learning picture stimuli, see Figure 2A and 2B, respectively).

While participants were aware that they would complete sentence judgement tasks at a later point, no explicit description of or feedback regarding grammatical rules was provided during the learning task. Each picture corresponded to multiple sentence variations, similar to the grammatical conditions in Figure 3A. Picture-sentence pairs were presented to participants as correct language input. Participants were presented with a fixation cross for 1000ms, followed by the picture illustrating the event between two entities for 5000ms. 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 96 reported combinations, until the end of the task, which took approximately 40 minutes. The 96 sentences included in this analysis included the flexible (i.e., AVU, UVA) and fixed (i.e., AbaUV) sentence constructions. Sentences considered as fillers contained a coverb that was not *ba*, and thus were not relevant to testing the predictions posited in the current analysis. 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, and each sentence contained a different combination of nouns and verbs. This was done to encourage learning of the underlying grammatical rules rather than episodic events of individual sentences. Further, the two lists of sentences were counterbalanced across participants and testing session. Following the sentence learning task, participants completed the baseline judgement task.

Baseline and delayed judgement tasks

The baseline sentence judgement task taken immediately after learning provided a baseline to control for level of encoding, while the delayed judgement task took place ~12hrs after the learning and baseline judgement tasks. During both judgement tasks, 288 sentences without pictures (144 grammatical, 144 ungrammatical), 156 of which are reported here, were presented word-by-word with a presentation time of 600ms and an ISI of 200ms. The 156 included sentences included a combination of grammatical and ungrammatical flexible and fixed sentence constructions, while the 132 sentences that were considered fillers contained coverbs that were not *ba*, and classifier-noun pair violations, and thus were not relevant to testing the predictions of the current analysis. 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 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 and the baseline and delayed sentence judgement tasks. 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.

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, with EEG recorded during both the learning and judgement task. Participants then completed the behavioural control tasks 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. EEG was also recorded during the delayed judgement task.

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, with EEG recorded during both the learning and judgement tasks. 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 behavioural control tasks. 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.

Data Analysis

Behavioural analysis

Two measures of behavioural performance were calculated. For the behavioural analysis, grammaticality ratings were calculated on a trial-by-trial basis, determined by whether participants correctly identified grammatical and ungrammatical sentences. For EEG analysers, memory performance was quantified using the sensitivity index (d’) from signal detection theory (Stanislaw and Todorov 1999). Hit Rate (HR) and False Alarm rate (FA) were computed to derive d’, defined as the difference between the z transformed probabilities of HR and FA (i.e., d’ = z[HR] – z[FA]), with extreme values (i.e., HR and FA values of 0 and 1) adjusted using the recommendations of (Hautus 1995).

EEG recording and pre-processing

Task-related EEG analyses during the baseline and delayed sentence judgement tasks were performed using MNE-Python (Gramfort et al. 2013). EEG data (C3, C4, CP1, CP2, CP5, CP6, Cz, F3, F4, F7, F8, FC1, FC2, FC5, FC6, Fp1, Fp2, Fz, O1, O2, P3, P4, P7, P8, Pz) were re-referenced offline to the average of both mastoids and filtered with a digital phase-true finite impulse response (FIR) band-pass filter from 0.1 – 40 Hz to remove slow signal drifts and high frequency activity. Data segments from -0.5 – 6.5s relative to the onset of each sentence were extracted and corrected for ocular artefacts using Independent

Component Analysis (fastica; Hyvarinen 1999). Epochs were dropped when they exceeded a 150 μV peak-to-peak amplitude criterion or were identified as containing recordings from flat channels (i.e., < 5 μV).

Task-related time frequency analysis.

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

We conducted task-related time-frequency analyses by convolving the pre-processed EEG with a family of complex Morlet wavelets using the MNE function tfr_morlet. Theta activity was analysed using wavelet cycles, with the mother wavelet defined as the centre frequency value divided by four. Relative power change values in the post-stimulus interval were computed as a relative change from a baseline interval spanning -0.5s to the onset of each sentence. 500ms was added to the beginning and end of each sentence epoch to avoid edge artefacts. From this, we derived power estimates from individually defined (i.e., based on participants' IAF values) theta activity from the start to end of each sentence stimulus, electrode, and from the baseline and delayed testing sessions.

Finally, in order to determine whether changes in neural activity between the sleep and wake conditions were truly oscillatory, we used the irregular-resampling auto-spectral analysis toolbox (IRASA v1.0; Wen and Liu 2016) to estimate the $1/f$ power-law exponent characteristic of background spectral activity (for a detailed description of this procedure, see the supplementary material), which was used as a covariate in EEG-based statistical models.

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) using 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: total sleep time, sleep onset latency, wake after sleep onset, time (minutes) and percent of time spent in each sleep stage (N1, N2, N3 and R). Slow oscillation-spindle coupling strength was extracted via the YASA toolbox (Vallat and Walker 2021) implemented in MNE-Python based on published algorithms (Helfrich et al. 2018; Staresina et al. 2015).

The EEG data were re-referenced to linked mastoids and filtered from 0.1 – 30 Hz using a digital phase-true FIR band-pass filter. Data were then epoched into 30 s bins and subjected to a multivariate covariance-based artifact rejection procedure. This approach estimates a reference covariance matrix for each sleep stage and rejects epochs that deviate too far from this reference, where deviation is established using Riemannian geometry (Barachant, Andreev, and Congedo 2013; Barthélemy et al. 2019).

For SOs, continuous NREM EEG data were filtered using a digital phase-true FIR band-pass filter from 0.3 – 2 Hz with a 0.2 Hz transition band to detect zero crossing events that were between 0.3 – 1.5 s in length, and that met a 75 to 500 microvolt criterion. These artifact-free epochs were then extracted from the raw EEG signal. For sleep spindles, the signal was filtered between 12 – 16 Hz with a wide transition bandwidth of 1.5 Hz, while the amplitude was calculated by applying a Hilbert transform which was then smoothed with a 200ms moving average. Events were only included if they were within 0.5 – 2 s. Artifact-free events were then defined as 4s (± 2 s) peak-locked sleep spindle epochs.

We calculated an event-locked cross-frequency coupling metric (for a detailed description of this method, see Helfrich et al., 2018). 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 and epoch, we detected the maximal sleep spindle amplitude and corresponding SO phase angle at each channel. The mean circular direction (phase) and resultant vector length (mean vector length [MVL]; coupling strength) across all NREM events were then determined using circular statistics implemented in the *pingouin* package (Vallat 2018). This procedure also normalises the MVL value, yielding a z-score, an approach based on recommendations by (Özkurt 2012), and which is in line with previous work (e.g., Canolty et al. 2006; Combrisson et al. 2017). Further, such statistical normalization has been shown to provide more robust estimates of phase-amplitude coupling than non-normalised metrics (Combrisson et al. 2017; Özkurt and Schnitzler 2011). Finally, the Rayleigh test was used to test for circular non-uniformity with $p < .01$.

Statistical analysis

Data were imported into *R* version 4.0.2 (R Core Team, 2020) and analysed using (generalised) linear mixed-effects models fit by restricted maximum likelihood (REML) using *lme4* (Bates 2010). For the behavioural model, we used a logistic mixed-effects regression, modelling response choice (correct, incorrect) as a binary outcome variable. This model also factored in by-item and by-participant differences by specifying them as random effects on the intercept. The behavioural model took the following form:

$$\mathrm{Logit}(response_i) = \beta_0 + \beta_1 grammaticality_i * \beta_2 type_i * \beta_3 condition_i + \beta_4 baseline_i + \beta_5 sss_i + subject_{0i} + item_{\,0i} + \epsilon,$$

Here, *grammaticality* encodes sentence grammaticality (grammatical, ungrammatical), *type* refers to word order (fixed, flexible), *condition* is sleep versus wake, *baseline* is performance on the baseline (i.e., pre-sleep and -wake) judgement task, and *sss* refers to self-perceived sleepiness estimated from the SSS. Asterisks denote interaction terms, including all subordinate main effects; pluses denote additive terms.

Cluster-based permutation testing (Maris and Oostenveld, 2007) on task-related EEG data was performed in *MATLAB R2022a* (v9.12.0.1884302; The MathWorks, Natick, MA, USA) using the *FieldTrip* toolbox (v20220810; Oostenveld et al. 2011). Baseline-corrected power estimates for each channel and frequency band (theta, alpha, beta) were averaged over the grammaticality factor for both fixed and flexible sentence types. The difference in spectral estimates between fixed and flexible word orders was calculated for each channel and frequency band within-subjects. These difference scores were then contrasted between sleep and wake conditions (thereby testing the interaction between type and condition). Between-subject *t*-statistics were computed using the *ft_statfun_indepsamplesT* function. Channels with *t*-values that exceeded an alpha threshold of .10 were considered as candidates for cluster inclusion. The *t*-values of resolved clusters were then summed and compared to the null distribution of *t*-statistics obtained from 1000 random partitions of the data. The cluster-level statistic was considered significant if it attained a *p*-value < .05.

Following the identification of significant topographical differences in oscillatory power, the following structure was used for the EEG models, where we were interested in predicting behaviour from task-related theta activity, and which did not include trial-based response accuracy:

$$dprime_i = \beta_0 + \beta_1 power_i * \beta_2 condition_i * \beta_3 type_i + \beta_4 baseline + \beta_5 aperiodic_i + \beta_6 channel_i + subject_{0i} + \epsilon,$$

power is theta power from the post-sleep and -wake testing session, *condition* is sleep versus wake, and *type* is sentence word order (fixed, flexible). *Baseline* is theta power from the baseline judgement task (pre-sleep and -wake session). a*periodic* refers to the $1/f$ exponent estimated from the task-related EEG (see the supplementary material for full model summaries and visualisations of the influence of $1/f$ on putative oscillatory activity), and *channel* refers to the significant channels isolated from the cluster-based permutation test. Subject was modelled as a random effect on the intercept. d' was specified as the outcome.

For sleep-related analyses, we first constructed linear mixed-effects model to predict judgement accuracy from the combination of SO-spindle coupling strength, sentence type, sagittality, and laterality, while controlling for baseline (i.e., pre-sleep and -wake) judgement accuracy and sleep stage (N2, N3), with a random intercept of subject. A second linear mixed-effects model was constructed predicting task-related theta power from SO-spindle coupling strength, sentence type, sagittality, and laterality, with random intercepts of subject and channel.

P-values for all models were estimated using the *summary* function from the *lmerTest* package, which is based on Satterthwaite's degrees of freedom (Kuznetsova, Brockhoff, and Christensen 2017), while effects were plotted using the package *effects (Fox and Hong 2010)* and *ggplot2* (Wickham and Wickham 2016). Post-hoc comparisons for main effects were performed using the *emmeans* package (Lenth et al. 2019). The Holm–Bonferroni method (Holm 1979) was used to correct for multiple comparisons, while outliers were isolated using Tukey's method, which identifies outliers as exceeding ± 1.5 × inter-quartile range. Categorical factors were sum-to-zero contrast coded, such that factor level estimates were compared to the grand-mean (Schad et al. 2020). Further, for modelled effects, an 83% confidence interval (CI) threshold was used given that this approach corresponds to the 5% significance level with non-overlapping estimates (Austin and Hux 2002; MacGregor-Fors and Payton 2013). In the visualisation of effects, non-overlapping CIs indicate a significant difference at *p* < .05.

Results

Sleep supports the consolidation of fixed word order rules

Across testing sessions and grammaticality, participants showed a moderate degree of accuracy for fixed (*M* = 64.00, *SD* = 48.00) and flexible (*M* = 58.00, *SD* = 49.00) word orders, with performance accuracy ranging from 37.18 to 93.75 percent. As shown in Table 1, performance also varied by sentence type, condition, and grammaticality, with the sleep relative to the wake condition performing higher for fixed word orders at delayed testing.

Generalised linear mixed-effects modelling of single trial response accuracy (controlling for baseline performance) revealed a significant Grammaticality × Sentence Type × Condition interaction ($\beta = 0.13$, *se* = 0.03, *p* < 0.001; see Figure 4). Holm-Bonferroni adjusted post-hoc comparisons revealed that response accuracy was higher for the sleep relative to wake condition for fixed grammatical (OR = 0.55, *se* = 0.12, $z = -2.60$, $p_{adj} = 0.03$) but not fixed ungrammatical (OR = 0.89, *se* = 0.19, $z = -0.52$, $p_{adj} = 1.00$) word orders.

Response accuracy was also higher in the sleep condition for grammatical fixed relative to grammatical flexible word orders (OR = 0.58, *se* = 0.06, $z = -4.63$, $p_{adj} < 0.001$)., The sleep condition also judged flexible over fixed word order sentences as ungrammatical (OR = 1.59, *se* = 0.23, $z = 3.10$, $p_{adj} = 0.01$; for a full model summary, see the supplementary material). These results indicate that sleep may benefit the consolidation of fixed (but not flexible) word order rules, although this pattern may be due to differing response strategies adopted between the sleep and wake conditions. To address this in subsequent analyses, we examine the sensitivity index d’ to account for potential response biases (see Table 1 for d’ values).

Table 1. Percent correct and the sensitivity index d’ by condition (sleep, wake), sentence judgement task (baseline, delayed), grammaticality (grammatical, ungrammatical) and sentence type (fixed, flexible). Standard deviations (SD) are given in parentheses.

Condition	Session	Grammaticality	Sentence Type	Correct (SD)	d’ (SD)
Sleep	Baseline	Grammatical	Flexible	65.14 (47.67)	0.79 (1.24)
			Fixed	67.44 (46.90)	0.90 (0.80)
		Ungrammatical	Flexible	58.88 (49.26)	
			Fixed	47.65 (50.00)	
	Delayed	Grammatical	Flexible	57.92 (49.38)	1.00 (1.90)
			Fixed	71.28 (45.28)	1.50 (1.34)
		Ungrammatical	Flexible	64.85 (47.80)	
			Fixed	49.50 (50.00)	
Wake	Baseline	Grammatical	Flexible	63.04 (48.28)	1.11 (1.34)
			Fixed	67.66 (46.81)	1.40 (0.91)
		Ungrammatical	Flexible	68.88 (46.35)	
			Fixed	51.14 (50.00)	
	Delayed	Grammatical	Flexible	66.82 (47.10)	1.41 (1.48)
			Fixed	61.11 (48.80)	1.20 (1.42)
		Ungrammatical	Flexible	71.12 (45.31)	
			Fixed	51.50 (50.00)	

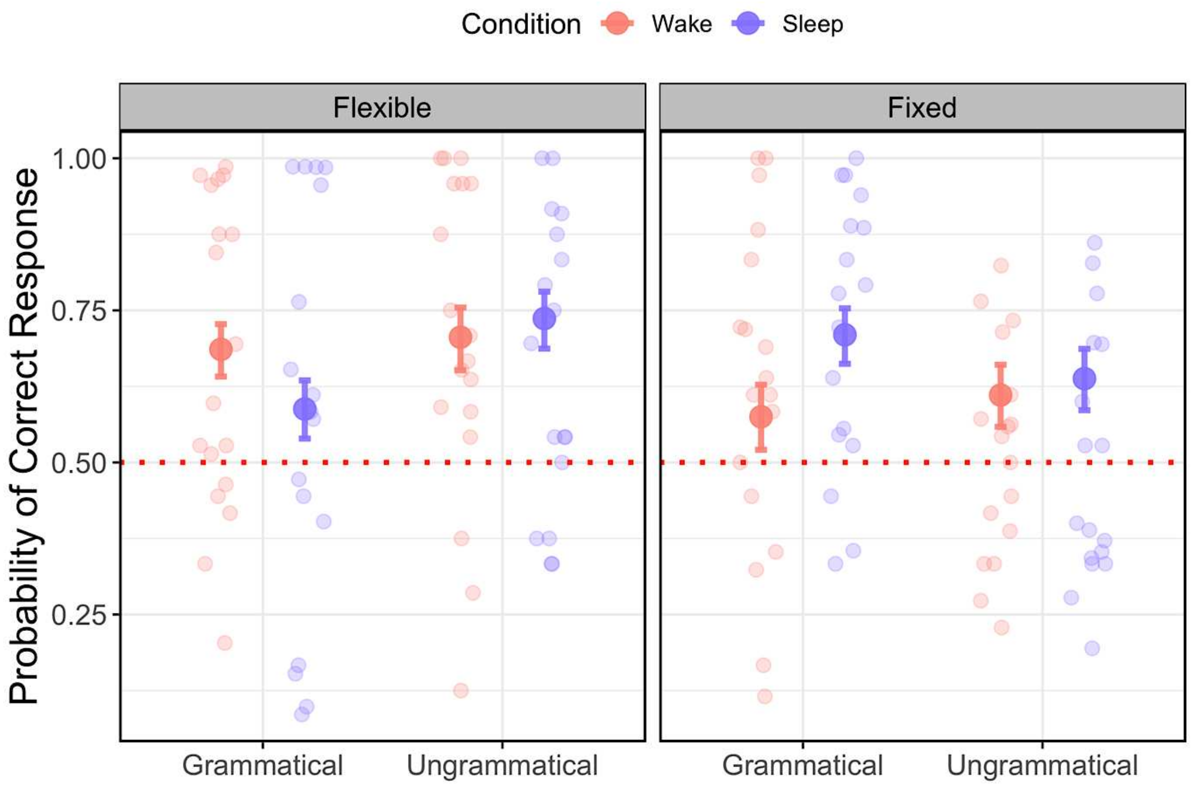


Fig 4. Visualisation of the behavioural results. Relationship between the probability of correct response (y-axis; higher values indicate a higher probability of a correct response), grammaticality (x-axis; grammatical, ungrammatical), sentence type (left column = flexible, right column = fixed), and condition (wake = salmon, sleep = purple). Bars represent the 83% confidence interval around group-level expected marginal mean estimates. Dots represent individual data points per subject for aggregated data.

Theta power after sleep is associated with increased memory for fixed, but decreased memory for flexible word order rules

Based on the differences in behavioural performance between the sleep and wake conditions on fixed and flexible word orders, we asked whether task-evoked theta power predicts differences in behaviour across sleep and wake. A non-parametric cluster-based permutation test (see Methods) contrasting Condition (sleep, wake) and Sentence Type (fixed, flexible) revealed a significant difference in beaseline-corrected theta power during the delayed session (Monte Carlo $p = .008$; see Figure 5A for topography and demarcation of the cluster). No significant clusters were identified for alpha- or beta-band estimates.

Given the significant theta-band effects, we constructed a linear mixed-effects model with judgement accuracy (d') as the outcome and task-related theta power (drawn from the significant cluster identified above), Condition (sleep, wake) and Sentence Type (fixed, flexible) as predictors. This analysis revealed a significant Theta × Condition × Sentence type interaction ($\beta = -1.09$, $se = 0.34$, $p = 0.001$). Holm-Bonferroni adjusted post-hoc comparisons revealed that for flexible word orders, an increase in theta power was associated with poorer judgement accuracy for the sleep but not wake condition. However, the inverse was observed for fixed word order sentences, such that an increase in theta power was associated with improved judgement accuracy for the sleep but not wake condition ($\beta = -4.70$, $se = 1.10$, $p_{adj} < 0.001$). Coupled with the behavioural model, the current analysis demonstrates that sleep preferentially consolidates fixed word order rules at the expense of flexible word order rules, and that this is reflected in task-related theta power. For a visualisation of these effects, see Figure 5C.

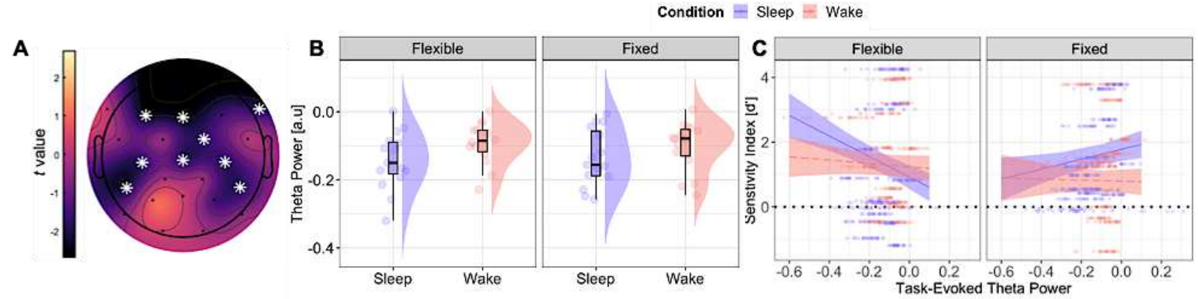


Fig 5. Theta power and judgement accuracy. (A). Cluster-based permutation testing on the theta band contrasting differences between Condition (sleep, wake) and Sentence Type (fixed, flexible). Warmer colours denote a higher *t* statistic. Significant channels are indicated by white asterisks. **(B)** Raincloud plots illustrating average theta power over significant channels between sentence type and condition. Higher values on the y-axis denote increased theta power. **(C)** Modelled effects of task-related theta power (x-axis; higher values indicate increased power) on judgement accuracy (y-axis; higher values indicate better performance) for the sleep and wake conditions (sleep = purple solid line; wake = dashed pink line) for flexible (left facet) and fixed (right facet) sentences. The black dashed line indicates chance-level performance, while the shaded regions indicate the 83% confidence interval. The x-axis reflects scaled power estimates, with negative values reflecting a decrease in power and positive values reflecting an increase in power from the pre-stimulus baseline period, respectively. Individual data points represent raw (single subject) values.

SO-spindle coupling is predictive of memory for fixed but not flexible word order rules

Having observed differences between the sleep and wake conditions on the relationship between task-related theta activity and behavioural performance, a logical next step was to test whether behavioural performance for fixed word order rules is associated with SO-spindle coupling. Based on previous work (e.g., Helfrich et al. 2018; Mikutta et al. 2019), we focussed on the coupling strength between maximal spindle amplitude and the phase of the SO (for a summary of typical sleep parameters and their correlation with d', see Table 2). There was a significant non-uniform distribution for the precise SO phase during the spindle peaks ($p < 0.0001$; Rayleigh test). In predicting behavioural performance, mixed-effects modelling revealed a significant Coupling Strength × Sentence Type × Sagittality interaction ($\beta = 7.94$, $se = 2.72$, $p = 0.003$). Pairwise contrasts further revealed that this effect was largest anteriorly for fixed sentences ($\beta = 35.76$, $se = 7.47$, $p_{\text{adj}} < 0.001$), with a progressive degradation proceeding posteriorly (central region: $\beta = 15.31$, $se = 5.00$, $p_{\text{adj}} = 0.002$; posterior region: $\beta = 8.45$, $se = 4.63$, $p_{\text{adj}} = 0.07$). Figure 6A illustrates an exemplary full-night spectrogram, group-level comodulagram and preferred phase of SO-spindle coupling for NREM sleep. Figure 6D also visualises the effect of SO-spindle coupling across the three levels of sagittality (anterior, central, posterior). Here, as SO-spindle coupling strength increased, judgement accuracy for fixed word order sentences improved, while the inverse relationship was present for flexible word order sentences.

Table 2. Descriptive statistics for sleep parameters and correlations with the difference between d' at delayed and baseline testing for fixed and flexible word order sentences.

Sleep Parameter	**Mean Minutes (SD)**	**% in Stage (SD)**	**Correlations with d' (Delayed – Baseline)**			
			Fixed		**Flexible**	
			r	***p***	***r***	***p***
TST	400.00 (67.02)		-.44	.42	.30	.96
SOL	15.23 (12.23)		.45	.42	-.47	.35
WASO	52.64 (55.60)		.41	.42	-.19	1.00
N1	38.05 (29.47)	10.05 (8.21)	.12	1.00	.10	1.00
N2	196.30 (46.29)	49.52 (10.36)	.26	.93	.33	.95
SWS	104.23 (42.27)	25.84 (9.60)	.02	1.00	-.48	.35
REM	61.30 (39.39)	14.57 (8.56)	-.46	.42	.04	1.00

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. Significance values are Holm-Bonferroni corrected (Holm, 1979).

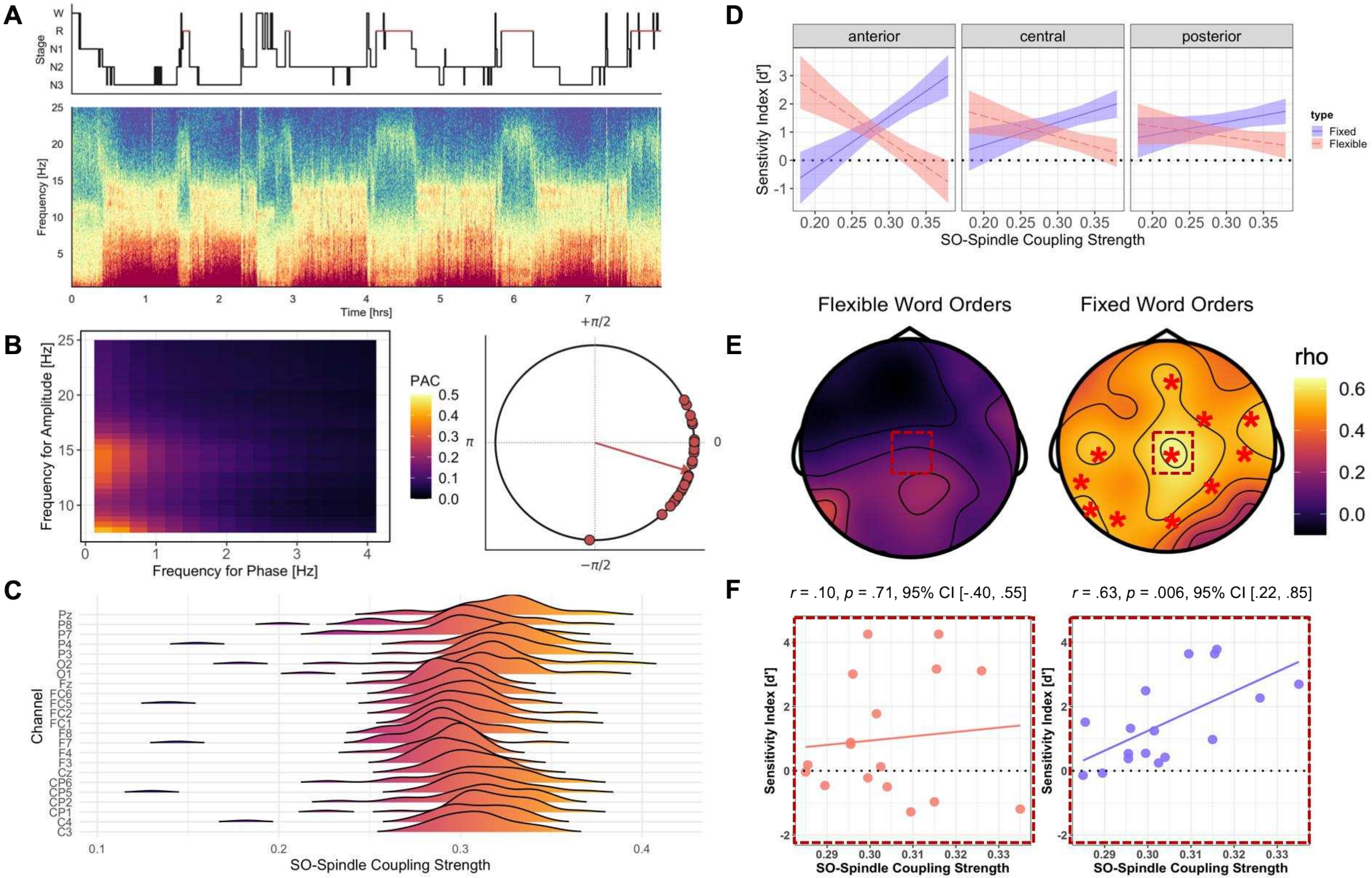

A
Stage
W
R
N1
N2
N3
Frequency [Hz]
25
20
15
10
5
0
1
2
3
4
5
6
7
Time [hrs]
B
Frequency for Amplitude [Hz]
Frequency for Phase [Hz]
PAC
0.5
0.4
0.3
0.2
0.1
0.0
+π/2
−π/2
π
0
C
Channel
Pz
P8
P7
P4
P3
O2
O1
Fz
FC6
FC5
FC2
FC1
F8
F7
F4
F3
Cz
CP6
CP5
CP2
CP1
C4
C3
0.1
0.2
0.3
0.4
SO-Spindle Coupling Strength
D
anterior
central
posterior
Sensitivity Index [d']
SO-Spindle Coupling Strength
0.20 0.25 0.30 0.35
type
Fixed
Flexible
E
Flexible Word Orders
Fixed Word Orders
rho
0.6
0.4
0.2
0.0
F
r = .10, p = .71, 95% CI [-.40, .55]
r = .63, p = .006, 95% CI [.22, .85]
Sensitivity Index [d']
SO-Spindle Coupling Strength
0.29 0.30 0.31 0.32 0.33

Fig 6. Sleep neurophysiology metrics and relationship between phase amplitude coupling and judgement accuracy. (A) Hypnogram and full-night multi-taper spectrogram for a single participant from channel Cz. **(B)** Group-level comodulagram illustrating the frequency for phase (x-axis) and frequency for power (y-axis) during NREM sleep SO-spindle coupling epochs from channel Cz. Across participants, the peak phase-amplitude coupling occurred for the amplitude at roughly 15 Hz coupled with the phase at 0.2 Hz. To the right is the preferred phase of SO-spindle coupling for NREM sleep (red circles indicate individual participants). Note that 0 represents the peak of the SO. **(C)** Ridge plot illustrating the distribution of SO-spindle coupling strength (x-axis; higher values indicate stronger coupling) across channels (y-axis). **(D)** Modelled effects of SO-spindle coupling strength (x-axis; higher values indicate stronger coupling) on judgement accuracy (y-axis; higher values indicate better performance) for fixed and flexible word order sentences (fixed = purple solid line; flexible = dashed pink line) across levels of anterior (left), central (middle) and posterior (right) regions. The black dashed line indicates chance-level performance, while the shaded regions indicate the 83% confidence interval. **(E)** Topographic visualisation of the relationship between SO-spindle coupling strength and judgement accuracy for flexible (left) and fixed (right) word orders. Warmer colours denote a higher rho value. Channels with a statistically significant relationship ($p < .05$) between SO-spindle coupling strength and judgement accuracy are indicated by red asterisks. **(F)** Scatterplot indicating the relationship between judgement accuracy (y-axis; higher values denote better memory performance) and SO-spindle coupling strength (x-axis; higher values denote stronger coupling) for flexible (left) and fixed (right) word order sentences at channel Cz.

Frontal SO-spindle coupling predicts task-evoked theta power

Having shown that SO-spindle coupling is associated with improved judgement accuracy for fixed word orders, and judgement accuracy is tracked by task-related theta power, we examined whether theta power is predicted by SO-spindle coupling strength. A mixed-effects model regressing SO-spindle coupling strength, laterality (left, midline, right), sagittality (anterior, central, posterior), and sentence type (fixed, flexible) onto task-related theta power revealed a significant four-way interaction between SO-spindle coupling strength, sentence type, laterality, and sagittality ($\beta = 0.73$, $se = 0.33$, $p = 0.03$). However, after performing Holm-Bonferroni adjusted pairwise comparisons, the only surviving effect was a contrast between right lateral anterior and central regions ($\beta = 3.21$, $se = 1.08$, $p_{adj} = 0.009$). As illustrated in Figure 7, stronger anterior SO-spindle coupling was positively associated with post-sleep theta power irrespective of sentence type, while no such relationship was observed over central channels.

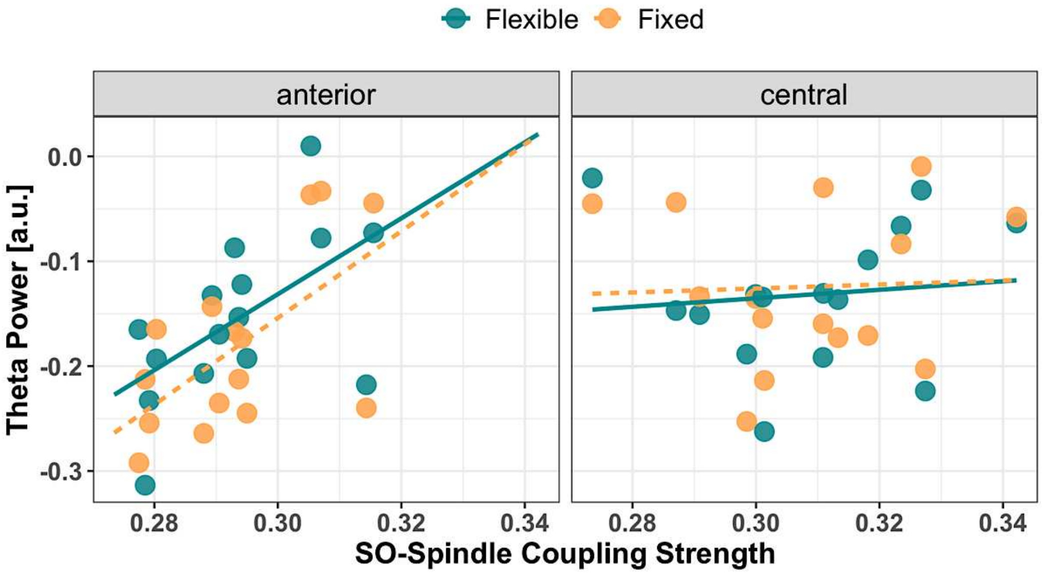


Fig 7. Theta power and SO-spindle coupling strength. Task-related theta power (y-axis; higher values denote increased power) and SO-spindle coupling strength (x-axis; higher values denote stronger coupling) average across left lateral regions and facetted by anterior (left) and central (right) channels. Fixed sentences are colour coded in teal, while flexible sentences are colour coded in yellow.

Discussion

Coordination between SOs and sleep spindles is hypothesised to provide an optimal temporal receptive window for hippocampal-cortical communication during sleep (Helfrich et al. 2019; Staresina et al. 2015) in the support of memory consolidation. Here, we show that the beneficial effect of SO-spindle coupling on memory extends to 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 SO-spindle coupling. Our results further reveal that SO-spindle coupling correlates with changes in task-evoked theta activity during sentence processing. In sum our results establish converging behavioural and neurophysiological evidence for a role of NREM SO-spindle coupling and task-related theta activity as signatures of successful memory consolidation and retrieval in the context of higher-order language learning

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

Using a complex modified miniature language paradigm (Cross et al. 2021), 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 sequential position of the noun phrases and verb (i.e., the first noun phrase is invariably the actor, and the sentence 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 sequential order-based interpretation and are more compatible with an English word-order-based processing strategy (Bornkessel and Schlesewsky 2006; Bornkessel-Schlesewsky et al. 2015; MacWhinney et al. 1984). Critically, this sleep-based enhancement for fixed word order rules was predicted by stronger SO-spindle coupling (Figure 6F).

Sleep-related memory effects are proposed to be biased toward stimuli following temporal or sequence-based regularities compared to relational information (for review, see Lerner and Gluck 2019). This is posited to occur via the hippocampal complex encoding temporal occurrences of sensory input (Durrant et al. 2011), which are replayed during SWS, potentially via SO-spindle coupling (e.g., Navarrete et al. 2020; Solano et al. 2020). Here, we provide evidence supporting this account. During learning, the hippocampus may have preferentially extracted the temporal regularities of fixed word order sentences. Sleep-associated memory processing, achieved via SO-spindle coupling, selectively strengthened these memory traces, facilitating the formation of neural representations of linguistic rules. During subsequent wake, these newly established representations would be used by cortical networks to detect the temporal regularities in novel sentences, resulting in greater sensitivity to fixed word order rules. From this perspective, sleep-based consolidation of higher order language favors sequence-based regularities, with mechanisms of sleep-related memory consolidation generalizing fixed over flexible word order rules, indexed by task-related theta activity.

It is important to note, however, that our sample of participants were native monolingual speakers, and as such, may have preferentially consolidated the fixed word order rules at the expense of the flexible rules. While behavioural work demonstrates sentence-level preferences of grammatical rules that are analogous to learners' native languages (e.g., Cross et al. 2021), less is known regarding the neural underpinnings of this phenomenon. We now turn to how the neurobiological processes underpinning the beneficial effect of SO-spindle coupling on memory consolidation extends to higher order language learning.

Slow oscillation-spindle coupling as a marker of sleep-associated memory consolidation and higher-order language learning

Coupling between SOs and spindles predicts successful overnight memory consolidation (Hahn et al. 2020, 2022; Helfrich et al. 2018; Mikutta et al. 2019). However, these studies often use old-new paradigms with single words (e.g., Helfrich et al. 2018; Mikutta et al. 2019) or word-image pairs (e.g., Muehlroth et al. 2019), leaving the role of NREM oscillations to more complex linguistic information unknown. Here, we found that the generalisation of sequence-based (or fixed word order) rules is facilitated by the strength of NREM SO-spindle coupling. Mechanistically, during SWS, the cortex is synchronised during the up state of the SO, allowing effective interregional communication, particularly between the prefrontal cortex and hippocampal complex (Helfrich et al. 2019). 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 (Niethard et al. 2018). Here we revealed that the interaction between these cardinal markers of sleep-related memory processing extend to sentence-level regularities. In the following, we discuss how SO-spindle coupling, as a marker of sleep-associated memory consolidation, modulates task-related oscillatory activity and how these interactions affect sentence processing.

Task-related theta oscillations index successful memory consolidation of complex linguistic rules

Theta is the dominant frequency in the hippocampal complex and surrounding structures during wake (Covington and Duff 2016; Duff and Brown-Schmidt 2012). Oscillations in this frequency range are critical for associative memory formation and coordinating hippocampal-cortical interactions, having been related to associative memory formation (Tort et al. 2009), tracking sequential rules (Crivelli-Decker et al. 2018) and predicting words based on contextual linguistic information (Corcoran et al. 2023; Piai et al. 2016). In the sleep and memory literature, increased theta oscillations have been reported for successfully remembered items, interpreted as reflecting a stronger memory trace induced by sleep-based consolidation (Köster et al. 2017; Schreiner and Rasch 2015). Here, we observed that an increase in theta oscillations predicted higher sensitivity for fixed word order rules after a 12hr delay period, and that the effect of theta on fixed word order processing was more pronounced in the sleep relative to wake condition. This finding accords with the general memory literature, possibly reflecting the binding of linguistic items in a sequence to generate a coherent sentential percept.

We also observed that NREM SO-spindle coupling was positively associated with task-evoked theta power. In line with systems consolidation theory (Born and 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 neocortical memory trace (Schreiner and Rasch 2015). From this perspective, when SO-spindle coupling is strong, hippocampal-based memory traces may become neocortically distributed and integrated with existing associative memory networks (Maingret et al. 2016; Navarrete et al. 2020), manifesting in stronger post-sleep, task-related theta oscillations.

Future directions and concluding remarks

Future studies may 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 and the $1/f$ exponent 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 SO-spindle coupling between cortical regions and the hippocampal complex, respectively (e.g., Helfrich et al. 2018, 2019). This approach could be complemented by demonstrating a selective reinstatement of memory traces during SO-spindle coupling using representational similarity analysis (Zhang, Fell, and Axmacher 2018). Identifying stimulus-specific representations during the encoding of sentence-level regularities and tracking the replay of stimulus activity related to SO-spindle coupling events would further demonstrate the critical role of sleep-based oscillatory mechanisms on higher-order language learning.

Taken together, our results demonstrate that the temporal coupling between NREM SOs and spindles supports the consolidation of complex sentence-level rules. We demonstrated that SO-spindle coupling promotes the consolidation of sequence-based rules and modulates task-evoked theta oscillations previously implicated in language learning (e.g., de Diego-Balaguer, Fuentemilla, and Rodriguez-Fornells 2011; Kepinska et al. 2017) and sentence processing (Vassileiou et al. 2018). Critically, these findings add to models of sleep-based memory consolidation (e.g., Born and Wilhelm 2012; Lewis and Durrant 2011) and help characterise how effects of sleep-related oscillatory dynamics on memory manifest in oscillatory activity during complex language-related operations.

Author Contribution. Conceptualization by Z.C., I.B-S., M.S. and M.J.K. Data curation by Z.C. and L.Z.W. Data pre-processing and analysis by Z.C., S.C., R.F.H., and A.W.C. Writing – original draft by Z.C.; writing – review & editing by all authors; Supervision of project by I.B-S., M.S., M.J.K and R.F.H. Visualization by Z.C.; Funding acquisition by I.B-S. and Z.C.

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