

Spontaneous Entry into an “Offline” State during Wakefulness: A Mechanism of Memory Consolidation?

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Abstract

■ Moments of inattention to our surroundings may be essential to optimal cognitive functioning. Here, we investigated the hypothesis that humans spontaneously switch between two opposing attentional states during wakefulness—one in which we attend to the external environment (an “online” state) and one in which we disengage from the sensory environment to focus our attention internally (an “offline” state). We created a data-driven model of this proposed alternation between “online” and “offline” attentional states in humans, on a seconds-level timescale. Participants ($n = 34$) completed a sustained attention to response task while undergoing simultaneous high-density EEG and pupillometry recording and intermittently reporting on their subjective experience. “Online” and “offline” attentional states were initially defined using a cluster analysis applied to multimodal measures of (1)

EEG spectral power, (2) pupil diameter, (3) RT, and (4) self-reported subjective experience. We then developed a classifier that labeled trials as belonging to the online or offline cluster with >95% accuracy, without requiring subjective experience data. This allowed us to classify all 5-sec trials in this manner, despite the fact that subjective experience was probed on only a small minority of trials. We report evidence of statistically discriminable “online” and “offline” states matching the hypothesized characteristics. Furthermore, the offline state strongly predicted memory retention for one of two verbal learning tasks encoded immediately prior. Together, these observations suggest that seconds-timescale alternation between online and offline states is a fundamental feature of wakefulness and that this may serve a memory processing function. ■

INTRODUCTION

“Zoning out” is often considered a waste of time, for example, when an inattentive student daydreams during a lecture. However, to the contrary, such “offline” moments of disengagement from the sensory environment may serve a critical cognitive function. Recent studies demonstrate that a brief period of eyes-closed waking rest after learning can facilitate the consolidation of new memories (Wamsley, 2019; Brokaw et al., 2016; Dewar, Alber, Butler, Cowan, & Della Sala, 2012) as well as promote cognitive processes including creativity (Ritter, Strick, Bos, van Baaren, & Dijksterhuis, 2012; Cai, Mednick, Harrison, Kanady, & Mednick, 2009), insight (Craig, Ottaway, & Dewar, 2018), and decision-making (Strick, Dijksterhuis, & van Baaren, 2010; Dijksterhuis, Bos, Nordgren, & van Baaren, 2006). Offline states like rest and sleep are thought to facilitate internally focused cognitive processing by virtue of reduced encoding demands (Mednick, Cai, Shuman, Anagnostaras, & Wixted, 2011) as well as state-specific neurophysiological events actively promoting consolidation (Wamsley, 2019; Brokaw et al., 2016).

To date, the literature on offline cognitive processing has focused on the effect of relatively long durations of offline time (ranging from a few minutes of rest to a full night of

sleep). However, accumulating evidence suggests that we may intermittently enter an offline state for brief moments during wakefulness, even while ostensibly engaged in a task (Reimer et al., 2016; Handy & Kam, 2015; Harris & Thiele, 2011; Schooler et al., 2011). In the current study, we explore the hypothesis that seconds-long bouts of offline wakefulness interspersed throughout our daily activities are a fundamental feature of wakefulness that supports memory consolidation.

Two primary lines of evidence suggest that this could be the case. First, a psychological literature on “mind wandering” describes our subjective experience as alternating between an external focus on what we are doing and an internal focus on task-unrelated thoughts, feelings, and imagery (mind wandering; Wang, Poerio, et al., 2018; Smallwood & Schooler, 2015; Smallwood, Beach, Schooler, & Handy, 2008). Mind wandering and task-related processing are proposed to be mutually exclusive, as the frequency of mind wandering is inversely related to the attentional demands of ongoing cognitive tasks and its occurrence can predict performance decrements (Stawarczyk, Majerus, Maquet, & D’Argembeau, 2011; Smallwood & Schooler, 2006; Antrobus, Singer, Goldstein, & Fortgang, 1970; Antrobus, Singer, & Greenberg, 1966), although not all studies have reported a clear link with impaired performance (Konishi, Brown, Battaglini, & Smallwood, 2017). Neurophysiological studies have linked mind

wandering to changes in the scalp-recorded EEG (Compton, Gearing, & Wild, 2019; Dhindsa et al., 2019; Kawashima & Kumano, 2017; Grandchamp, Braboszcz, & Delorme, 2014) and pupil diameter (Konishi et al., 2017; Grandchamp et al., 2014; Smallwood et al., 2012). These observations are proposed to indicate that mind wandering arises from an intermittent “perceptual decoupling,” during which we disengage from the sensory environment in favor of internally focused processing (Schooler et al., 2011). Thus, this research suggests an intermittent “switching” between externally and internally focused attentional states that may be a pervasive but little-noticed feature of wakefulness.

However, defining “mind wandering” based on participant self-report limits the ability to track movement between attentional states over time. First, participants are only sometimes aware that they have begun mind wandering (Schooler et al., 2011). Second, even if the subjective experience of mind wandering is accurately recalled and reported, participants’ experience may nonetheless be imperfectly correlated with the underlying neurobiological states of interest. Here, our interest is in the global neurobiological state of being “offline,” rather than in participants’ conscious experience of their attentional state *per se*. Third, participants can be queried about their subjective experience only infrequently, as the very act of reporting on attention lapses itself interferes with fluctuation of attention. The current study seeks to overcome some of these limitations inherent to defining attentional states based on subjective report alone.

In parallel, an emerging animal literature provides evidence of a seconds-timescale alternation between distinct and behaviorally relevant “cortical states” during wakefulness, defined using single-unit and local field potential (LFP) recordings during animal behavior. During what has been termed the “synchronized” state, cortical neurons show coordinated fluctuations in firing rate on a timescale of ≈ 100 msec, resulting in increased low-frequency power in the LFP (Harris & Thiele, 2011). In contrast, in the “desynchronized” state, this coordinated fluctuation in unit firing rate is not observed, and low-frequency power in the LFP is reduced. Fluctuation between “synchronized” and “desynchronized” states occurs every few seconds and is seen even during extended periods of immobility, indicating that changes in state are not driven solely by the onset of movement/behavior (Reimer et al., 2014). These states are behaviorally relevant in animals, with the desynchronized state predicting better behavioral performance in monkeys (Beaman, Eagleman, & Dragoi, 2017) and modulating evoked responses in rodents (McGinley et al., 2015). Mirroring the human literature, fluctuation between synchronized and desynchronized states is correlated with rapid changes in pupil diameter, with pupil diameter tracking rapid changes in noradrenergic and cholinergic neuromodulation (Reimer et al., 2016).

Thus, both the human and animal literature suggest at least two substates that spontaneously occur during

immobile wakefulness—one in which attention to external sensory stimuli is enhanced, pupil diameter is increased, and cortical neuronal activity is desynchronized, and an opposing state in which processing of external sensory stimuli is decreased, the pupil constricts, and cortical neuronal activity is synchronized. No data-driven description of the substates of wakefulness has yet emerged to become widely accepted, however, and entry into offline wakefulness has never been tracked on a rapid, seconds-level timescale in human participants. As a result, the vast majority of research in cognitive neuroscience has continued to treat wakefulness as homogenous.

Although the structure and characteristics of these waking states remain poorly understood in humans, recent work has made progress in defining the various forms that subjective experience might take during wakefulness as well as their neural correlates. One useful approach has been to apply data-driven techniques to decompose complex subjective report data into a discrete set of fundamental experience dimensions (Turnbull et al., 2019; Sormaz et al., 2018; Wang, Bzdok, et al., 2018; Wang, Poerio, et al., 2018). Much of this work suggests the existence of more than two categories of waking experience, potentially including multiple forms of “off-task” thought (Turnbull et al., 2019; Sormaz et al., 2018; Wang, Bzdok, et al., 2018). Neurophysiological correlates of subjective experience categories have then been explored using techniques including fMRI (Turnbull et al., 2019; Sormaz et al., 2018) and EEG (Compton et al., 2019; Dhindsa et al., 2019; Kawashima & Kumano, 2017).

Instead of defining waking states on the basis of subjective experience, here we aim to define a set of mind–brain states in which participants’ self-reported experience is only one of several imperfect indicators of a waking state. Wang et al.’s work provides a rare example of this approach in the human literature, using fMRI in combination with self-report data to jointly define mind–brain states (Wang, Bzdok, et al., 2018; Wang, Poerio, et al., 2018). Here, we extend this general approach to define mind–brain states based on the multimodal neurocognitive measurements of (1) high-density EEG, (2) pupillometry, (3) RT, and (4) subjective experience.

Critically, the function of entering an offline state during wakefulness remains unknown. From a survival perspective, it would perhaps seem most adaptive to maintain constant attention to the external environment. Why should it be necessary to go “offline” at all? A clue may come from evidence that extended periods of offline time during sleep (Tucker et al., 2006; Stickgold, 2005; Mednick, Nakayama, & Stickgold, 2003; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002; Plihal & Born, 1997) and waking rest (Wamsley, 2019; Brokaw et al., 2016; Dewar et al., 2012; Mednick et al., 2011; Mednick, Makovski, Cai, & Jiang, 2009) both facilitate memory. The memory benefits of sleep and rest have been attributed to a neurobiological milieu favoring the consolidation of memory, characterized by EEG slowing, decreased cholinergic neuromodulation,

reduced processing of sensory stimuli, and the emergence of hippocampal ripples (strongly linked to the offline reactivation of memory; for a review, see Buzsáki, 2015). However, notably, some of these consolidation-promoting features are also engaged during briefer, seconds-long bouts of offline time. As a result, we hypothesize that even very brief, seconds-long bouts of an offline state might support the earliest stages of memory consolidation (see Table 1).

To test these hypotheses, we modeled the alternation between online and offline waking states during the performance of an attentional task in human participants. To do so, we applied machine learning algorithms to multimodal neurocognitive measurements of (1) high-density EEG, (2) pupillometry, (3) RT, and (4) subjective experience. Our goals were, first, to develop a data-driven method of defining “offline” time with high temporal resolution, without relying exclusively on self-report. Second, using this data-driven definition of offline time, we tested the hypothesis that spontaneously entering an offline state for even a few seconds might support the early stages of memory consolidation. Thus, we examined the amount of “offline time” after a learning task as a predictor of subsequent memory retention.

METHODS

Overview of the Approach

During two laboratory visits, participants’ EEG, pupil diameter, and RTs were recorded while they performed a sustained attention to response task (SART; see below). On 24 of 324 total SART trials (“thought probe trials”), participants also self-reported the current contents of their subjective experience. Using these data, our initial goals were to (1) define statistically discriminable substates of wakefulness and (2) determine which state participants were in during each 5-sec SART trial. To accomplish this, first, we used an expectation maximization (EM) algorithm to optimally separate SART trials into two clusters, which we term the “online” and “offline” states. This initial clustering was applied

only to thought probe trials. After labeling each thought probe trial as “online” or “offline,” we used these labeled trials to train a classifier to categorize SART trials using the EEG, pupil diameter, and RT data alone. As a final step, we used this classifier to now label all trials as either “online” or “offline,” even when subjective report data were not present. This approach allowed us to model participants’ movement between online and offline states during the entirety of the 30-min SART, with 5-sec temporal resolution, and to calculate the proportion of this interval that each participant spent offline. This information was then used to predict participants’ subsequent memory for two verbal learning tasks encoded before the SART.

Participants

Participants were full-time students between 18 and 30 years old, were native English speakers, and reported no prior knowledge of the Icelandic language (because of the nature of one of the memory tasks). By self-report, participants had not been diagnosed with any sleep disorders or attention-deficit disorders. Thirty-four participants meeting these criteria successfully completed the study ($M_{\text{age}} = 19.9$ years, $SD = 1.2$; 31 female, three male). This research was approved by Furman University’s institutional review board. All participants signed informed consent and were compensated for their participation with either payment or course credit. Participants were asked to keep a regular sleep schedule for the three nights before the study and to refrain from consuming caffeine after 10 a.m. on the day of the study. Table 2 summarizes participant-level characteristics including measures of sleepiness, task performance, and questionnaire responses.

Procedures

All participants completed two sessions in counterbalanced order, utilizing a different verbal memory task during each session. In one session, the memory task was the Short

Table 1. Hypothesized Characteristics of Online and Offline Waking States

Measurement	Online State	Offline State
EEG	↓ Alpha and slow oscillation	↑ Alpha and slow oscillation
Pupillometry	↑ Pupil diameter reflecting increased NE and ACh neuromodulation	↓ Pupil diameter reflecting decreased NE and ACh neuromodulation
Mental experience	Focus on the present sensory environment	Focus on task-unrelated thought and imagery
RT	↓ SART RTs reflecting increased attention to the present sensory environment	↑ SART RTs reflecting decreased attention to the present sensory environment
Memory processes	↑ Encoding ↓ Consolidation	↓ Encoding ↑ Consolidation

The current study was motivated by the hypothesized existence of at least two statistically discriminable states of wakefulness—an “online” state optimized for encoding the present sensory environment and an “offline” state optimized for consolidation of previously encoded information.

Table 2. Participant Characteristics

	<i>Mean</i>	<i>SD</i>
Epworth Sleepiness score	14.3	3.2
MAAS score	3.9	0.5
Daydream frequency score	34.2	9.5
Baseline Icelandic words correct (of 20)	8.5	3.7
Baseline story elements recalled (of 25)	15.6	3.9
SART % trials correct	90.3	15.1
RT to nontarget SART trials (msec)	515.5	201.5

Daydream frequency score = total score from the daydream frequency subscale of the Imaginal Processes Inventory; MAAS score = mean score on the Mindfulness Attention Awareness Scale.

Story Task, and in the other session was the Icelandic Word Pairs Task, each described below. These tasks were selected because both have been observed to benefit from short durations of posttraining rest (Mercer, 2015; Dewar et al., 2012). Upon arrival for their first session, participants signed

informed consent and completed initial questionnaires including demographics forms, the Epworth Sleepiness Scale (Johns, 1991), the daydream frequency subscale of the Imaginal Processes Inventory (a measure of trait daydream frequency [Singer & Antrobus, 1972]), the Mindfulness Attention and Awareness Scale (a measure of trait mind-wandering propensity [Brown & Ryan, 2003]), and a two-night retrospective sleep log.

Participants were then prepared for EEG and pupillometry recording. Sixty-four EEG electrode locations were recorded using a high-density cap following the 10–10 system of electrode placement. Impedance was kept under 10 k Ω . Participants' heads were immobilized in a chin rest positioned a fixed distance from the computer monitor, to facilitate the accurate recording of pupil data using an EyeTribe infrared eye tracker positioned below the computer monitor. Participants then completed measures of state sleepiness, including the Stanford Sleepiness Scale (Johns, 1991) and visual analog scales assessing perceived ability to concentrate and how refreshed participants felt.

Participants then trained on one of the two memory tasks, just before beginning a \approx 30-min SART (see Figure 1

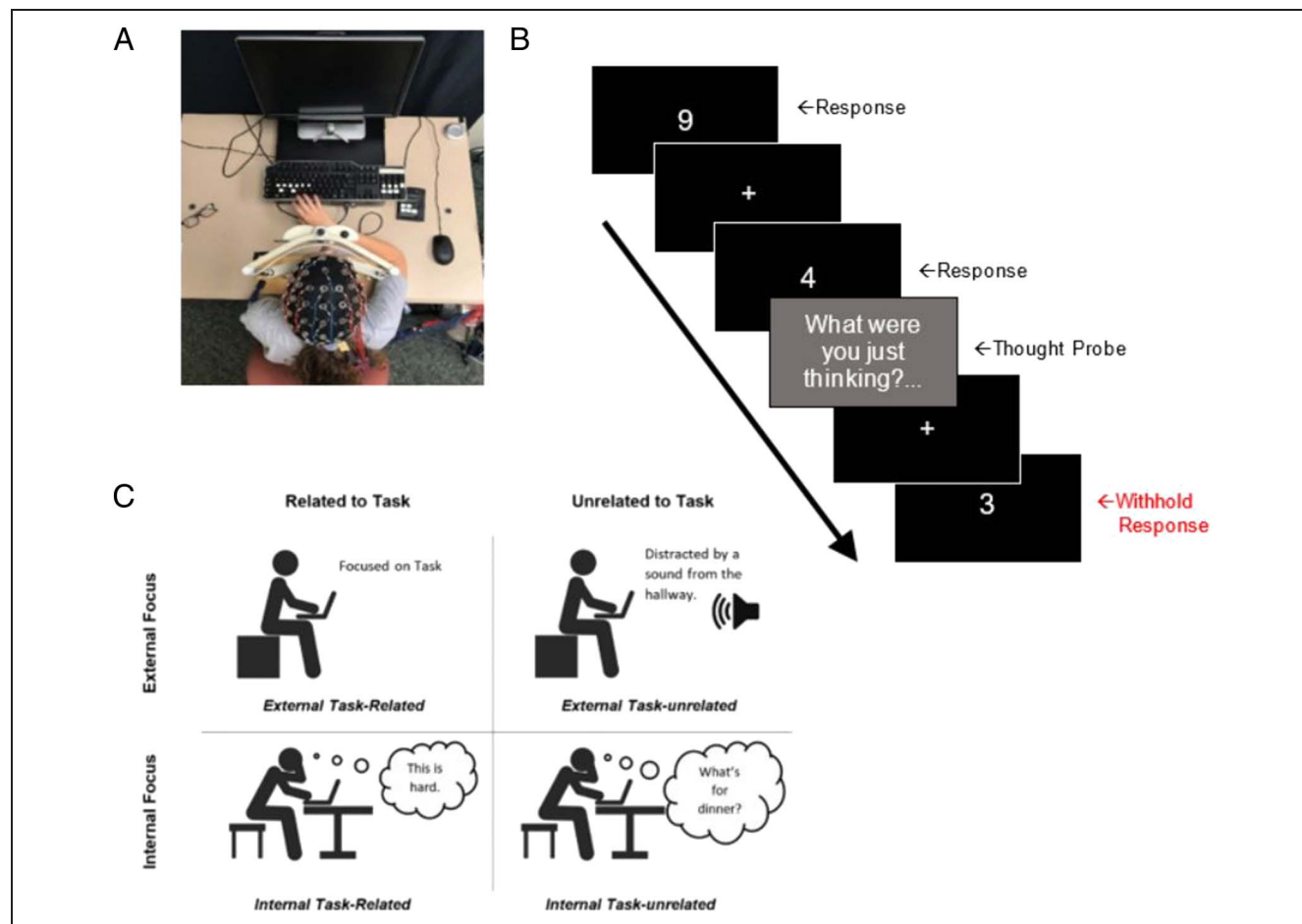


Figure 1. Experimental paradigm. (A) Participant undergoing simultaneous EEG and pupillometry while completing the SART. (B) During the SART, participants responded to successive numeric stimuli with a button press but were instructed to withhold response to the target digit (“3”). (C) Experience was intermittently sampled using a forced-choice thought probe that prompted participants to categorize their immediately preceding experience as either related or unrelated to the experimental stimuli and either externally or internally directed.

and below). During the SART, EEG and pupillometry data were continuously recorded as participants completed the task in a dimly lit room. The eye tracker was calibrated before beginning the SART, and pupil diameter of both eyes was recorded at 30 Hz for the duration of the task (measured in arbitrary units). EEG data were acquired at 400 Hz for the duration of the SART. Immediately after completion of the SART, participants were again tested on their memory for the verbal learning task, as described below.

Finally, participants completed an exit questionnaire about their subjective experiences during the SART retention interval. Participants were first asked to indicate, using a 5-point scale, the extent to which they had “thought about,” “imagined,” or “tried to remember” the verbal learning task while completing the SART. They were then asked to indicate the proportion of the SART interval they spent in one or more of 13 predefined mental categories: “thinking about the [short story/word pairs] from earlier,” “thinking about the past” (something earlier today/yesterday to a week ago/past year or several years ago), “imagining the future” (remainder of the day/tomorrow to next week/next year or several years), “thinking about the numbers task,” “mind was blank,” “counting the time,” “doing focused meditation,” “sleeping,” and “other.” For purposes of analysis, these categories were collapsed into the superordinate groupings of (1) thinking about the past, (2) thinking about the future, (3) thinking about the SART, and (4) other. Finally, participants provided an open-ended response to the question “Please describe your thoughts, feelings, or daydreams while performing the numbers task in as much detail as you can remember.”

Tasks

SART

The SART is a simple attention task designed to facilitate mind wandering while also measuring fluctuations in RT (Stawarczyk, Majerus, Maquet, et al., 2011; Christoff, Gordon, Smallwood, Smith, & Schooler, 2009). Participants were serially presented with the digits 1–9 on the computer monitor and were instructed to press the spacebar as quickly as possible as each digit appeared but to refrain from responding to the digit “3” (the “target”). Each digit was on-screen for 450 msec, with a 5-sec SOA. This relatively long SOA was necessary to be certain that evoked pupil and EEG responses returned to baseline well in advance of the next stimulus, allowing epochs of tonic prestimulus activity to be selected for analysis, uncontaminated by evoked responses.

Stimulus sequences were randomly generated with the following constraints: (1) Target probability was set to 0.29; (2) digit sequences were generated in blocks of 9, 12, 15, or 18 stimuli, with each of these blocks containing at least one but no more than three targets; and (3) targets were always separated by at least one nontarget.

Two different randomized sequences were generated, with a different sequence presented on each of the two experimental visits (order counterbalanced) to guard against sequence-specific learning effects. The last trial in every block was a “probe trial,” in which the digit stimulus (always a nontarget) was followed by a forced-choice question asking participants to reflect on the content of their current subjective experience. As illustrated in Figure 1C, participants classified their experience into one of five categories: (a) external focus on sensory aspects of the experimental stimuli (“external task-related”); (b) external focus on other sensory stimuli in the environment (“external task-unrelated”); (c) internal thoughts, feelings, or imagery about the experimental stimuli (“internal task-related”); (d) internal thoughts, feelings, or imagery unrelated to the current sensory environment (“internal task-unrelated,” e.g., daydreaming); or (e) mind blank/unable to recall any experience. There were 324 total trials, including 24 probe trials. Total task duration was approximately 30 min, with participants allowed a short break at the halfway point, during which they could stretch and reposition themselves.

Icelandic Word Task

Participants learned a list of 20 Icelandic words paired with their English translation (e.g., “*árekstur* – crash”). During encoding, participants were presented with each pair in sequence. Trials began with a 100-msec fixation cross, followed by display of the Icelandic–English pair for 5 sec, and then a 3-sec intertrial interval. An immediate recall test was then administered, in which participants were presented with the full list of 20 Icelandic words and were asked to type the corresponding English translation for each. An identical cued recall test was again administered after the SART.

Short Story Task

This short story recall task was adapted from the Wechsler Memory Scale (Wechsler, 1987) following Dewar et al. (2012). Participants listened to a digital recording of a short story, approximately 3 sec long, and then freely recalled as much of this story as they could, and as accurately as possible, by typing everything that they remembered into an electronic form. They were given as much time as needed to complete their responses. After the 30-min SART, a delayed recall test was administered in which they again typed everything they could remember about the short story. Free recall responses were scored by two raters blind to the experimental condition. Correctly recalled elements were scored according to the methods described in the Wechsler Memory Scale manual. All reports were scored by both raters, and the final score for each report was calculated as the average score of the two raters.

Data Preprocessing

EEG Recordings

EEG analyses were conducted in BrainVision Analyzer 2. Before analysis, recordings were filtered at 0.3–35 Hz, and bad channels were removed and interpolated using spherical splines. Ocular artifacts were then removed using an independent component analysis, and any remaining artifacts were manually marked via visual inspection. For all artifact-free trials, power spectral density was calculated for the 4-sec window of prestimulus EEG ending 200 msec before stimulus presentation (to account for jitter in EEG marker timing), in five a priori frequency bands known to covary with vigilance and mind wandering (Braboszcz & Delorme, 2011): slow oscillation (0.3–1 Hz), delta (1–4 Hz), theta (4–7 Hz), alpha (8–12 Hz), and beta (13–35 Hz). Power was normalized to the 0.3- to 100-Hz frequency range and then z scored before further analysis. To avoid excessive redundancy in the features provided to the cluster analysis (in a pilot study, this impeded our ability to arrive at a meaningful clustering model), only a single electrode (Fz) was considered for this procedure. The specific choice of Fz was based, first, on a prior study from our laboratory, which found the strongest associations between EEG and memory retention across rest frontally (Brokaw et al., 2016). In addition, we hypothesized that inhibition of frontal attention and executive control networks might be a relevant feature of the offline state that could be reflected in the EEG. Trials marked as including excessive artifacts were excluded from all subsequent analysis steps.

Pupil Diameter

Datapoints during which the pupil failed to be detected because of blinks or other artifact were deleted, as were datapoints where extreme variations in score were present (defined as a change of ≥ 1 in a single sample, after a 10-Hz low-pass filter). Linear interpolation was used to replace missing datapoints. Overall signal quality was then quantified by calculating the percentage of interpolated points across the whole recording, and only the eye with the highest overall signal quality was passed on for further processing. Data were then low-pass filtered at 10 Hz and z scored before obtaining the mean pupil diameter for the 1-sec window just before each SART stimulus presentation (less than a 6-datapoint buffer to allow for stimulus marker jitter). The 1-sec window was chosen to ensure that the pupil response evoked by the previous stimulus had returned to baseline, such that our analysis reflects only tonic, baseline pupil size just before presentation of the next stimulus.

Some participants had large amounts of missing pupil data because of failure of the tracker to maintain accurate pupil detection for the duration of the recording. Thus, individual trials were included in further analysis only when $\leq 20\%$ of the datapoints for that trial were interpolated, and experimental sessions were included in further analysis

only if at least 25% of trials from the session were usable according to this criterion. For these reasons, $n = 7$ participants were completely excluded from further analysis, and an additional $n = 9$ participants had one of their two experimental sessions excluded from further analysis. As a result, the final data set consisted of $n = 45$ sessions collected from $n = 27$ participants.

Clustering and Classification Procedures

Identification of Waking States via Cluster Analysis

Clustering and classification analyses were carried out using Weka 3.8 (Hall et al., 2009). Only nontarget trials were considered. To define waking states in a data-driven manner, an EM cluster analysis was applied to all probe trials. Input features included EEG spectral power at Fz (preprocessed and z scored as described above), RT to SART stimuli (RTs > 1000 msec excluded as extreme values), pupil diameter (preprocessed and z scored as described above), and participants' forced-choice response to the experience sampling probe (Figure 2). Finally, for all measures, datapoints more than 4 SD s above or below the mean were removed before EM clustering. Three different EM clustering models were evaluated (describing the data using two, three, or four clusters). Distance metrics (including the Silhouette index, Davies–Bouldin index, and Calinski–Harabasz index; see Table 3) uniformly confirmed that optimal cluster separation was obtained with two clusters, which we term the “online” and “offline” states. All subsequent analyses considered only this two-state model.

Classification of Nonprobe Trials into “Online” and “Offline” States

Because mind wandering is reduced when experience is sampled too frequently (Seli, Carriere, Levene, & Smilek, 2013), probes of conscious experience were administered at only 24 time points per session, and the above cluster analysis included only these trials. Yet, the full 30-min retention interval contains much richer data collected across hundreds of 5-sec trials, each with EEG, pupillometry, and associated RT data. Because of our interest in examining seconds-level fluctuations in waking state, a primary analytic goal was to be able to classify all trials into EM-defined online and offline states, even when experience sampling data were not present on that trial. As a next step, we thus trained a classifier to determine the EM cluster assignment (online vs. offline) of each probe trial based on the EEG, pupil, and RT data alone.

Selection of the classification approach. The classification approach best suited to our data was empirically determined by building five classifiers using different algorithms (ZeroR, OneR, J48, support vector machine,

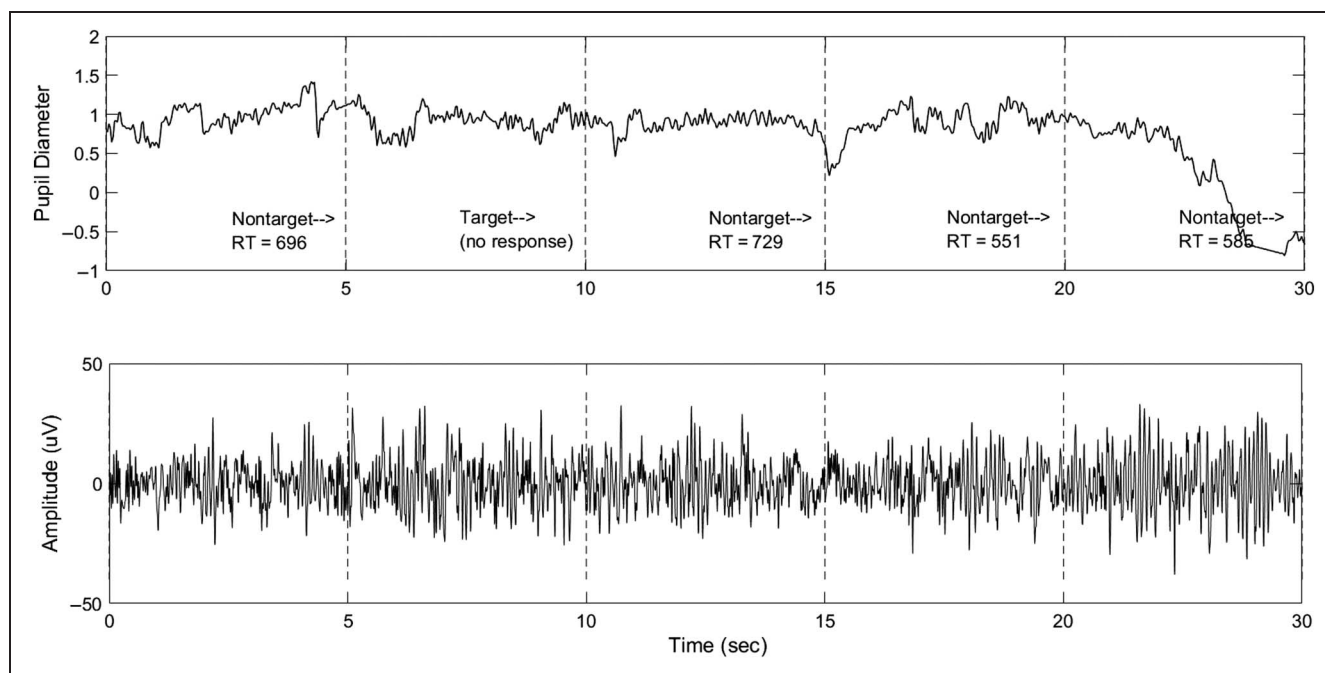


Figure 2. Example raw data for a single participant. Example pupil diameter (top) and EEG (bottom) time series for five consecutive 5-sec trials in a single participant. Dotted lines indicate the onset of SART stimuli. Labels indicate whether each stimulus was a “target” (requiring a button press) or a “nontarget” (requiring response withholding). RT is in milliseconds. Pupil diameter is expressed in z-score units.

and naive Bayes) and comparing their performance in correctly determining the cluster assigned to trials by the EM algorithm. Classifier performance was assessed using 10 iterations of stratified 10-fold cross-validation. The naive Bayes classifier significantly outperformed all other approaches, achieving an average of 95.4% accuracy in correctly labeling trials by cluster using EEG, pupil, and RT data alone (relative to 53.9% accuracy for ZeroR, 73.4% for OneR, 89.9% for J48, and 88.1% for support vector machine). We thus chose to move forward using the naive Bayes classification approach.

Development and validation of the classifier. The naive Bayes classifier was initially trained on data from two thirds of the participants ($n = 18$). Classifier performance was then tested on data from the remaining one third of the participants ($n = 9$), which the classifier had not been exposed to. On the test set, 95.4% accuracy was achieved in determining cluster assignment using EEG, pupil, and RT data alone.

Applying the classifier to assign “online” and “offline” labels to all trials. Having developed a classifier able to accurately determine waking state cluster based on EEG, pupil, and RT data alone, we then moved forward in applying this classifier to label all trials as “online” or “offline,” allowing us to define these states across the full length of the recording with 5-sec temporal resolution.

Statistical Analyses

Parametric statistics were used to describe the features of these data-driven “online” and “offline” states. To test for

an association between time spent in the offline state and memory retention, for each participant, we calculated off-line probability as the mean probability of being offline during the SART (posterior probability that a trial belongs to the offline state, as determined by the naive Bayes classifier and averaged across all trials for that participant). This metric was used to assess the association between offline time and memory retention for each of the verbal learning tasks.

Calculation of Bout Length

Online and offline bout lengths were calculated as mean number of trials that participants remained in the current state (online or offline) before switching states. As described above, participants often had missing trials because of low pupil detection quality and/or EEG artifact. To avoid the influence of missing data discontinuities on

Table 3. Distance-Based Cluster Evaluation Metrics

	Number of Clusters		
	2	3	4
Calinski–Harabasz index	74.88	20.31	24.72
Davies–Bouldin index	2.13	7.32	24.82
Silhouette index	0.17	−0.05	−0.21

For the Calinski–Harabasz and Silhouette indices, higher values indicate a greater separation between clusters. For the Davies–Bouldin index, lower values indicate greater cluster separation.

this calculation, individual bouts were assessed only within continuous runs of trials with no missing data and not across points of missing-trial discontinuity.

Regression Models

Finally, we used multiple linear regression to predict memory retention based on a combination of features including offline state probability, EEG, pupil diameter, RT, and thought probe responses. These exploratory analyses were motivated by our strong hypothesis that memory consolidation can best be predicted by a combination of features that together index a brain state, rather than by any single of these measurements alone. Because we reasoned that our definition of “offline state” might not perfectly capture the particular feature combinations relevant to memory, multiple regression constituted a complementary method for exploring how neurophysiology during the SART might relate to consolidation. We separately predicted memory for the Icelandic Word and Short Story tasks, applying backward elimination linear regression ($p \geq .1$ removal criterion) using the following predictors: mean offline state probability, proportion of thought probe responses in each of the five categories (external task-related, external task-unrelated, internal task-related, internal task-unrelated, and mind blank), mean RT on the SART, mean pupil diameter, and spectral power in the slow oscillation (0.3–1 Hz), delta (1–4 Hz), theta (4–7 Hz), alpha (8–12 Hz), and beta (13–35 Hz) frequency ranges.

RESULTS

Task Performance and Subjective Experience

Participants were highly accurate in their SART responses, performing correctly on $90.3 \pm 15.1\%$ *SD* of trials (Table 2). As expected, accuracy was greater for nontarget than for target stimuli (target percent correct: $69.0 \pm 18.6\%$ *SD*; nontarget percent correct: $94.5 \pm 18.9\%$ *SD*). Subsequent clustering and classification analyses considered only nontarget trials yielding a correct response. Baseline recall scores for the Icelandic Word and Short Story tasks were consistent with past observations (Brokaw et al., 2016; Mercer, 2015).

During the SART, thought probe responses most frequently indicated internal task-unrelated thought ($37.6 \pm 23.3\%$ *SD* of probes), followed by external task-related ($25.2 \pm 22.1\%$ *SD*), internal task-related ($18.6 \pm 16.5\%$ *SD*), external task-unrelated ($12.6 \pm 11.7\%$ *SD*), and mind blank ($6.0 \pm 8.3\%$ *SD*) responses. On the retrospective exit questionnaire, participants most commonly indicated that they had been thinking about the future ($31.1 \pm 21.2\%$ *SD* of time), followed by thinking about the SART ($29.3 \pm 26.9\%$ *SD*), thinking about the past ($22.2 \pm 19.9\%$ *SD*), and “other” categories of thought ($17.4 \pm 24.1\%$ *SD*).

Cluster and Classification Analyses

Cluster Analysis of Thought Probe Trials to Define States of Wakefulness

States of wakefulness were initially defined by applying EM cluster analysis to thought probe trial EEG, RT, pupil, and subjective experience data ($n = 579$ trials; see Methods). This revealed two distinct clusters of trials, which we refer to as the “online” trial cluster (46% of trials, green points in Figure 3A) and the “offline” trial cluster (54% of trials, blue points in Figure 3A). A moderately positive silhouette index of 0.17 indicated that trials tended to be relatively closer in multidimensional state space to points in their own cluster and relatively farther away from points in the other cluster.

As illustrated in Figure 3, cluster characteristics largely matched our a priori predictions. Relative to the online cluster, the offline cluster was characterized by slowed RTs, $t(537) = 8.65$, $p < 1 \times 10^{-10}$, $d = 0.72$ (Figure 3B); increased alpha and slow oscillation EEG power (alpha: $t(577) = 9.76$, $p < 1 \times 10^{-10}$, $d = 0.81$; slow oscillation: $t(577) = 6.99$, $p < 1 \times 10^{-10}$, $d = 0.58$; Figure 3C); and decreased theta, $t(577) = 7.74$, $p < 1 \times 10^{-10}$, $d = 0.64$ (Figure 3C), and delta, $t(577) = 17.43$, $p < 1 \times 10^{-10}$, $d = 1.45$, power (Figure 3C). The offline cluster was also associated with decreased subjective focus on the SART (external task-related thought probe response: $\chi^2(1, n = 579) = 30.50$, $p = 3.34 \times 10^{-8}$, $d = 0.47$; Figure 3D) and an increase in internal task-unrelated thought, $\chi^2(1, n = 579) = 19.07$, $p = 1.26 \times 10^{-5}$, $d = 0.37$ (Figure 3D). The remaining thought probe categories did not differ significantly between clusters. Neither pupil diameter nor beta power differed significantly between clusters.

Classification of Non-Thought-Probe Trials into Online and Offline States

To categorize the remaining trials (those not including thought probes) as online or offline, we developed a naive Bayes classifier. This classifier was 95.4% accurate in labeling an independent test set of probe trials by their EM-defined cluster, using EEG, RT, and pupil diameter alone (see Methods). Developed and tested using probe trial data, the classifier was then applied to label all trials, including $n = 4916$ without thought probes, as online or offline. For this much larger sample of trials, we describe the characteristics of online and offline states in two ways: (1) Trial-level statistics compare the characteristics of all online trials versus those of all offline trials, using the individual “trial” as the unit of analysis, and (2) participant-level statistics are computed by first calculating participant averages for each variable, separately for online and offline trials. We then use paired-samples *t* tests to compare the characteristics of the online versus offline state using “participant” as the unit of analysis.

Trial-level statistics. Applying this classifier to all $n = 5945$ trials, 55% were classified into the online state, and

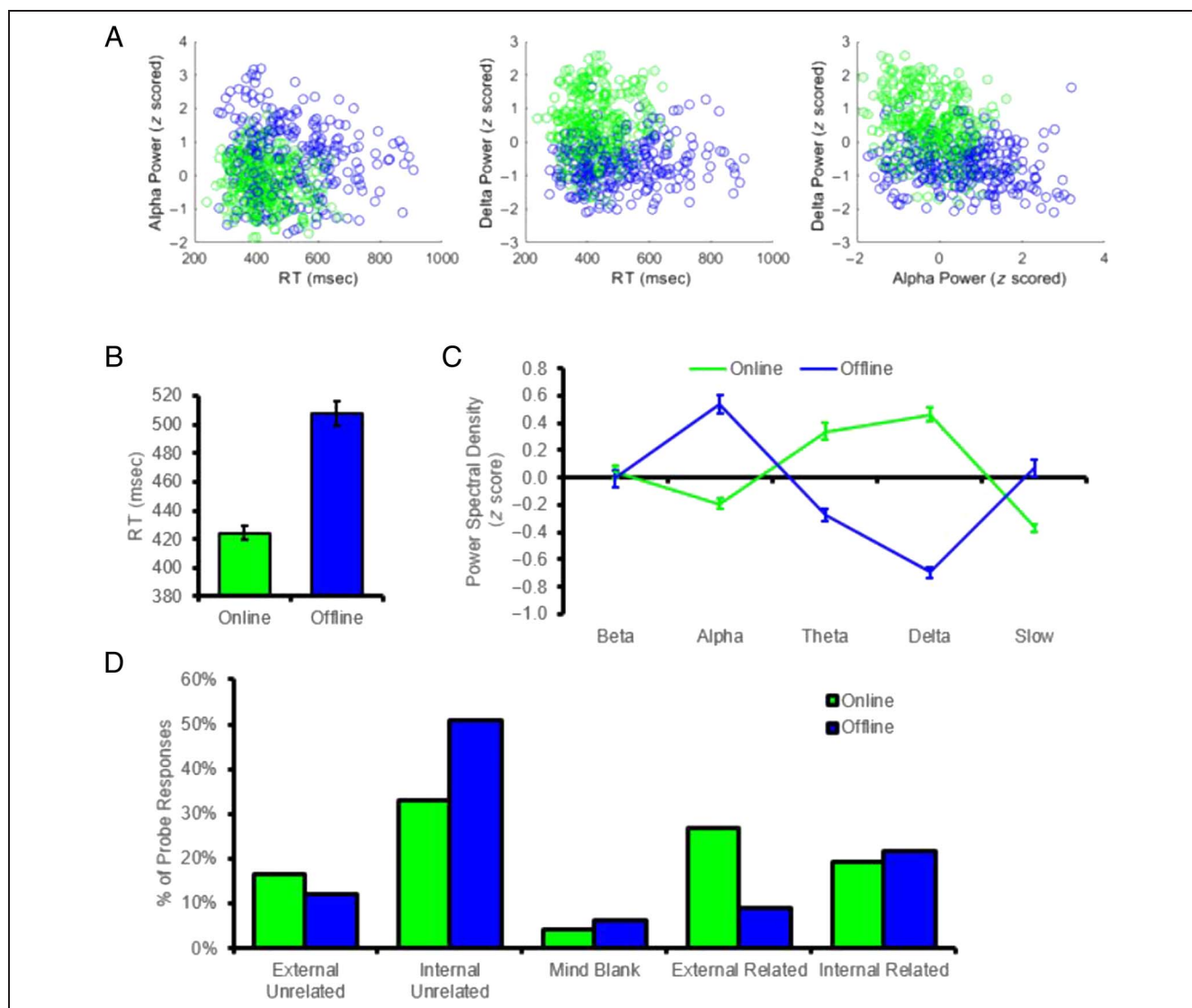


Figure 3. EM cluster analysis to define online and offline states using $n = 579$ thought probe trials. EM-based clustering indicated optimal separation using two states, the features of which largely conformed to our a priori hypotheses. Data for the “online” state cluster are shown in green, and for the “offline” state cluster, data are shown in blue. (A) Representative scatterplots illustrating the shape of the online and offline clusters in selected 2-D state spaces. (B) RT was significantly slower on offline, relative to online, trials. (C) EEG spectral power differed between states in the alpha, theta, delta, and slow oscillation bands. (D) During the offline state, participants indicated daydreaming more frequently (internal task-unrelated thought) and indicated that they were attending to the SART less frequently (external task-related thought).

45% were classified into the offline state. On a per-trial basis, the offline state was again characterized by slowed RTs, $t(5628) = 24.86$, $p < 1 \times 10^{-10}$, $d = 0.67$ (Figure 4B), along with increased EEG alpha, $t(5943) = 31.35$, $p < 1 \times 10^{-10}$, $d = 0.82$ (Figure 4C) and slow oscillation power, $t(5943) = 25.13$, $p < 1 \times 10^{-10}$, $d = 0.66$ (Figure 4C), as well as decreased theta, $t(5943) = 23.49$, $p < 1 \times 10^{-10}$, $d = 0.61$ (Figure 4C) and delta activity, $t(5943) = 52.98$, $p < 1 \times 10^{-10}$, $d = 1.38$ (Figure 4C). Again, trials in the offline cluster were associated with a decrease in focus on the SART (external task-related thought: $\chi^2(1, n = 579) = 13.93$, $p = .0002$; Figure 4D) and an increase in internal task-unrelated thought, $\chi^2(1, n = 579) = 7.92$, $p = .005$ (Figure 4D). The remaining thought probe categories

did not differ significantly between online and offline trials, nor did pupil diameter or beta-frequency EEG power.

Participant-level statistics. Every participant was classified as having a mix of online and offline trials. On average, participants were classified as spending 56.6% of the SART in an online state (range = 25.4–83.2% online, $SD = 12.5\%$). Mirroring the trial-level comparisons, relative to their own online trials, participants’ RTs were slowed when they were offline, $t(26) = 6.62$, $p = .0000006$, $dz = 1.30$, and alpha and slow oscillation power were substantially increased (alpha: $t(26) = 13.30$, $p < 1 \times 10^{-10}$, $dz = 2.56$; slow: $t(26) = 6.89$, $p = .0000003$, $dz = 1.33$), whereas both theta, $t(26) = 14.13$, $p < 1 \times 10^{-10}$,

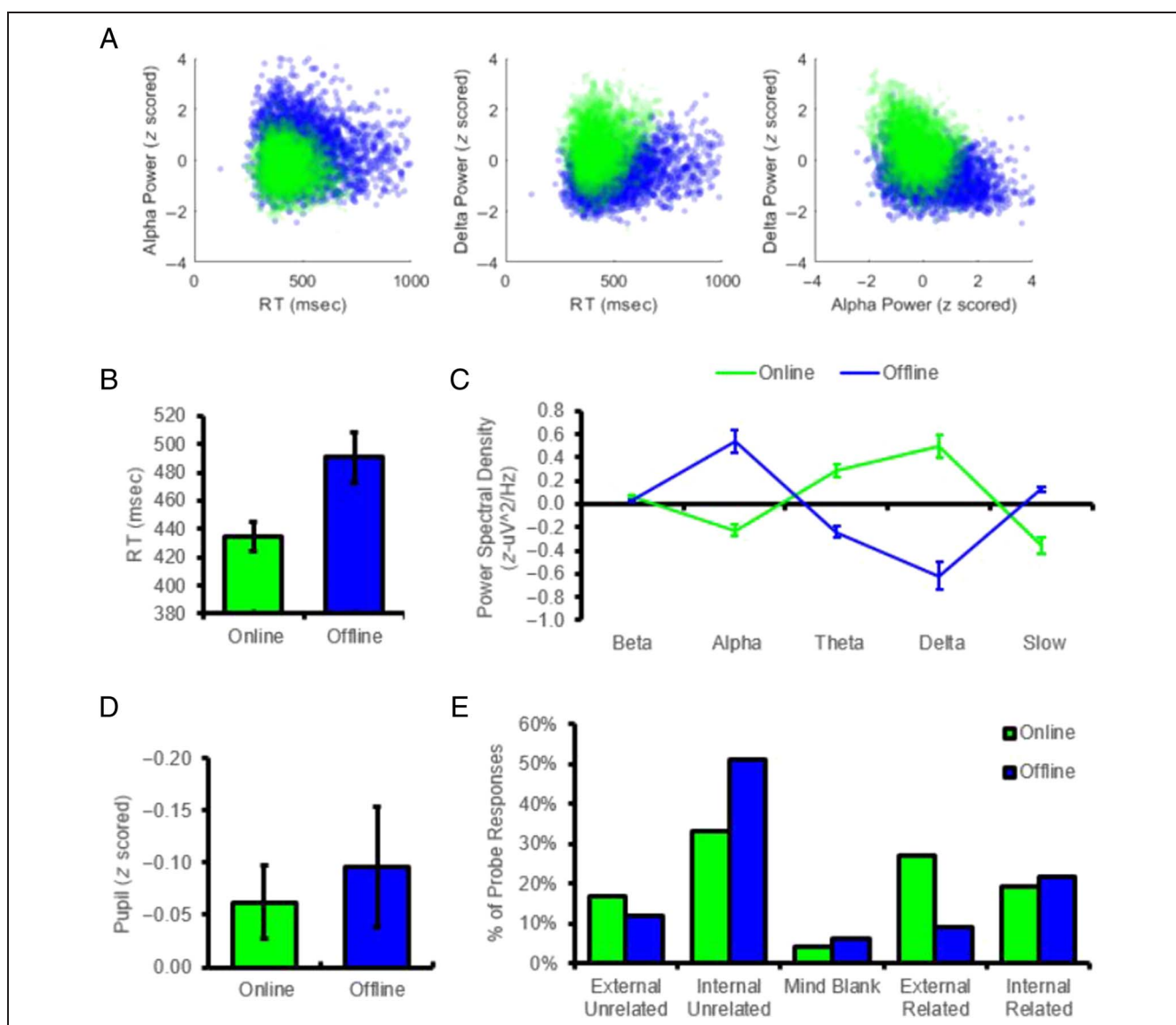


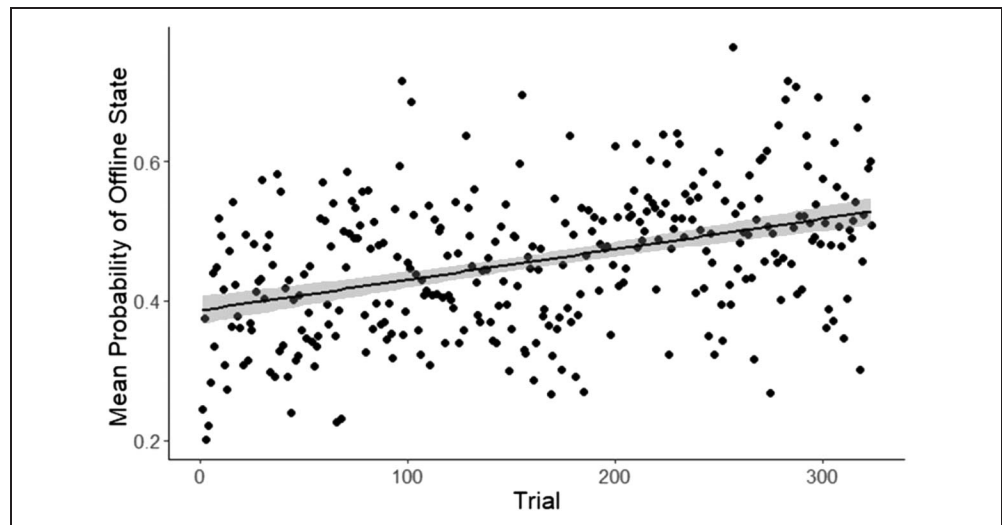
Figure 4. Naive Bayes classifier results: characteristics of online versus offline trials. Applying the naive Bayes classifier to label all $n = 5495$ trials by state yielded state features that strongly mirrored the initial EM cluster analysis of probe trials. (A) Representative scatterplots illustrating the shape of the online and offline clusters in selected 2-D state spaces. (B) RTs were significantly slowed during offline trials. (C) EEG spectral power again differed between states in the alpha, theta, delta, and slow oscillation bands. (D) Pupil diameter was nonsignificantly smaller during offline, relative to online, trials. (E) Using classifier-based labeling, the offline state was again characterized by increased daydreaming (internal task-unrelated thought) and decreased attention to the SART (external task-related thought).

$dz = 2.72$, and delta, $t(26) = 42.48$, $p < 1 \times 10^{-10}$, $dz = 8.17$, power were substantially decreased. Again, while offline, there was an increase in internal task-unrelated thought, $t(26) = 1.98$, $p = .02$, $dz = 0.35$. Accompanying this, there was a marginal decrease in focus on the SART (external task-related: $t(26) = 1.81$, $p = .08$, $dz = 0.49$) and also in external task-unrelated thought, $t(26) = 1.98$, $p = .06$, $dz = 0.39$. Again, pupil diameter did not differ significantly between states ($p = .24$), although the mean difference was in the hypothesized direction, with pupil size being numerically larger during the online state (-0.08 ± 0.03 SEM) and numerically smaller during the offline state (-0.13 ± 0.05 SEM).

Temporal features of the transition between states. As predicted, the offline state became increasingly prevalent as time on task increased ($r = .40$, $p < 1 \times 10^{-10}$; Figure 5). Mean duration of any one bout of online or offline time (see Methods) was approximately equal between states (mean number of trials spent online before switching states = 1.9 ± 0.09 SEM, mean number of trials spent offline before switching states = 1.7 ± 0.09 SEM; $p = .26$).

EEG features of online and offline states. As described above, state classification relied on EEG activity from a single electrode (Fz), in a selection five a priori frequency bands. However, after classification, we described spatiotemporal

Figure 5. Offline state probability increases with time on task. As hypothesized, the mean probability of being offline increased significantly across trials.



features of the EEG in more detail by examining spectral power during online and offline trials, across all electrode sites and frequencies. After Benjamini–Hochberg correction for multiple comparisons, mean EEG spectral power across electrode sites differed significantly between offline and online trials in the slow oscillation and alpha ranges as well as at select frequencies in the delta, theta, and beta ranges (Figure 6A). Time–frequency decomposition revealed that the prominent increase in alpha power during offline trials was, on average, strongest early in the SART trial (Figure 6B). Finally, we examined the scalp topography of offline–online differences in spectral power. After correction for multiple comparisons, offline trials were associated with significant increases in slow oscillation and alpha power primarily over frontal electrode sites (Figure 6C). Meanwhile, offline trials were also characterized by significant decreases in delta power over frontal electrodes (Figure 6C). No individual electrode comparisons survived correction for multiple comparisons in the theta or beta bands (Figure 6C).

Predictors of Memory Retention

Probability of the Offline State as a Predictor of Memory Retention

There was a nonsignificant positive association between participants' probability of being offline during the SART and their subsequent improvement on the Story Recall Task, $r(18) = .31$, $p = .19$ (Figure 8, top). This association did not reach significance for the Icelandic Word Task, $r(22) = -.12$. Offline probability was not associated with baseline memory performance before the SART, for either the Icelandic Word Task ($r = .20$, $p = .36$) or the Story Recall Task ($r = -.12$, $p = .63$).

Component Features of the Offline State as Predictors of Memory Retention

Next, we examined the association between memory change across the SART and each of the component features used

to define the online and offline states (Table 4). Multiple metrics of subjective experience during the SART predicted subsequent memory for the Icelandic Word Task. First, internal task-unrelated thought (i.e., daydreaming) was negatively associated with retention of memory for the word pairs (Table 4). This was mirrored in a similar negative correlation between trait daydreaming propensity and memory for the Icelandic words (Table 4). Conversely, external task-related thought (i.e., focus on the SART) was positively associated with subsequent memory for the Icelandic words (Table 4).

Regression Models Predicting Memory Based on a Combination of Features

Finally, we used multiple linear regression to predict memory retention for the Short Story and Icelandic Word tasks based on a combination of features including offline probability, EEG, pupil diameter, RT, and thought probe responses (see Methods). As summarized in Table 5, for both tasks, $\approx 50\%$ of variance in memory retention across the SART was successfully predicted by a combination of these metrics.

For the Story Recall Task, the regression model explained 53% of the variability in memory retention, $F(4, 15) = 4.28$, $p = .02$, $R^2 = .53$, adjusted $R^2 = .41$ (Table 5). Four predictors remained in the model after backward elimination ($p \geq .1$ elimination criterion). Offline state probability ($p = .02$) and proportion of external task-related probe responses ($p = .02$) were both significant positive predictors of subsequent memory. Meanwhile, both delta ($p = .07$) and slow oscillation ($p = .07$) power were marginally negatively associated with memory retention. Thus, as illustrated in Figure 8, although the above-reported 0.31 zero-order correlation between offline state probability and memory retention did not reach significance, a stronger association was uncovered when controlling for these other predictors (partial correlation

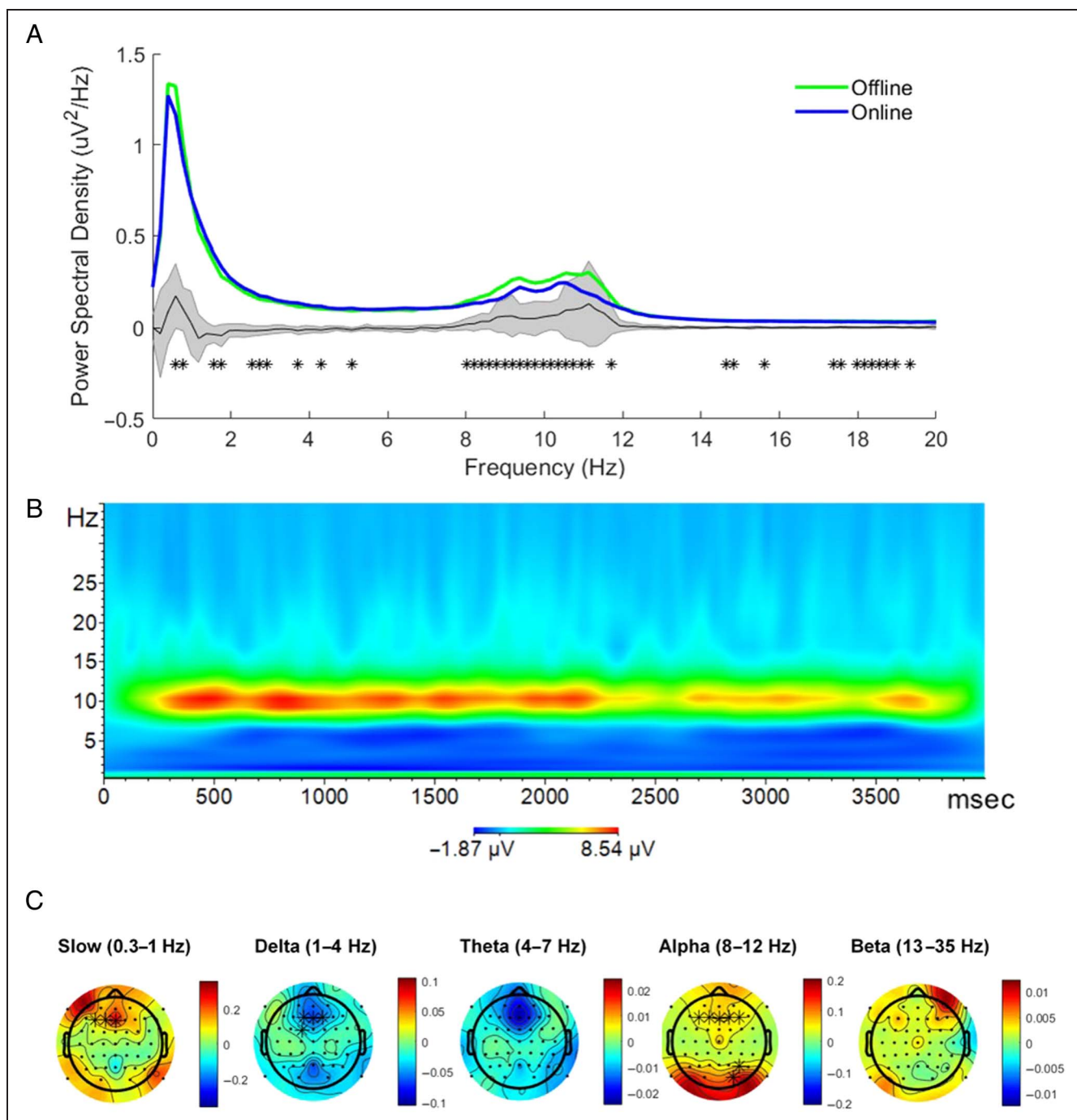


Figure 6. EEG features of offline versus online trials. (A) Spectral power averaged across all frequencies and electrodes. Shaded line represents mean offline–online difference scores, $\pm SD$. ***frequencies at which the difference between online and offline trials reached statistical significance, controlling for false discovery rate using the Benjamini–Hochberg method. (B) Time–frequency plot displaying offline–online difference scores for spectral power, across the duration of the 4-sec EEG analysis window. Warm colors indicate time/frequency points at which power was greater during offline trials, relative to online trials. Apparent is the prominent offline increase in ~ 10 -Hz alpha power, which was stronger earlier in the SART trial. As the first second after stimulus onset was excluded from EEG analyses, time = 0 on this plot falls 1 sec after onset of the SART stimuli. (C) Topographical plots representing the spatial distribution of offline–online differences in spectral power in each frequency band (units = $\mu V^2 / \text{Hz}$, spherical spline interpolation between sensors, *individual electrodes at which the offline–online difference retained statistical significance after correcting for multiple comparisons).

between offline state probability and percent improvement in story recall, when controlling for delta/slow power and external task-related thought: $r = .57$, $p = .009$; Figure 8, bottom).

For the Icelandic Word Task, the overall regression model also significantly predicted memory retention, explaining 43% of the variability in recall scores, $F(3, 24) = 5.33$, $p = .007$, $R^2 = .43$, adjusted $R^2 = .35$ (Table 5). For

Table 4. Retention Interval Features as Predictors of Memory Performance

	<i>Icelandic % Change</i>		<i>Short Story % Change</i>	
	<i>n = 24</i>		<i>n = 20</i>	
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
Thought probe responses				
External task-unrelated thought	.297	.159	.075	.754
Internal task-unrelated thought	−.489	.015*	−.220	.352
External task-related thought	.447	.029*	.189	.424
Internal task-related thought	−.057	.792	−.041	.865
Mind blank	−.131	.540	.206	.382
EEG spectral power				
Beta (13–35 Hz)	.254	.232	.202	.393
Alpha (8–12 Hz)	.062	.773	.357	.123
Theta (4–7 Hz)	.092	.669	−.293	.210
Delta (1–4 Hz)	−.052	.808	−.387	.092
Slow oscillation (0.3–1 Hz)	−.025	.907	−.328	.158
SART RT	−.118	.582	.141	.565
Pupil diameter	−.019	.929	.258	.272
MAAS	−.016	.942	.207	.382
Daydream frequency	−.375*	.038*	.027	.892
Offline probability	−.119	.580	.305	.191

In this table, Pearson's correlations between memory performance and features of the retention interval are shown. MAAS = Mindfulness Attention and Awareness Scale; Daydream frequency score = total score from the daydream frequency subscale of the Imaginal Processes Inventory. Boldface highlights statistically significant values.

* $p < .05$.

this task, three predictors remained in the model after backward elimination ($p \geq .1$ criterion): EEG alpha positively predicted subsequent memory ($p = .04$), whereas the proportions of internal task-unrelated ($p = .001$) and internal task-related ($p = .07$) probe responses were both negatively associated with subsequent memory.

Bivariate Associations between Component Features

Pearson's correlations were used to examine the bivariate associations between EEG, pupil, RT, and subjective experience during the SART, on a per-participant basis (Figure 7). Pupil diameter was negatively associated with EEG power in the delta and theta ranges but was positively associated with slow oscillation EEG power and with thought probe responses in the external task-unrelated category. RT showed a significant negative correlation

with EEG spectral power in the delta, theta, and beta bands. Attention to the SART (external task-related probe responses) was positively associated with EEG theta power. As summarized in Figure 7, there were also moderate intracorrelations between EEG variables as well as between probe response thought categories (Figure 8).

Association of Offline Time with Retrospective Exit Questionnaire Responses

For the Icelandic Word Task, extent to which participants reported "thinking about" the words during the SART was associated with offline state probability, such that participants who reported "not at all" thinking about the word pairs had higher offline probabilities than those who thought of the word pairs "once or twice" ($p = .006$) or "a few times" ($p = .04$; one-way ANOVA: $F(2, 22) = 5.49$, $p = .01$). Offline state probability was

Table 5. Regression Models Predicting Memory Retention from Offline Probability and Component Features

	<i>Beta Coeffs</i>	<i>t</i>	<i>p</i>	<i>Corr with % Recall Change</i>		<i>Collinearity</i>	
				<i>Zero Order</i>	<i>Partial</i>	<i>Tolerance</i>	<i>VIF</i>
Short Story Task: $R^2 = .53$							
Probability offline	.555	2.673	.017*	.305	.568	.722	1.385
External task-related thought	.521	2.548	.022*	.189	.550	.744	1.345
Delta power	−.370	−1.926	.073	−.387	−.445	.843	1.186
Slow oscillation power	−.372	−1.980	.066	−.328	−.455	.881	1.136
Icelandic Words Task: $R^2 = .43$							
Internal task-unrelated thought	−.792	−3.967	.001**	−.489	−.654	.678	1.475
Internal task-related thought	−.339	−1.895	.072	−.057	−.382	.843	1.187
Alpha power	.417	2.227	.037*	.061	.437	.772	1.296

Coeffs = coefficients; Corr = correlation; VIF = variance inflation factor. Boldface highlights statistically significant values.

* $p < .05$.

** $p < .01$.

not associated with reports of “imagining” or “trying to remember” the word pairs, nor was it associated with any form of rehearsal for the Short Story Task. Offline state probability was not associated with exit questionnaire ratings of the proportion of time that participants spent thinking about any particular topic, for either learning task.

DISCUSSION

Psychologists and neuroscientists have traditionally studied the mind and brain by observing how organisms respond to external stimuli. However, in actuality, we may spend as little as half of our waking hours attending to our immediate environment, with the remainder of our

Figure 7. Bivariate associations between participants' mean RT, pupil diameter, EEG power, and proportion of thought probe responses in each category. Pearson's correlations were used to assess associations between these individual component features. Numerical values and color scaling represent the correlation coefficient (r). Only statistically significant values are plotted (at $p < .05$; $df = 25$ for all comparisons). Ext = external; Int = internal.

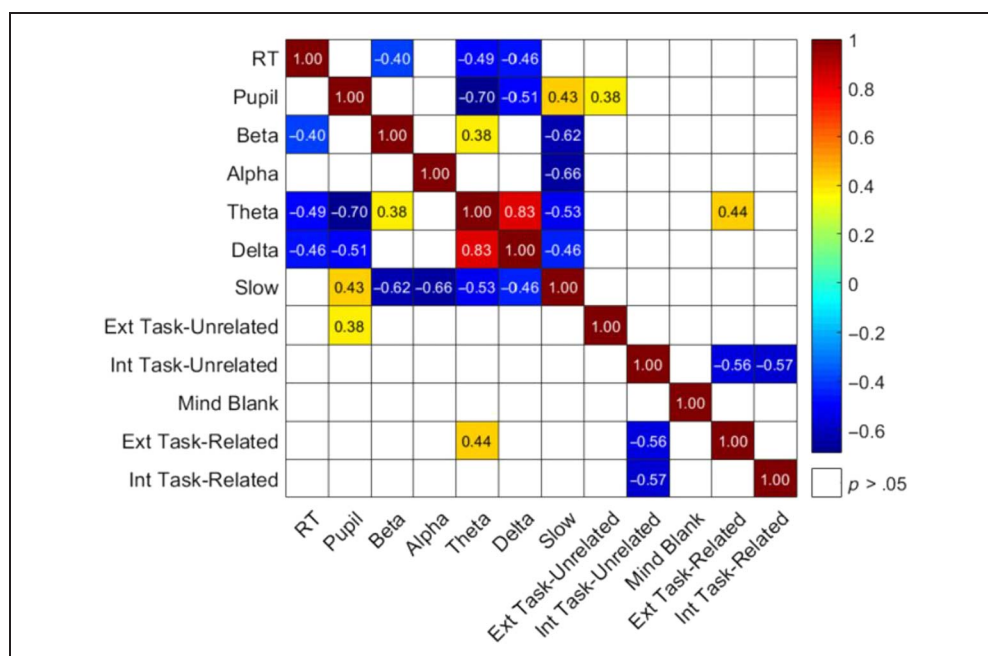
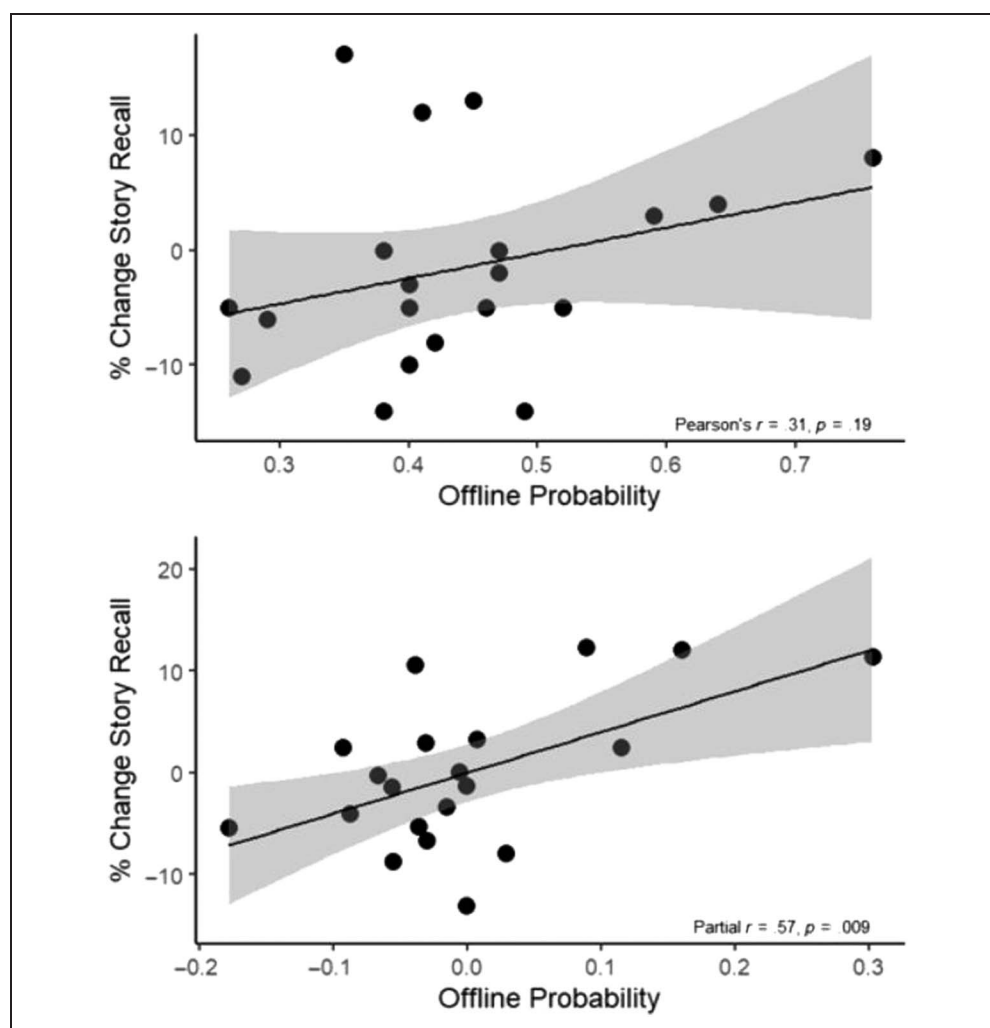


Figure 8. The offline state as a predictor of memory retention. Although the bivariate association between offline state probability and memory retention did not reach significance (top), offline state probability was a significant predictor of memory for the Short Story Task when included in a regression model along with measures of low-frequency EEG power and external task-related thought. Thus, offline state probability strongly predicted memory for the Short Story Task in a partial correlation controlling for delta/slow power and proportion of external task-related thought probes (bottom).



time focused on internally generated thoughts, feelings, and imagery (Smallwood & Schooler, 2006, 2015; Killingsworth & Gilbert, 2010). Why? Emerging evidence suggests that periods of inattention to the environment may support critical cognitive functions (Craig et al., 2018; Ritter et al., 2012; Cai et al., 2009; Dijksterhuis et al., 2006). Here, we explore the role that very brief offline moments play in the consolidation of recently formed memory, even while we are awake and ostensibly performing a task.

The structure and function of offline waking time still remain largely unknown, and the absence of a reliable, objective method of defining the offline state has been an impediment to research in this area. Although self-report is a critically important source of information in human studies, experience can be sampled only infrequently and relies on participants' ability to accurately detect and report attentional shifts. An emerging animal literature suggests that entry into an offline state can be measured without need of self-report—recent studies have described a rapid alternation between distinct “cortical states” in rodents, in which the intermittent emergence of synchronous fluctuations in neuronal firing

rate is accompanied by inhibition of sensory processing and a decrease in NE and ACh neuromodulation (Reimer et al., 2014, 2016; Harris & Thiele, 2011). Here, we hypothesized that a rapid, seconds-level alternation between online attention to the current environment and offline attention to internally generated thought and imagery is a fundamental feature of wakefulness, reflected in both the human mind-wandering literature and the animal literature on cortical states.

We created a data-driven model of how “online” and “offline” substates of wakefulness might operate in humans, illustrating a novel method of operationally defining this concept without exclusive reliance on self-report measures. Prior studies have used data-driven methods to define categories of neurocognitive experience (Turnbull et al., 2019; Sormaz et al., 2018; Wang, Bzdok, et al., 2018; Wang, Poerio, et al., 2018) or to predict mind wandering from neurophysiological data (Dhindsa et al., 2019; Jin, Borst, & van Vugt, 2019). However, our model is one of the first using a machine-learning approach to operationally define the concept of an “offline” state based on a combination of subjective and objective

measures and the first to relate brief, seconds-long bouts of offline wakefulness to memory consolidation.

Our results are consistent with the notion that continuous recordings of wakefulness can be usefully described as an alternation between brief periods during which participants report paying attention to the sensory environment (accompanied by rapid RTs + increased theta/delta EEG power), alternating with brief periods during which participants report attending to internally generated thoughts (accompanied by slowed RTs + increased alpha/slow oscillation power).

Offline trials were characterized by a large increase in alpha and slow oscillation power. Increased slow oscillation power during wakefulness is a prominent feature of the “synchronized” cortical state, as described in the animal literature, arising as a result of synchronized fluctuations in firing rate at the unit level and ultimately influencing the processing of incoming sensory input (Beaman et al., 2017; Harris & Thiele, 2011). In our data, we propose that the offline increase in low-frequency EEG power similarly indicates transient entry into an altered mode of cortical processing that functions to reduce processing of the external sensory environment, freeing cognitive resources to be devoted to internal processing. We interpret large increases in alpha power as indicating inhibition in task-irrelevant brain regions (Klimesch, 1997, 2012). Seen through this lens, occipital alpha is decreased during the offline state because of a decrease in processing of external visual information. Meanwhile, alpha increases over the frontal lobe during offline trials could indicate inhibition of frontal attention or executive control networks.

Conversely, increased delta and theta power during online trials could reflect task-related processing. Delta and theta oscillations have both been previously observed to increase during performance of a go/no-go task that, much like the SART, requires monitoring for a cue that will instruct participants whether to respond or withhold a response on each trial (Harmony, 2013; Harmony, Alba, Marroquín, & González-Frankenberger, 2009).

Importantly, classification of trials into online and offline states was based on an entirely atheoretical, data-driven clustering procedure. That the resulting states largely conform to our theoretically driven *a priori* hypotheses indicates that the latent structure of these data are indeed consistent with the existence of online and offline waking substates. In one notable exception, pupil diameter did not differ between online and offline trials as hypothesized. Yet, we did observe that trial-by-trial fluctuations in pupil diameter were associated with both subjective experience (reports of external task-unrelated cognition) and multiple EEG features, suggesting that pupil diameter may yet prove to be relevant to the concepts of interest here. As predicted, the offline state became increasingly frequent with increasing time on task, mirroring the temporal pattern of subjectively defined mind wandering (Risko, Anderson, Sarwal, Engelhardt,

& Kingstone, 2012; Stawarczyk, Majerus, Maj, Van der Linden, & D’Argembeau, 2011).

The Offline State as an Ideal Environment for Memory Consolidation

Theoretical Basis for Our Predictions

Our interest in the offline state was motivated by evidence that this form of wakefulness may be ideally suited to support the early stages of memory consolidation. The initial encoding of memory and its subsequent consolidation are thought to be mutually exclusive processes, with consolidation requiring a brain state during which processing of external sensory stimuli is reduced, while the neuromodulatory (Hasselmo & McGaughy, 2004; Hasselmo, 1999) and electrophysiological (Jadhav, Kemere, German, & Frank, 2012; Ego-Stengel & Wilson, 2010; Axmacher, Elger, & Fell, 2008; Eschenko, Ramadan, Molle, Born, & Sara, 2008) environment shifts to facilitate consolidation, as opposed to encoding (Mednick et al., 2011; McClelland & O’Reilly, 1995). A growing literature thus explores offline memory consolidation in the context of sleep, demonstrating that sleep after encoding benefits memory performance at delayed test (Wamsley, Tucker, Payne, & Stickgold, 2010; Tucker et al., 2006; Stickgold, James, & Hobson, 2000; Plihal & Born, 1997). This mnemonic benefit of sleep has been attributed to neurophysiology including sleep slow waves (Alger, Lau, & Fishbein, 2012; Diekelmann, Biggel, Rasch, & Born, 2012; van Dongen et al., 2012), hippocampal sharp-wave ripples and associated memory “replay” (Bendor & Wilson, 2012; Ramadan, Eschenko, & Sara, 2009; Eschenko et al., 2008; Ji & Wilson, 2006), and decreased acetylcholine levels during non-rapid eye movement sleep (Hasselmo & McGaughy, 2004).

Yet clearly, at least some consolidation processes must occur balanced with the demands of new encoding during wakefulness. Local cellular-level consolidation beginning immediately after encoding is sufficient to stabilize memory against interference over the short term (hours), even in the absence of sleep. This is evident, first, in our ability to recall what we did a few hours ago without taking a nap. Empirical evidence includes that molecular cascades underlying memory consolidation begin just minutes after encoding (Redondo & Morris, 2011; Bailey & Kandel, 2008), and behavioral studies showing performance stabilization over minutes to hours of wakefulness (Cohen, Pascual-Leone, Press, & Robertson, 2005).

The brief moments of offline time under study here could provide an ideal opportunity for wakeful consolidation, as offline trials share some of the consolidation-promoting neurophysiological features that have been attributed to sleep. First, attention to new external stimuli is reduced during offline trials. In our data, this was evident in the shift of subjective experience away from task-focused cognition and toward task-unrelated cognition as well as in slowed RTs to task stimuli. Second, offline trials

were characterized by increased power in the <1-Hz slow oscillation band. The <1-Hz cortical slow oscillation is hypothesized to play a vital role in the hippocampal–cortical communication thought to underlie system consolidation of declarative memory during sleep (Mölle & Born, 2011; Marshall, Mölle, Hallschmid, & Born, 2004). Recent studies now link memory improvements to increased slow oscillation activity during resting wakefulness as well (Sattari, Whitehurst, Ahmadi, & Mednick, 2019; Brokaw et al., 2016), suggesting that this EEG rhythm could retain a similar functional role even outside sleep. Finally, we had hypothesized that offline trials would be characterized by decreased pupil diameter, reported to track reductions in ACh neuromodulation (Reimer et al., 2016; also thought to favor consolidation [Hasselmo & McGaughy, 2004; Hasselmo, 1999]). However, as described above, pupil diameter did not end up differing significantly between online and offline trials.

Evidence for a Link between the Offline State and Memory Consolidation in the Current Study

Our data provide partial support for the hypothesis that memory is facilitated by brief entry into an offline state, characterized by momentary EEG slowing and reduced sensory processing. A regression model including offline probability successfully explained over 50% of the variance in memory for a short story learned just prior. Indeed, the probability of being offline during the 30-min retention interval was the strongest individual predictor of subsequent story memory. Surprisingly, the only other statistically significant predictor of story memory was external task-related thought (i.e., attending to the SART)—a feature that was most prevalent during online trials. This latter unexpected association could have arisen if attention to the SART acted as a “suppressor” variable in the regression model, strengthening the relationship between offline probability and memory by removing memory-irrelevant variance from these measures. In support of this conjecture, we note that external task-related thought had a near-zero bivariate correlation with memory, only predicting memory retention in combination with the other factors in the regression. This pattern of results could have arisen from imperfections in our classification method, such that only a subset of “offline”-labeled trials are truly part of a functional state related to memory.

Interestingly, Icelandic word memory was predicted by entirely different features of the retention interval than was short story memory. Contrary to our hypotheses, Icelandic word memory was negatively associated with both state and trait measures of internally focused thought and positively associated with reports of being task focused (as reported in Tables 4 and 5). We originally hypothesized that both internal-task unrelated thought and trait daydreaming would be positively associated with memory, on the basis of prior work showing that

quiet rest, during which such thoughts are prominent, facilitates memory (Brokaw et al., 2016; Dewar et al., 2012). However, in addition to the current data, another recent study from our laboratory similarly found that increased trait daydreaming was associated with more forgetting of a verbal learning task across a brief retention interval (Humiston, Tucker, Summer, & Wamsley, 2019). Thus, we now hypothesize that within “rest,” moments of high internal task-unrelated thought may actually not represent the optimal conditions for memory consolidation to occur. Instead, although quiet rest enhances memory relative to an attention-demanding distractor task and quiet rest tends to be high in internal task-unrelated thought, the form of rest that most optimally facilitates consolidation may yet be an offline state in which internal task-unrelated thought (i.e., daydreaming) is low.

The two verbal memory tasks we employed may have relied on different mechanisms, causing them to be promoted by different forms of wakefulness. For example, memory for story narratives relies heavily on temporal, semantic, and associative features that were less relevant to the Icelandic Word Task. Notably, prior research has reported that the offline state of sleep shows a greater benefit for highly associative materials, perhaps because of the engagement of the hippocampus in associative learning tasks (Studte, Bridger, & Mecklinger, 2015). We thus speculate that memory for the Icelandic words was better able to be maintained even in tandem with focused attention to the SART, whereas memory for the story was preferentially promoted by the proposed “offline” form of wakefulness, because of its associative nature.

Together, these observations add to a growing body of evidence that memory consolidation is not uniformly distributed throughout all wakefulness but, to the contrary, occurs preferentially during periods characterized by reduced attention to the sensory environment and accompanying changes in cortical activity (Wamsley, 2019; Craig et al., 2018; Brokaw et al., 2016; Dewar et al., 2012; Mednick et al., 2009). However, unlike prior studies utilizing relatively long (minutes to tens of minutes) enforced periods of task-free “rest,” here we report that even brief, spontaneously occurring bouts of offline time are similarly associated with a memory benefit. Thus, we propose that, even while we are ostensibly engaged in performing a task, the brain is spontaneously entering a memory-promoting offline state for short, seconds-long bouts.

Limitations

Limitation of the Two-State Model

The model presented here describes wakefulness as consisting of only two states, one with an external attentional focus and one with an internal attentional focus. This may be an oversimplification, as the literature on human mind

wandering strongly suggests the existence of multiple distinct forms of task-unrelated thought (Wang, Bzdok, et al., 2018; Smallwood & Schooler, 2015; Unsworth & McMillan, 2014; Stawarczyk, Majerus, Maquet, et al., 2011). In our own data, during periods that participants report not being focused on the SART, this might be because they are daydreaming, because they are distracted by some other sensation in the environment, or because they simply cannot recall their experience. A dichotomous distinction between “online” and “offline” does not capture these or other potentially crucial subtleties. We used a two-state model because this parsing was best able to describe trial-by-trial variability in our particular data set. Yet, in reality, we suspect that what we refer to as the “offline” state may actually consist of multiple substates.

In support of this latter conjecture, we note that offline trials were much more variable on several features than online trials, including RT and alpha power. For example, as shown in Figure 4A, when participants are classified as “online,” they invariably have relatively fast RTs in concert with low alpha power. However, when participants enter the offline state, this sometimes consists of an increase in alpha power while maintaining swift RTs, and other times, this consists of a slowing of RTs without an increase in alpha power. Potentially, this could suggest that the “offline” state actually reflects multiple forms of offline wakefulness, only one of which is associated with an increase in alpha power. Future studies may discover ways in which methods similar to those used here can be leveraged to meaningfully parse several different forms of “offline” state that better capture the full heterogeneity of wakefulness.

Limitations of the regression analyses. As a caveat regarding the exploratory regression models, we note that, because of our relatively small sample size, overfitting is a potential danger. Although these analyses suggest a novel relationship between offline time and memory retention for the short story, this should not be accepted as an established conclusion until future studies can confirm these observations using *a priori* planned analyses.

Possible Influence of Individual Differences

Here, we have interpreted associations between waking state and memory as consistent with a causal role for offline time in promoting memory consolidation. Indeed, prior work from our laboratory and others has demonstrated that experimentally induced periods of task-free rest improve memory for previously learned information (Brokaw et al., 2016; Dewar et al., 2012). However, because entry into the offline state was not experimentally manipulated in the current study, associations between offline time and memory could also be driven by individual differences that cause both an increased amount of offline time and greater retention of short story memory.

Individual differences are also a plausible explanation for the observed negative associations between internally focused cognition and Icelandic word memory. Icelandic word memory was associated not only with internally focused thought reported during the SART but also with trait daydreaming frequency as measured by the Imaginal Processes Inventory. This suggests that a stable trait related to daydreaming could explain reduced memory for the Icelandic words in these participants.

There is substantial individual variability in the extent to which participants engage in mind wandering, which may be a trait rooted in stable individual differences in intrinsic network connectivity (Turnbull et al., 2019; Godwin et al., 2017; Kucyi & Davis, 2014). For example, connectivity between regions of the default mode network (DMN) is associated with trait mind wandering (Godwin et al., 2017; Kucyi & Davis, 2014). Given the strong association of the DMN with memory, it is plausible that individual differences in DMN connectivity could predict both the occurrence of the offline state and memory retention across a period of rest.

Conclusions

Here, we present a method of parsing continuous periods of wakefulness into “online” and “offline” states, without the need to exclusively rely on self-report. This data-driven model suggests that wakefulness can be usefully described as a series of transitions between brief periods during which we are attending to the current sensory environment, alternating with brief periods during which external sensory processing is reduced. Together with converging evidence from other literature, these observations suggest that, even while we are ostensibly engaged in performing a task, the mind intermittently disconnects from the current sensory environment in favor of internal processing.

We suggest that this “offline” state may function to support the consolidation of recently formed memory. The offline consolidation of memory has already been extensively described in studies of sleep (Wamsley et al., 2010; Ellenbogen, Hu, Payne, Titone, & Walker, 2007; Tucker et al., 2006; Stickgold et al., 2000; Plihal & Born, 1997) and, more recently, in studies of enforced periods of postlearning rest (Brokaw et al., 2016; Dewar et al., 2012). Yet, during our hectic lives, many days pass where obtaining even a few continuous minutes of unoccupied rest is impossible. Our current observations provide the first evidence that spontaneously “going offline” for even only a few seconds at a time could help us to balance the demands of new encoding with the offline consolidation of learned information.

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