

## NREM sleep spindles are associated with dream recall

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Both rapid eye movement (REM) sleep dreaming and non-rapid eye movement (NREM) sleep spindles have been linked to processes of memory consolidation. However, relationships between the two phenomena have yet to be explored. In a heterogeneous sample of 53 healthy subjects who had participated in a memory consolidation protocol and who varied in their self-reported recall of dreams and nightmares, we assessed overnight polysomnography, N2 sleep spindle density, REM dream word count, and retrospective estimates of how often they recall dreams, bad dreams (dysphoric dreams, no awakening), and nightmares (dysphoric dreams, with awakenings). Fast spindle density positively correlated with all measures of dream recall but was most robustly associated with bad dream recall and REM dream word count. Correlations with bad dream recall were particularly strong for spindles occurring in sleep cycles 2 and 3 and correlations with word count for cycles 1, 4, and 5. While slow spindle density showed opposite correlations with all of these measures, partialing out slow spindles attenuated, but did not eliminate, the fast spindle correlations. Results are largely consistent with the conclusion that fast sleep spindles are associated with a common trait factor that also influences dream recall. However, the results also raise the possibility that both spindles and dreaming are expressions of memory consolidation mechanisms, such as neural replay, that transcend sleep stage.

**Keywords:** dreaming; sleep spindles; memory consolidation; REM sleep; N2 sleep

## HIGHLIGHTS

- Dream recall measures are correlated with the density of fast spindles from N2 sleep
- The association is most prominent for measures of bad dream recall and REM dream word count
- The two dream measures are associated with different N2 cycles of the night
- Dreaming and spindles may reflect a shared trait or mechanism of sleep-dependent memory consolidation

## INTRODUCTION

Two prevalent sleep phenomena – non-rapid eye movement (NREM) sleep spindles and rapid eye movement (REM) sleep dreaming – have been linked to the consolidation of new memories. Yet, direct relationships between the two phenomena have never been investigated. That these events occur in different sleep states might seem to preclude them being related, yet their joint association with memory consolidation processes and their correlations with other trait characteristics such as intelligence (Bodizs, Gombos, Ujma, and Kovacs, 2014; Foulkes, 1985) suggest that there

may well be more direct links. Connections between the two are also suggested by many theories that consider memory consolidation to be a function of both REM and NREM sleep stages at different times of the sleep episode (Buzsaki, 1989; Ficca and Salzarulo, 2004; Fogel, Smith, and Beninger, 2009; Giuditta, 2014; Giuditta et al., 1995). Accordingly, the general goal of this study was to assess potential relationships between measures of N2 sleep spindles and dream recall.

*Sleep spindles are a reliable index of intelligence and memory consolidation*

The essential features of sleep spindles and methods for their detection are well described (for reviews, see Andrillon et al., 2011; O'Reilly, Godbout, Carrier, and Lina, 2015; O'Reilly and Nielsen, 2014; Wallant, Maquet, and Phillips, 2016). Their use as an index of intellect and memory

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consolidation has also been repeatedly validated, with robust associations being documented between sleep spindles and (a) trait measures of intelligence (for reviews, see [Fogel and Smith, 2011](#)) and (b) sleep-related measures of memory improvement (for reviews, see [Astori, Wimmer, and Luthi, 2013](#); [Fogel and Smith, 2011](#); [Rasch and Born, 2013](#)). As an indicator of trait abilities, spindle density correlates positively with intellectual competencies, such as general intelligence (*Wechsler Memory Scale*; [Schabus et al., 2008](#)), performance IQ (Multidimensional Aptitude Battery–II; [Fogel, Nader, Cote, and Smith, 2007](#)), fluid intelligence (*Raven Progressive Matrices Test*; [Bódizs et al., 2005](#)), verbal memory (*Auditory Verbal Learning Test*; [Lafortune et al., 2014](#)), and visuospatial memory (Rey–Osterrieth Complex Figure Test, ROCFT; [Bódizs, Lazar, and Rigo, 2008](#)).

As an indicator of memory processing during sleep, sleep spindles correlate with a number of different sleep-dependent memory consolidation measures. This is especially the case for higher frequency (“fast”) spindles (13–16 Hz), more prevalent over central, parietal, and occipital regions, than for lower frequency (“slow”) spindles (10–13 Hz), more prevalent over frontal regions ([Andrillon et al., 2011](#); [O’Reilly and Nielsen, 2014](#)). For example, fast spindle density is elevated when participants show sleep-related improvement on tasks of verbal memory ([Clemens, Fabo, and Halasz, 2005](#)), visuospatial memory ([Clemens, Fabo, and Halasz, 2006](#)), and integration of new semantic information ([Tamminen, Lambon Ralph, and Lewis, 2013](#); [Tamminen, Payne, Stickgold, Wamsley, and Gaskell, 2010](#)). A causal role for sleep spindles in memory is further demonstrated by protocols that enhance consolidation of new memories by increasing spindle density either pharmacologically ([Kaestner, Wixted, and Mednick, 2013](#)) or with transcranial alternating current stimulation ([Lustenberger et al., 2016](#)).

Neural theories of memory consolidation link sleep spindles to sleep “replay” events, that is, the reactivation of neural sequences learned during wake, by their observed associations with slow oscillations and sharp-wave ripples ([Born, 2010](#); [Ritter et al., 2015](#); [Siapas and Wilson, 1998](#)). Although most studies of memory replay find that neural replays occur during NREM sleep, which in humans is associated with less frequent and less vivid dreaming than is REM sleep, neural replay events also take place in REM sleep ([Hennevin, Hars, Maho, and Bloch, 1995](#); [Louie and Wilson, 2001](#); [Poe, Nitz, McNaughton, and Barnes, 2000](#); [Poe, Walsh, and Bjorness, 2010](#)). Some characteristics of neural replay events during NREM sleep suggest a similarity to those seen during dreaming. For example, the finding that complete sequences are replayed much less often than that are short sequence fragments ([Mahoney, Titiz, Hernan, and Scott, 2016](#)) parallels the observation that dreaming about complete episodic memories is rare, whereas dreaming about short memory fragments is not ([Fosse, Fosse, Hobson, and Stickgold, 2003](#); [Malinowski and Horton, 2014](#)). On the other hand, many features of NREM sleep replays have no clear phenomenological analog in human dreaming; for example, replays may occur in reverse order ([Diba and Buzsaki, 2007](#)) or accelerated by as much as 7–10 times ([Euston, Tatsuno, and McNaughton, 2007](#); [Kudrimoti, Barnes, and McNaughton, 1999](#)).

### *Dreaming is a possible index of memory consolidation*

Unlike findings for sleep spindles, a role for dreaming in memory consolidation remains uncertain. Theories have long held that dreaming serves a memory-enhancing function ([Breger, 1969](#); [Dewan, 1970](#); [Palombo, 1976](#)) with a wide variety of mechanisms having been proposed. Most theories implicate some form of replay of waking memory during dreaming; these may be quite general, as in the reprocessing of unassimilated “lessons” from waking experience ([Dewan, 1970](#)) or the realistic simulations of real-world threats ([Revonsuo, 2000](#)), or they may be relatively restrained and fragmented, such as the reactivation of fear elements in safe contexts ([Nielsen and Levin, 2007](#)) or the repetition of memory fragments in novel or bizarre contexts ([Horton and Malinowski, 2015](#)).

Empirical tests have supported this notion of replay during dreaming to a limited extent (for reviews, see [Smith, 2010](#); [Wamsley and Stickgold, 2011](#)) with several studies supporting a role for dreaming in memory improvement ([Cipolli, Fagioli, Mazzetti, and Tuozi, 2004](#); [De Koninck, Christ, Hebert, and Rinfret, 1990](#); [De Koninck, Christ, Rinfret, and Proulx, 1988](#); [De Koninck, Prévost, and Lortie-Lussier, 1996](#); [Dumel et al., 2015](#); [Erlacher and Schredl, 2010](#); [Fiss, Kremer, and Lichtman, 1977](#); [Pantoja et al., 2009](#); [Schredl and Erlacher, 2010](#); [Wamsley, Tucker, Payne, Benavides, and Stickgold, 2010](#)) and several others finding no such effect ([Cipolli, Bolzani, Tuozi, and Fagioli, 2001](#); [Nguyen, Tucker, Stickgold, and Wamsley, 2013](#); [Nielsen et al., 2015](#); [Plailly, Villalba, Nicolas, and Ruby, 2016](#); [Sabourin, Forest, Hebert, and De Koninck, 2006](#); [Schredl and Erlacher, 2010](#); [Wamsley, Perry, Djonlagic, Reaven, and Stickgold, 2010](#)). To illustrate one positive finding, in a frequently cited study ([Wamsley, Tucker, et al., 2010](#)), participants learned to navigate a virtual maze on a computer screen and were tested following a 90-min period of either napping or wakefulness. Participants who slept improved the most, and those who showed the biggest gains were also those who reported dreams in which the “the task was explicitly and unambiguously mentioned” (p. 853). Having had task-related thoughts in the waking condition did not predict improved performance. As compelling as such findings might be, the work has weaknesses such as the exclusive use of NREM dreams and very little dreaming about the task ( $n = 4/50$  subjects). However, unlike most others studying this question, Wamsley’s group attempted to replicate their findings using either the same ([Wamsley, Nguyen, Tucker, Olsen, and Stickgold, 2012](#)) or a similar virtual task ([Nguyen et al., 2013](#); [Wamsley, Perry, et al., 2010](#)). They claim to have succeeded on one of these attempts ([Wamsley, 2014](#)) although a detailed report has not yet been published ([Wamsley, Nguyen, et al., 2012](#)).

An indirect connection between sleep spindles and dreaming is that both phenomena are related to trait measures of cognitive processes. First, like sleep spindles, dream recall has been linked to measures of intelligence. Laboratory dream recall through childhood and adolescence is quite reliably associated with high performance scores on the Block Design of the Wechsler scales ([Foulkes, 1985](#)). Second, intelligence (reasoning, verbal abilities) assessed by the Cambridge Brain Sciences Trials ([Hampshire, Highfield,](#)

Parkin, and Owen, 2012) is correlated with the extent of dreaming about a newly learned task (Fogel, Ray, Sergeeva, and Owen, 2016). Third, like sleep spindles, dream recall frequency has been linked to visual memory in adults (Butler and Watson, 1985; Cory, Ormiston, Simmel, and Dainoff, 1975; Schredl and Montasser, 1996). Fourth, like sleep spindles, dream recall capacity may have trait-like electroencephalography (EEG) signatures, such as increased theta oscillations (Scarpelli et al., 2015) or delayed P3 reactivity (Eichenlaub, Bertrand, Morlet, and Ruby, 2013). Finally, the association of both dreaming and sleep spindles with various psychopathologies, such as schizophrenia (Lusignan et al., 2009; Wamsley, Tucker, et al., 2012), is consistent with the notion that these two phenomena are linked.

Briefly, whereas sleep spindles are a well-characterized, well-validated marker of intellectual abilities and sleep-dependent memory mechanisms, dreaming's association with intelligence and memory is less certain. Contemporary theories are nonetheless consistent with the possibility that the two sleep phenomena are interrelated by virtue of neural replay mechanisms occurring in different forms during different sleep stages. Research with human subjects suggests a range of dream replay phenomena in which participants dream to different degrees about experimental stimuli (for reviews, see Arkin and Antrobus, 1991; Smith, 2010), whereas research with animals suggests that neural replays occur in both REM and NREM sleep and match the phenomenological features of dream replays in some respects (e.g., fragmentary nature) but not in others (e.g., reverse or accelerated replay). Thus, there are both empirical and conceptual grounds on which to expect that NREM sleep spindles may be related to dreaming. This study addresses this open question.

### Objectives and hypotheses

This study aimed to examine relationships between sleep spindles and measures of dream recall. We focused on spindles recorded from six standard electrode derivations (F3, F4, C3, C4, O1, and O2) for the whole sleep period. And, because spindle attributes have been observed to change with increasing depth of sleep (Andrillon et al., 2011), we assessed spindles separately for each of the first five consecutive N2 sleep cycles. We used available polysomnography (PSG) recordings for a heterogeneous sample of healthy, non-clinical participants who varied in their self-reported frequencies of recalling dreams and nightmares. To assess differences in dream recall frequency, retrospective measures of recalling dreams, bad dreams, and nightmares were used. We hypothesized that fast spindle density in particular would correlate positively with measures of dream recall frequency.

## METHODS

### Participants

A total of 53 participants [20 males (M) and 33 females (F) with the mean age of  $24.2 \pm 4.2$  years] were available in the Dream & Nightmare Laboratory database who had all completed the same night-time protocol. These included 35 participants (17 M and 18 F with the mean age of  $24.8 \pm 4.1$  years)

whose results are published in a paper on sleep-related memory among high- and low-frequency dream recallers (Dumel et al., 2015) and 18 participants (3 M and 15 F with the mean age of  $23.2 \pm 4.1$  years) whose results are unpublished; some of these participants reported high frequencies of dream recall, bad dreams, and/or nightmares, whereas the others reported low frequencies. All participants were initially recruited by word of mouth and advertisements on campus and on our Center website. Potential participants then completed a telephone screening interview that included reporting their retrospective monthly recall of dreams (*Dream recall*), bad dreams (*Bad dream recall*), and nightmares (*Nightmare recall*). To be included, participants had to be 18–35 years old and fluent in English or French. They were excluded if they reported a major sleep disorder, if their sleep efficiency score was  $<80\%$  on the polysomnographic evaluation, or if they reported an emotional or psychological disorder, a major medical or psychiatric condition, excessive consumption of alcohol, cigarettes/nicotine, or recreational drugs or use of medications that affect sleep. In short, all participants reported themselves to be physically and psychologically fit – even if some recalled nightmares or bad dreams more often than others. Each participant gave written informed consent and received \$110 plus compensation for transport and breakfast expenses. The research was approved by institutional scientific and ethical boards.

### Procedures

Participants completed a sleep and dream log from home by telephone 1 week prior to and 1 week following their overnight stay in the laboratory. They also completed a variety of questionnaires that are not all reported here [Beck Depression Inventory-II (BDI), State-Trait Anxiety Inventory (STAI), Morningness-Eveningness Questionnaire, Boundaries Short Form, Inventory of Dreams: Experiences and Attitudes, Sleep Disorders Questionnaire, Pittsburgh Sleep Quality Index, and Toronto Alexithymia Scale-20]. Only the Beck Depression and State-Trait Anxiety measures are considered further in the present analyses.

Participants underwent a pre-sleep testing session during which four cognitive tasks were administered: the Mirror-Tracing Task (MTT), Tower of Hanoi (ToH), Corsi Block-Tapping (CBT) Task, and ROCFT. Two intellectual tasks from the Wechsler Adult Intelligence Scales were also given: Block Design and Digit Span (total). Participants were prepared for polysomnographic recordings and allowed to sleep uninterrupted through the night. In the morning, they were awakened from REM sleep and asked to report and self-rate their sleep and dream experiences using the same rating scales contained in the home logs. They were subsequently given a light breakfast and then retested on the MTT and ROCFT. They returned to the laboratory 1 week later and completed a retest of all four tasks. Pre-/post-sleep measures of task improvement were available for three of the four tasks: MTT, CBT, and ToH.

### PSG

An electrode montage of six EEG (F3, F4, C3, C4, O1, and O2) referenced to A1 (including A2 for re-referencing

offline to A1 + A2), four electrooculography (EOG; vertical, horizontal), and four electromyography (EMG; chin, finger extensor, toe flexor, and corrugator) channels was recorded using a Grass M12 or M15 Neurodata Acquisition System (−6 dB filters, 0.30 and 100 Hz cutoffs) with 16-bit precision under the control of Harmonie 6.2b (Natus/Stellate Systems Inc., Montreal, Canada). The sampling rate for EEG, EOG, EMG, and reference derivations was 256 Hz; for electrocardiography (ECG), it was 512 Hz. The F4 derivation was defective for one participant and removed from further analyses. PSG tracings were scored with American Academy of Sleep Medicine standards (Silber et al., 2007) by an experienced PSG technician. REM sleep for laboratory awakenings was determined online by an experimenter familiar with PSG scoring. Standard sleep variables (e.g., REM min, REM%, N2 min, N2%, and total sleep time) were calculated offline by in-house software.

### Spindle detection

Each spindle was detected automatically on six artifact-free derivations (F3, F4, C3, C4, O1, and O2; re-referenced to A1 + A2 offline) for the entire night. For nights on which the first REM sleep episode was skipped (Nielsen et al., 2010), cycle timing was adjusted by inserting a faux epoch of REM sleep at the point in the hypnogram where an experienced technician familiar with partial REM sleep signs (descending N2, muscle atonia, phasic EMG activity, rapid eye movements, and saw-tooth waves) determined that the skipped REM sleep episode should have occurred. This allowed accurate segmentation of each night into relatively equal length cycles, of which the first five N2 episodes were selected for more detailed analysis of spindles. Raw digitized signals were bandpass filtered from 11 to 16 Hz using a linear phase finite impulse response filter (−3 dB at 11.1 and 15.9 Hz). Forward and reverse filtering was performed to

obtain zero-phase distortion and double the filter order. The root mean square (RMS) of the filtered signal was then calculated with a 0.25-s time window and thresholded at the 95th percentile (Martin et al., 2013). A spindle was identified when at least two consecutive RMS time points exceeded this threshold and the event duration met the criterion of 0.5 s. The resulting output files were processed to verify the distribution of sleep spindle frequency; a cutoff of 12.99 Hz was used to distinguish slow (11.00–12.99 Hz) from fast (13.00–16.00 Hz) spindles; counts of slow and fast spindles were conducted automatically and spindle densities for the entire night and for each of the first five cycles were calculated by dividing each spindle count on each channel by the number of minutes of time elapsed in artifact free N2 over the entire night or over the corresponding sleep cycle as appropriate. In Fig. 1, distributions of the entire sample of recorded spindles for the 53 participants are plotted by 0.25 Hz frequency bin (11.0–16.0 Hz range) for each electrode derivation. The normal preponderance of slow spindles in frontal derivations is clearly evident from this plot as is the normal distribution of faster spindles in the central and parietal derivations.

### Statistics

Since the dream recall measures were not normally distributed, they were log transformed. In addition, correlations between spindle densities and other measures were determined using the conservative non-parametric Spearman coefficients when possible (partial correlations were performed with Pearson correlations). Multiple linear regressions (forward stepwise) were used to assess which dream recall measures (predictors) correlated most strongly with fast spindle density (criterion). Task improvement differences on the MTT, CBT, and ToH tasks between groups high and low in dream recall were determined by defining

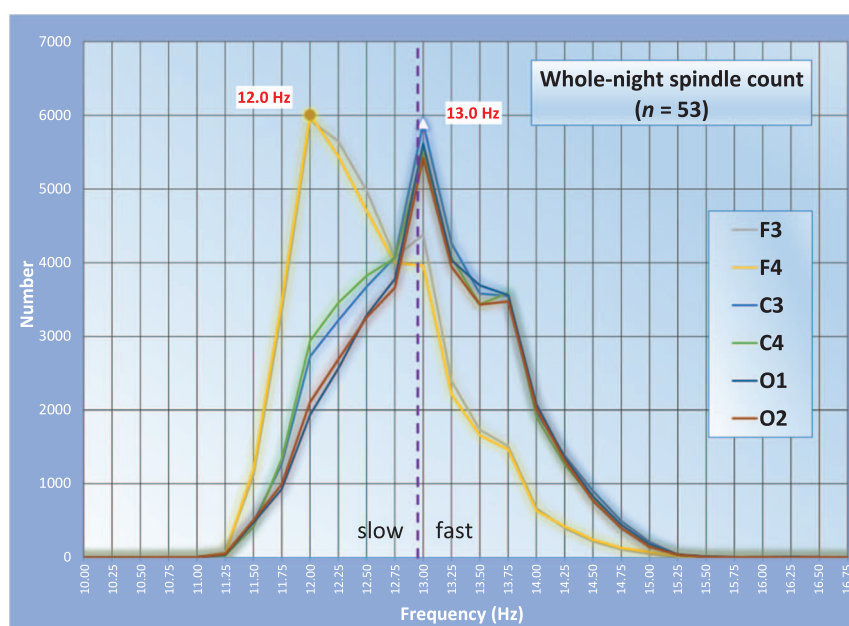


Fig. 1. Distributions of all-night spindle counts by frequency (bin = .25 Hz) and derivation for all participants. The predominance of slow spindles (11.00–12.99 Hz) in frontal derivations (F3, F4) and fast spindles (13.00–16.00 Hz) in all other derivations is apparent



High and Low groups (median splits) on each of the four dream recall measures and then comparing these groups using four separate multivariate ANOVAs each of which used Group (High, Low) as an independent variable and improvement scores on the MTT, CBT, and ToH tasks as multiple dependent measures. Follow-up ANCOVAs were applied to determine which dream recall measures best accounted for the group differences observed.

## RESULTS

Demographic and personality characteristics of the study cohort are shown in *Table 1* and sleep architecture attributes are shown in *Table 2*.

### *Dream recall measures*

The three retrospective measures of dream recall frequency were very highly correlated with coefficients between .57 and .67 (all  $p < .000001$ ; *Table 3*) but only *Dream recall* was moderately correlated with the *#Words/report* measure ( $r = .341, p = .013$ ). Furthermore, although all three retrospective dream recall measures correlated negatively with depression and trait anxiety, these were significant only for *Dream recall* (all  $p < .01$ ) and *Bad dream recall* (all  $p < .05$ ); none were significant for *Nightmare recall* or *#Words/report*.

### *Fast versus slow sleep spindle densities*

Spearman correlations revealed that the within-derivation densities of fast and slow spindles were inversely related (*Table 4*, diagonal). The average coefficient for the six derivations was  $r = -.875$  ( $p < .001$ ) and substantially larger than the average of between-derivation correlations ( $r = .759, p < .001$ ). The highest within-derivation correlations occurred centrally (C3:  $-.919$ ; C4:  $-.914$ ), the lowest frontally (F3:  $-.828$ ; F4:  $-.806$ ), and intermediate values occipitally (O1:  $-.890$ ; O2:  $-.895$ ). To control for this covariance, partial correlations were conducted in examining the relationships between spindle densities and dream recall.

## RELATION OF SLEEP SPINDLES TO DREAMING

As shown in *Fig. 2* and *Table 5*, all-night spindle density scores were correlated with the four dream recall measures. Fast spindle correlations were uniformly positive and robust for both *Bad dream recall* and *#Words/report*, where all six

*Table 2.* Sleep characteristics of the cohort

	Mean $\pm$ SD	Range
Sleep latency (min)	15.0 $\pm$ 13.0	2.0–65.5
Latency to persistent sleep (min)	19.1 $\pm$ 15.0	2.0–75.0
N1 latency (min)	14.2 $\pm$ 12.5	2.0–63.0
N2 latency (min)	22.4 $\pm$ 15.1	6.5–83.0
N3 latency (min)	20.7 $\pm$ 22.5	5.0–153.5
REM latency (min)	79.1 $\pm$ 25.8	50.0–181.5
Sleep duration (min)	419.8 $\pm$ 49.0	279.5–513.0
Wake duration (min)	43.9 $\pm$ 39.0	7.5–187.0
Number of awakenings (number)	13.8 $\pm$ 8.2	1–37
Sleep efficiency (%)	90.6 $\pm$ 8.0	62.5–98.4
Wake (min)	43.9 $\pm$ 39.0	7.5–187.0
N1 (min)	35.8 $\pm$ 20.1	11.0–122.5
N2 (min)	189.1 $\pm$ 38.3	102.5–262.0
N3 (min)	109.1 $\pm$ 33.7	45.5–181.5
REM (min)	85.8 $\pm$ 24.0	42.0–153.5
NREM (min)	334.0 $\pm$ 41.5	233.5–418.5
Sleep (min)	419.8 $\pm$ 49.0	279.5–513.0
Wake (%)	9.3 $\pm$ 7.9	1.6–35.8
N1 (%)	8.7 $\pm$ 5.5	2.8–37.5
N2 (%)	44.9 $\pm$ 6.9	30.4–60.0
N3 (%)	26.0 $\pm$ 7.4	11.4–40.5
REM (%)	20.3 $\pm$ 4.8	65.2–88.1
NREM (%)	79.7 $\pm$ 4.8	11.9–34.8
Number of sleep cycles (number)	4.7 $\pm$ 1.0	3–8

derivations surpassed at least the  $p < .05$  significance threshold, and *Dream recall*, where five of the six correlations did. Correlations were least robust for *Nightmare recall*, where only C3 surpassed the  $p < .05$  threshold.

Slow spindle correlations with the four dream recall measures were uniformly negative, although these were consistently beyond the  $p < .05$  threshold only for *Dream recall*. Correlations between fast spindle density and *Bad dream recall* were attenuated but not eliminated for four derivations by partialing out slow spindle densities: F3 ( $r_{52} = .259, p = .064$ ), C4 ( $r_{52} = .287, p = .039$ ), O1 ( $r_{52} = .264, p = .059$ ), and O2 ( $r_{52} = .326, p = .018$ ); correlations were more severely reduced for the remaining two derivations: F4 ( $r_{51} = .149, p = .298$ ) and C3 ( $r_{52} = .247, p = .078$ ). For *#Words/report*, partialing out slow spindle densities reduced or eliminated all fast spindle correlations except O2, that is, F3 ( $r_{52} = .114, p = .423$ ), F4 ( $r_{51} = .110, p = .441$ ), C3 ( $r_{52} = .065, p = .645$ ), C4 ( $r_{52} = .238, p = .089$ ), O1 ( $r_{52} = .207, p = .140$ ), and O2 ( $r_{52} = .272, p = .051$ ). For *Dream recall* and *Nightmare recall*, partialing out slow spindle densities eliminated all correlations with fast spindle densities (all  $p > .120$  and  $> .414$ , respectively). In all cases, the reverse procedure – partialing out fast spindle densities from correlations with slow spindle densities – completely eliminated the slow spindle correlations (all  $p > .258$ ). Thus, there were unique relationships with fast spindle densities only for *Bad dream recall* and, to a lesser extent, for *#Words/report*.

A second set of partial correlations was, therefore, conducted to remove possible modulating effects of depression and trait anxiety from the *Bad dream recall*  $\times$  fast spindle correlations because, as shown in *Table 3*, these two pathology measures were also correlated with *Bad dream recall*. Partialing out BDI scores attenuated but did not eliminate the

*Table 1.* Demographic and personality attributes of the cohort ( $n = 53$ )

	Mean $\pm$ SD	Range
Age	24.2 $\pm$ 4.2	18–35
Dreams/month	16.4 $\pm$ 14.4	0.5–70
Bad dreams/month	5.2 $\pm$ 6.7	0–28
Nightmares/month	2.1 $\pm$ 4.4	0–22
#Words/report	138.2 $\pm$ 146.1	10–650
STAI: trait	40.3 $\pm$ 8.9	24–60
STAI: state	33.8 $\pm$ 9.3	20–60
BDI-II	8.3 $\pm$ 7.0	0–33

Table 3. Spearman correlations (upper right) and *p*-values (lower left) between age, dream recall measures, anxiety, and depression scores

	Age	Dream recall	Bad dream	Nightmare	#Words/report	STAI: trait	STAI: state	BDI
Age		-.090	-.168	-.173	.056	.295*	.212	.039
Dream recall	.521		.631*	.572*	.341*	-.360*	-.125	-.431*
Bad dream recall	.229	.000		.672*	.121	-.284*	.076	-.362*
Nightmare recall	.217	.000	.000		.098	-.149	.067	-.165
#Words/report	.691	.013	.386	.487		-.034	.107	-.196
STAI: trait	.034	.009	.041	.293	.811		.644*	.719*
STAI: state	.132	.376	.592	.638	.448	.000		.428*
BDI	.786	.001	.008	.243	.164	.000	.002	

Note. Dream recall: log (dreams/month + 1); Bad dream recall: log (bad dreams/month + 1); Nightmare recall: log (nightmares/month + 1); #Words/report: number of content-bearing words in laboratory dream report; STAI: State-Trait Anxiety Scale, trait and state measures; BDI: Beck Depression Inventory-II.

\*Correlations surpassing  $p < .05$ .

Table 4. Spearman correlations between all-night fast and slow spindle densities.

	F3-fast	F4-fast	C3-fast	C4-fast	O1-fast	O2-fast	Mean
F3-slow	<b>-0.828</b>	-0.783	-0.748	-0.729	-0.584	-0.588	<i>-0.710</i>
F4-slow	-0.808	<b>-0.806</b>	-0.732	-0.737	-0.576	-0.586	<i>-0.708</i>
C3-slow	-0.892	-0.835	<b>-0.919</b>	-0.856	-0.747	-0.752	<i>-0.834</i>
C4-slow	-0.883	-0.869	-0.875	<b>-0.914</b>	-0.739	-0.759	<i>-0.840</i>
O1-slow	-0.727	-0.684	-0.780	-0.780	<b>-0.890</b>	-0.900	<i>-0.794</i>
O2-slow	-0.719	-0.682	-0.769	-0.786	-0.875	<b>-0.895</b>	<i>-0.788</i>
Mean	<i>-0.810</i>	<i>-0.777</i>	<i>-0.804</i>	<i>-0.800</i>	<i>-0.735</i>	<i>-0.747</i>	<b><i>-0.779</i></b>

Note. Values in bold indicate within-derivation correlations; Values in italics denote derivation mean correlations; All  $p < .001$ .

correlations for five of the six derivations, that is, F3 ( $r_{52} = .265$ ,  $p = .061$ ), F4 ( $r_{51} = .206$ ,  $p = .152$ ), C3 ( $r_{52} = .287$ ,  $p = .041$ ), C4 ( $r_{52} = .322$ ,  $p = .021$ ), O1 ( $r_{52} = .323$ ,  $p = .021$ ), and O2 ( $r_{52} = .342$ ,  $p = .014$ ). Similarly, partialing out STAI-trait scores attenuated but did not eliminate the correlations for the same five derivations, that is, F3 ( $r_{52} = .278$ ,  $p = .048$ ), F4 ( $r_{51} = .215$ ,  $p = .133$ ), C3 ( $r_{52} = .307$ ,  $p = .028$ ), C4 ( $r_{52} = .344$ ,  $p = .014$ ), O1 ( $r_{52} = .349$ ,  $p = .012$ ), and O2 ( $r_{52} = .369$ ,  $p = .008$ ).

To determine which of the dream recall measures was most highly correlated with fast spindle density, first, a series of six linear multiple regressions was conducted in which the three retrospective recall measures – *Dream recall*, *Bad dream recall*, and *Nightmare recall* – served as predictor variables and all-night fast spindle densities for each of the six derivations served as the criterion variables. As shown in Table 6A, *Bad dream recall* was the sole significant predictor for five of the six derivations (F3, C3, C4, O1, and O2), but for F4, it was as predictive as were the other two measures.

Second, a similar set of six linear regressions was conducted in which #Words/report was added to the previous three predictors (Table 6B). In this analysis, *Bad dream recall* again predicted spindle density for C4, O1, and O2 derivations, whereas #Words/report predicted spindle density for F3 and F4. Both #Words/report and *Bad dream recall* independently predicted spindle density for C3.

#### Sleep spindle relationships by cycle of night

To assess if the observed relationships between dreaming and sleep spindles were uniform for spindles sampled from

different times of night, Spearman correlations were calculated between the best two predictive measures – *Bad dream recall* and #Words/report – and fast spindle densities for each of the first five NREM sleep periods of the night. Some participants lacked cycles 4 ( $n = 5$ ) and 5 ( $n = 22$ ), whereas some lacked a recalled dream ( $n = 8$ ), and thus sample sizes were reduced for these cycles. As shown in Fig. 3, correlations were uniformly positive for all cycles and for both measures. For *Bad dream recall*, correlations surpassed the  $p < .05$  threshold consistently only for cycles 2 and 3. For #Words/report, they surpassed  $p < .05$  for all cycles on at least one derivation, especially F3, but never on all derivations in any one cycle. The largest number of significant correlations here (four of six derivations) was seen for cycle 4, but the largest coefficients (F3, C4;  $r > .40$ ) were seen for cycle 5.

#### Relation of dream recall and spindle density to task improvement

To determine whether dream recall frequencies and spindle densities were associated with improved performance on any of the three administered tasks, we calculated (a) Spearman correlations between improvement scores on the MTT, ToH, and CBT tasks and all-night fast spindle densities for the six derivations and (b) task improvement scores for participants scoring High and Low on the four dream recall measures as determined by median splits of the distributions. First, no substantial correlations were observed between task improvement scores and all-night spindle densities (all  $p > .14$ ). Even when correlations were calculated for the five sleep cycles separately, correlations were minimal for the most part; the

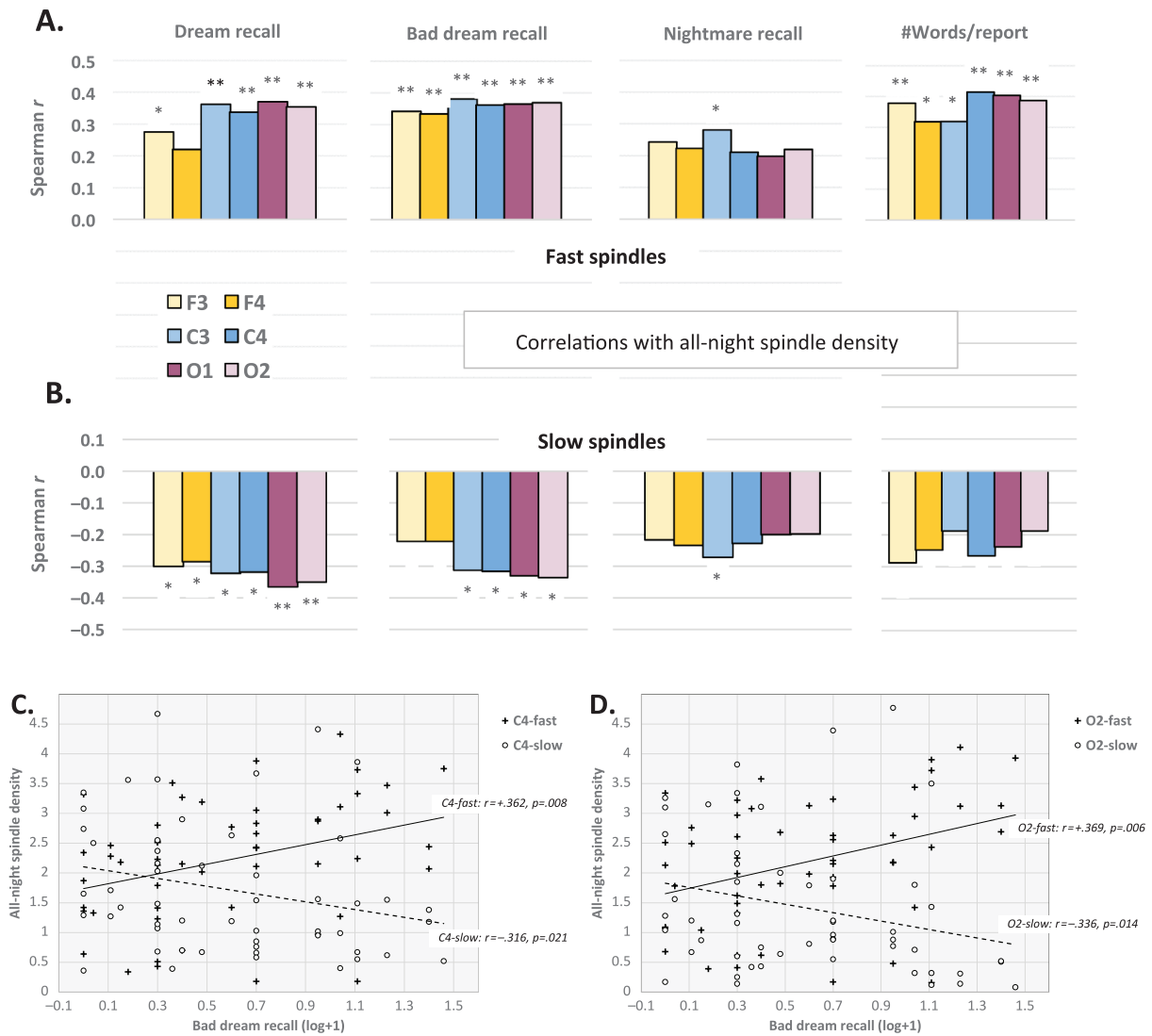


Fig. 2. Spearman correlations between (A) all-night fast (13.00–15.00 Hz) and (B) all-night slow (11.00–12.99 Hz) spindle densities and measures of Dream recall, Bad dream recall, Nightmare recall, and #Words/dream report. Scatter plots and Spearman correlations with Bad dream recall for (C) C4 derivation and (D) O2 derivation. \* $p < .05$ ; \*\* $p < .01$

Table 5. Spearman coefficients and two-tailed  $p$ -values for all-night fast (13.00–16.00 Hz) and slow (11.00–12.99 Hz) spindle density correlations with four dream recall measures

	Spearman $r$				$p$ (two-tailed)			
	Dream recall	Bad dream recall	Nightmare recall	#Words/report	Dream recall	Bad dream recall	Nightmare recall	#Words/report
F3-fast	0.275*	0.342*	0.243	0.367*	0.047	0.012	0.079	0.007
F4-fast	0.220	0.334*	0.223	0.314*	0.118	0.016	0.112	0.023
C3-fast	0.362*	0.381*	0.281*	0.348*	0.008	0.005	0.041	0.011
C4-fast	0.337*	0.362*	0.211	0.424*	0.014	0.008	0.130	0.002
O1-fast	0.370*	0.365*	0.198	0.321*	0.006	0.007	0.154	0.019
O2-fast	0.354*	0.369*	0.220	0.330*	0.009	0.006	0.114	0.016
F3-slow	-0.301*	-0.222	-0.217	-0.331*	0.029	0.111	0.119	0.015
F4-slow	-0.286*	-0.222	-0.235	-0.291*	0.040	0.114	0.093	0.036
C3-slow	-0.323*	-0.313*	-0.272*	-0.275*	0.018	0.022	0.049	0.046
C4-slow	-0.319*	-0.316*	-0.228	-0.317*	0.020	0.021	0.101	0.021
O1-slow	-0.366*	-0.331*	-0.200	-0.211	0.007	0.016	0.151	0.129
O2-slow	-0.351*	-0.336*	-0.199	-0.186	0.010	0.014	0.154	0.183

\*Coefficients with  $p < .05$ .

Table 6. Forward stepwise multiple regression solutions and 95% confidence intervals for dream recall predictors of all-night fast spindle density

	Predictor	<i>R</i>	<i>R</i> <sup>2</sup>	<i>F</i>	<i>p</i>	<i>B</i>	95% CI	SE
(A) Dream recall, Bad dream recall, and Nightmare recall								
F3	Bad dream recall	.287	.082	4.571	.037*	0.562	0.03–1.09	0.263
F4 <sup>a</sup>	Bad dream recall	.230	.053	2.794	.101	0.420	−0.09–0.93	0.765
C3	Bad dream recall	.306	.093	5.258	.026*	0.773	0.10–1.45	0.337
C4	Bad dream recall	.341	.116	6.723	.012*	0.817	0.18–1.45	0.315
O1	Bad dream recall	.354	.126	7.322	.009*	0.908	0.23–1.58	0.336
O2	Bad dream recall	.370	.137	8.084	.006*	0.906	0.27–1.55	0.319
(B) A + #Words/report								
F3	#Words/report	.334	.111	6.392	.015*	0.002	0.00–0.003	0.001
F4	#Words/report	.333	.111	6.224	.016*	0.002	0.00–0.003	0.001
C3	Bad dream recall	.306	.093	5.258	.026*	0.773	0.10–1.45	0.337
C4	1. #Words/report	.356	.127	7.399	.009*	0.002	0.00–0.004	0.001
	2. Bad dream recall	.452	.204	4.882	.032*	0.680	0.06–1.30	0.308
O1	Bad dream recall	.354	.126	7.322	.009*	0.908	0.23–1.58	0.336
O2	Bad dream recall	.370	.137	8.084	.006*	0.906	0.27–1.55	0.319

<sup>a</sup>Forced solution: three predictors contributed equally to the regression solution.

\*Coefficients with  $p < .05$ .

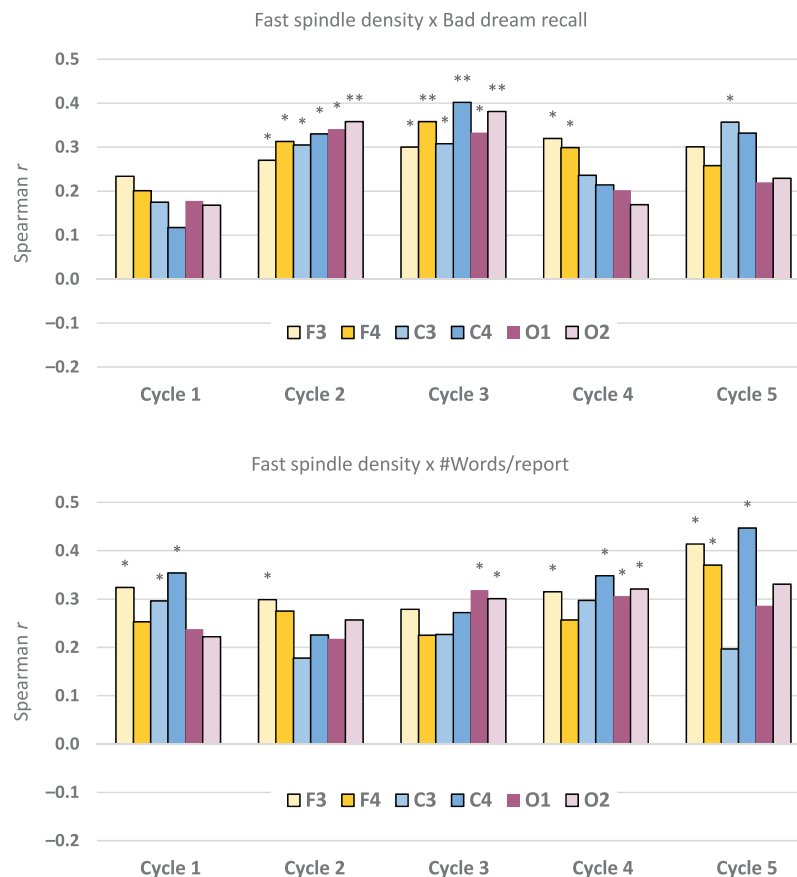


Fig. 3. Correlations between fast spindle density and self-reported frequencies of Bad dream recall (top panel) and #Words/report (bottom panel) for the first five NREM cycles of the night. *N* by cycle for Bad dream recall: 53, 53, 53, 48, and 31; for #Words/report: 45, 45, 45, 43, and 30. \* $p < .05$ ; \*\* $p < .01$

only exception was between improvement on the CBT task and fast spindle densities calculated for the fifth cycle. For this cycle, positive correlations were observed for all six derivations: F3 ( $r_{31} = .388$ ,  $p = .031$ ), F4 ( $r_{31} = .393$ ,  $p = .029$ ), C3 ( $r_{31} = .393$ ,  $p = .029$ ), C4 ( $r_{30} = .421$ ,  $p = .018$ ), O1 ( $r_{31} = .412$ ,  $p = .024$ ), and O2 ( $r_{31} = .353$ ,

$p = .051$ ). However, none of these correlations would withstand a conservative correction for multiple testing at .05/30 correlations or  $p < .002$ .

Second, multivariate ANOVAs revealed that the largest multivariate effect was for *Bad dream recall* (Hotelling's  $T = .259$ ,  $F_{4,48} = 3.121$ ,  $p = .023$ ,  $\eta^2 = .206$ ) which included



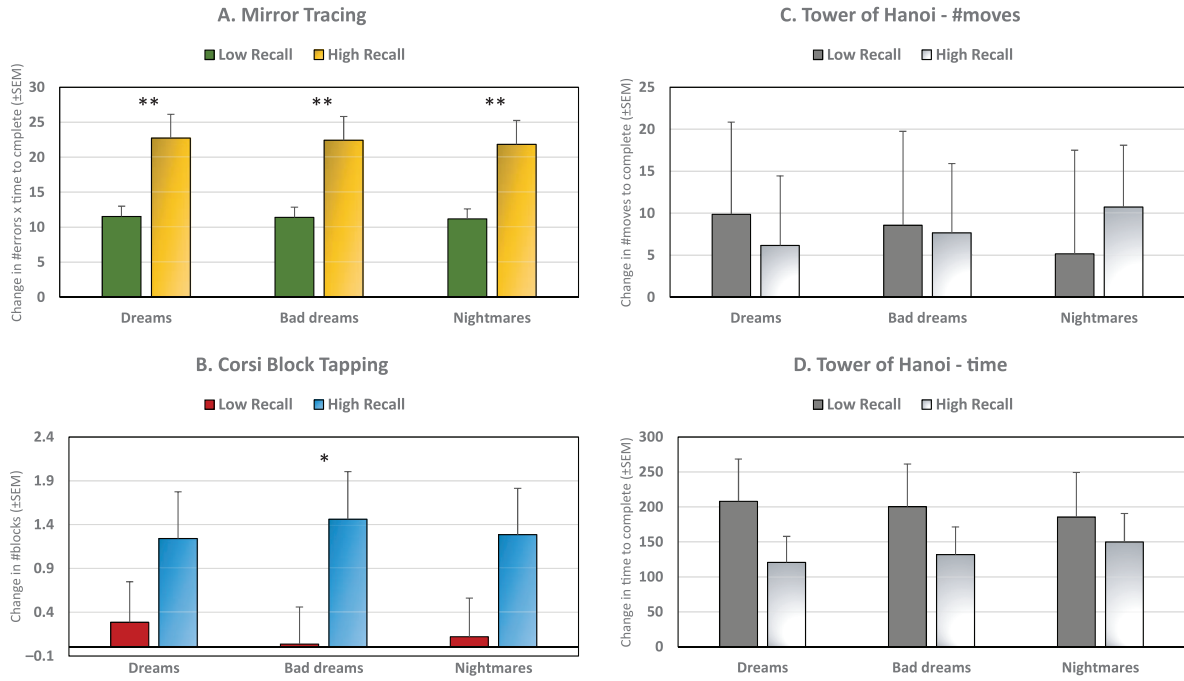


Fig. 4. Overnight levels of improvement on (A) Mirror-Tracing Task, (B) Corsi Block-Tapping Task, and (C and D) Tower of Hanoi #moves and time to completion for participants' self-reporting high and low levels of recalling dreams, bad dreams, and nightmares. \* $p < .05$ ; \*\* $p < .01$

univariate effects for both MTT improvement ( $F_{1,51} = 8.357, p = .006, \eta^2 = .141$ ) and CBT improvement ( $F_{1,51} = 4.318, p = .043, \eta^2 = .078$ ). As shown in Fig. 4, High *Bad dream recall* participants showed more improvement on the MTT ( $M: 22.44 \pm 18.42$ ) and the CBT ( $M: 1.46 \pm 2.77$ ) than did Low *Bad dream recall* participants (MTT:  $11.40 \pm 7.27$ ; CBT:  $0.04 \pm 2.19$ ). Entering *Dream recall* as a covariate in this analysis reduced, but did not completely eliminate, these two effects, that is, neither MTT ( $F_{1,50} = 4.005, p = .051, \eta^2 = .074$ ) nor CBT ( $F_{1,50} = 3.313, p = .075, \eta^2 = .062$ ). However, entering *Nightmare recall* as a covariate eliminated the MTT effect ( $F_{1,50} = 0.674, p = .416, \eta^2 = .013$ ) and attenuated the CBT effect ( $F_{1,50} = 3.204, p = .079, \eta^2 = .060$ ).

For the *Dream recall* measure, a multivariate main effect ( $T = .227, F_{4,48} = 2.721, p = .040, \eta^2 = .185$ ) revealed only a single univariate difference: High *Dream recall* participants showed greater MTT improvement ( $M: 22.73 \pm 18.79$ ) than did Low participants ( $M: 11.53 \pm 7.05; F_{1,51} = 8.602, p = .005, \eta^2 = .144$ ). This effect was eliminated by entering either *Bad dream recall* ( $F_{1,50} = 1.761, p = .191, \eta^2 = .034$ ) or *Nightmare recall* ( $F_{1,50} = 1.161, p = .286, \eta^2 = .023$ ) as covariates.

Finally, for the *Nightmare recall* measure, a significant multivariate effect ( $T = .224, F_{4,48} = 2.683, p = .042, \eta^2 = .183$ ) revealed one univariate effect for MTT improvement ( $F_{1,51} = 7.728, p = .008, \eta^2 = .132$ ). As for the other two measures, High *Nightmare recall* participants showed more MTT improvement ( $M: 21.86 \pm 17.94$ ) than did Low participants ( $11.16 \pm 7.28$ ). This effect was not eliminated by covarying *Dream recall* ( $F_{1,50} = 4.791, p = .033, \eta^2 = .087$ ) but was by covarying *Bad dream recall* ( $F_{1,50} = 2.273, p = .138, \eta^2 = .043$ ). Finally, participants with High and Low recall on any measure did not improve differentially on the ToH improvement measures.

Briefly, retrospective dream recall measures were associated with improvements on MTT (all three measures) and CBT (*Bad dream recall* only) with the most robust differences being shown by participants differing in High and Low *Bad dream recall*.

For the prospective dream recall measure, in contrast, the results were consistently negative. Participants High ( $\geq 91$  words) and Low ( $< 91$  words) on *#Words/report* did not differ on any of the task improvement scores (all  $p > .301$ ).

#### Relation of dream recall and spindle density to intellectual abilities

Spearman correlations between dream recall measures and intellectual abilities (Block Design and Digit Span) are shown in Table 7. For Block Design, we replicated, albeit marginally, an expected (Foulkes, 1985) positive correlation with *#Words/report* ( $r = .282, p = .061$ ) but also observed a negative, again marginal, correlation with *Bad dream recall* ( $r = -.265, p = .055$ ). There were no correlations with Digit Span; Block Design and Digit Span were also not correlated ( $r = .067, p = .635$ ).

Table 7. Spearman correlations between dream recall measures and Wechsler Adult Intelligence Scales (Block design and Digit Span)

		Dream recall <sup>a</sup>	Bad dream recall <sup>a</sup>	Nightmare recall <sup>a</sup>	#Words/report <sup>b</sup>
Block design	$r$	-.137	-.265	-.112	.282
	$p$	.329	.055	.426	.061
Digit span	$r$	.144	-.075	.053	.136
	$p$	.305	.595	.705	.373

<sup>a</sup> $n = 53$ ; <sup>b</sup> $n = 45$  due to lack of dream recall from REM awakening.

Correlations between all-night fast spindle densities and Block Design and Digit Span were consistently null (Block Design: all  $p > .265$ ; Digit span: all  $p > .210$ ). Similarly, when calculated by sleep cycle, there were no significant correlations for Block Design (all  $p > .154$ ) and only two significant correlations for Digit Span, both in cycle 4 (C3,  $r = .319, p = .027$ ; C4,  $r = .294, p = .043$ ). Neither survives a correction for multiple analyses.

## DISCUSSION

Overall, these results confirm our general expectation of a relationship between measures of dream recall and fast N2 sleep spindles. On three retrospective and one prospective measures of dream recall frequency, we observed positive correlations between levels of recall and the density of fast spindles. The correlations were somewhat stronger for the *Bad dream recall* measure in that only this measure withstood partialing out of the slow spindle density measures for most derivations, but positive correlations were nonetheless obtained for all recall measures. The correlations were also independent of depression and trait anxiety scores. Furthermore, the correlations were apparent for spindles assessed at different points in the sleep period – but especially in cycles 2 and 3 for *Bad dream recall* but in all cycles except 2 for *#Words/report*. While there was some evidence that retrospective dream recall measures were related to learning (two of the three tasks), there was no relationship between task improvement and spindle density scores.

### *A possible trait factor common to spindles and dreaming*

While there might seem to be no reason to expect an association between sleep spindles, a predominantly NREM sleep phenomenon, and dreaming, a predominantly REM sleep phenomenon, there is ample evidence of the interdependence of NREM and REM sleep processes, as suggested by sequential (Giuditta, 2014; Giuditta et al., 1995), “two-stage” (Buzsaki, 1989; Fogel et al., 2009), and “sleep organization” (Ficca and Salzarulo, 2004) models of memory consolidation. As described in the Introduction section, such interrelatedness is suggested by the fact that measures of cognitive abilities that are correlated with sleep spindles are also correlated with REM sleep measures – and in some cases with dreaming measures as well. For example, Auditory Verbal Learning Test scores are correlated with REM sleep time as well as with NREM sleep spindles (Lafortune et al., 2014). Similarly, IQ is associated with both REM sleep eye movements (Smith, Nixon, and Nader, 2004) and sleep spindle density (Fogel et al., 2007), whereas intelligence is also correlated with some measures of dreaming (Fogel et al., 2016; Foulkes, 1999; Sándor, Szakadát, and Bódizs, 2016). In light of such findings, the most parsimonious explanation for the present results may be that sleep spindles and dream recall are related by virtue of a common cognitive trait. While the precise nature of this trait remains unknown for the present, several possibilities might be considered. The trait of general intelligence is a salient candidate, although we found no correlations between spindle density and the Block Design or Digit Span intelligence subtests. However, these two subtests tap a relatively

restricted range of cognitive abilities (visuospatial competence and working numeric memory, respectively) and more thorough testing may well find links with general intelligence. Other possible trait factors include an individual's ability to either generate visuospatial imagery or to accurately recall visuospatial images and memories (e.g., dreams). The latter abilities may be reflected in our *#Words/report* measure, which could conceivably reflect the typical salience of visuospatial imagery or an ability to describe it in a detailed narrative form. Further study could readily clarify this issue.

### *A possible sleep-dependent consolidation mechanism common to spindles and dreaming*

The present findings are also consistent with the possibility that sleep spindles and dream recall are affected by a shared mechanism for sleep-related memory consolidation that spans both NREM and REM sleep, rather than – or perhaps in addition to – a trait factor explanation. This possibility is supported by several findings. First, spindle density was reliably correlated with the *#Words/report* variable, which is widely viewed as a measure of local REM sleep memory or arousal processes (Palagini, Gemignani, Feinberg, Guazzelli, and Campbell, 2004; Rosenlicht, Maloney, and Feinberg, 1994). Furthermore, when considered by sleep cycle, the correlations between *#Words/report* and spindles were largely different from those between *Bad dream recall* and spindles, suggesting a different mechanism. The former correlations were more pervasive for cycles 1, 4, and 5, whereas the latter correlations were more pervasive for cycles 2 and 3. Similarly, when considered by derivation, the two types of correlations differed: multiple regressions showed spindle correlations with *#Words/report* to be strongest for F3 and F4, whereas correlations with *Bad dream recall* were predominant for C3, O1, and O2. Finally, elevated dream recall was found to be associated with better improvement on two of the three consolidation tasks; high *Bad dream recall* in particular was associated with improvement on MTT and CBT tasks. However, this possible mechanistic explanation is not entirely consistent with either the finding that the *#Words/report* measure was not associated with task improvements or the finding that spindle densities were uncorrelated with such improvements.

Nonetheless, the findings taken together may belie a more complex interaction between trait and sleep state factors. Such an interaction was demonstrated in a recent memory consolidation study in which participants high on a general cognitive trait factor (“baseline memory performance”) had higher spindle densities but also demonstrated the strongest sleep-dependent memory consolidation effects (Wisłowska, Heib, Griessenberger, Hoedlmoser, and Schabus, 2016). The fact that our multiple regression analyses found at least one derivation (C4) for which spindle density independently predicted both the trait (*Bad dream recall*) and sleep state (*#Words/report*) measures supports such an interaction between trait and sleep-related mechanisms.

The possibility that sleep spindles are associated with dreaming due to a shared sleep-dependent mechanistic factor is also broadly consistent with sequential (Giuditta, 2014; Giuditta et al., 1995), two-stage (Buzsaki, 1989;

Fogel et al., 2009), and sleep organization (Ficca and Salzarulo, 2004) models of NREM–REM sleep states, and has parallels in previous research. First, it is consistent with the finding that overnight improvements in visual discrimination are linked most strongly to a combination of NREM and REM sleep stages, that is, early-night NREM sleep and late-night REM sleep percentages, rather than to either measure alone (Stickgold, Whidbee, Schirmer, Patel, and Hobson, 2000). Second, it is consistent with the finding that targeted memory activation during NREM sleep leads to functional magnetic resonance imaging-detected brain changes in both NREM and REM sleep (Cousins, El-Deredy, Parkes, Hennies, and Lewis, 2016). The latter study found that targeted stimulation in NREM sleep produced REM sleep-related increases in bilateral superior parietal cortex, cerebellum, premotor cortex, sensorimotor cortex, and left dorsolateral prefrontal cortex, as well as changes in NREM sleep. Third, the notion that spindles and dreaming share a common mechanism is consistent with clinical observations; patients with *auto-activation deficit* are deficient in sleep spindles and report infrequent dreams and dreams that are short, simple, and devoid of normal bizarre and emotional elements, even though measures of sleep duration, continuity, and stage percentages do not differentiate patients from healthy controls (Leu-Semenescu et al., 2013). Finally, some neuroanatomical evidence points to brain regions that are implicated in both spindles and dreaming. For example, whereas spindles in one study were accompanied by activations in thalamus, anterior cingulate cortex, insular cortex, and superior temporal gyrus (Schabus et al., 2007), a review of imaging studies (Hobson, Stickgold, and Pace-Schott, 1998) found activation in the same regions during REM sleep, when dreaming is most abundant. Similarly, while fast spindles are associated with increased gray matter volume in bilateral hippocampus (Saletin, van der Helm, and Walker, 2013), hippocampal volume is also associated with increased dream bizarreness (De Gennaro et al., 2011) and REM sleep hippocampal connectivity is associated with both successful dream recall (Fell et al., 2006) and visual dream vividness (De Gennaro et al., 2011).

Together, these findings illustrate that consolidation mechanisms, such as those underlying both sleep spindles and dreaming, may well span NREM and REM sleep stages. There may be a neural substrate for memory consolidation that implicates both sleep stages and, within these stages, both spindles and dream imagery.

#### *Spindles, dreaming, and memory replay*

A consolidation mechanism that may link sleep spindles directly to dreaming is that of memory replays that manifest in different forms in NREM and REM sleep. According to one influential model (Born, 2010; Ritter et al., 2015; Siapas and Wilson, 1998), NREM replay events, as indexed by hippocampal sharp-wave ripples and sleep spindles, are synchronized by a third wave form: neocortical slow oscillations (0.5–1.0 Hz). Slow oscillations cause sharp-wave ripples in the hippocampal CA1 to occur in close temporal proximity to spindles recorded in neocortical regions such as medial prefrontal cortex (Peyrache, Battaglia, and Destexhe,

2011; Siapas and Wilson, 1998). This produces *spindle–ripple events* (Siapas and Wilson, 1998) that facilitate information transfer between the hippocampal and neocortical cell assemblies (Sirota, Csicsvari, Buhl, and Buzsaki, 2003). Critically, during sleep spindles, the cortex is “functionally deafferented” from hippocampal inputs, presumably through the strong recruitment of inhibitory interneurons (Peyrache et al., 2011). There is anatomical evidence supporting such a view (Varela, Kumar, Yang, and Wilson, 2014) as well as evidence of the expected directionality of activity from hippocampus to prefrontal cortex (Wierzynski, Lubenov, Gu, and Siapas, 2009).

Although this specific mechanism may be suppressed during REM sleep (Wierzynski et al., 2009), when in humans dreaming is more abundant, neural replay events also do take place at this time (Hennevin et al., 1995; Louie and Wilson, 2001; Poe et al., 2000, 2010). Furthermore, it is generally thought that the cortex is functionally deafferented from the hippocampus during REM sleep and that this disengagement supports consolidation (Diekelmann and Born, 2010). Thus, as inhibitory processes, NREM sleep spindles and tonic REM sleep may function similarly to enable replay-related consolidation. However, it remains to be shown more precisely how the neural bases of NREM sleep replay events differ from those of REM sleep and how these may implicate dream formation processes.

#### *A privileged role for bad dreams?*

The fact that it was *Bad dream recall*, rather than either *Dream recall* or *Nightmare recall*, that most reliably correlated with both spindles and task improvement in this study requires further clarification. If bad dreams are a sign of pathology, it may seem counterintuitive for them to be associated with neural indicators of adaptive memory consolidation. However, the negative correlations we observed between *Bad dream recall* and STAI and BDI scores are opposite to what is typically reported in studies of nightmare populations (Nielsen and Levin, 2007). This may be because our laboratory volunteers were not clinical patients and were not seeking treatment; thus, their associated suffering may have been low, despite the high frequency of their nightmares. In other words, the participants with bad dreams and nightmares in this study may have been high functioning and resilient to comorbidities to different degrees. Another possibility is that bad dreams may, in fact, be an adaptive form of emotional dreaming. That bad dreams represent dysphoric emotions without sleep being disturbed by awakenings, which is the definition of bad dreams, might point to these dreams having successfully consolidated a dysphoric emotion by an ostensible adaptive function. Dreaming has been theorized to modify emotion and memory through various mechanisms (for review, see Nielsen and Carr, 2016), including by modulating fear extinction (Nielsen and Levin, 2007) and affect depotentiation (Walker and van der Helm, 2009). From this perspective, our finding that *Dream recall* had large and significant negative correlations with both depression ( $r = -.431$ ,  $p = .001$ ) and anxiety ( $r = -.360$ ,  $p = .009$ ) is consistent with the possibility that normal dreaming helps down-regulate negative affect. At the other extreme, however, that frequent *Nightmare*



*recall* was non-significantly correlated in the same negative direction with the two measures ( $r = -.165$ ,  $p = .243$  and  $r = -.149$ ,  $p = .293$ ) suggests that nightmares may have little or no regulatory effect on negative emotions. Finally, our findings show that correlations for *Bad dream recall* were also significantly negative, but smaller than those for *Dream recall* ( $r = -.362$ ,  $p = .008$  and  $r = -.284$ ,  $p = .041$ ), suggesting that bad dreams may be more like normal dreams than they are like nightmares in having a somewhat smaller regulatory effect on negative emotions. Nonetheless, in such a scenario, it remains unclear why *Nightmare recall* and *Bad dream recall* were so highly correlated ( $r = .672$ ,  $p < .00001$ ) and why *Nightmare recall*, like *Bad dream recall*, also correlated positively with sleep spindles in the present analyses. It also remains unclear why *Bad dream recall* was negatively associated with Block Design scores, while *Dream recall* was positively correlated, even though both measures were positively associated with sleep spindles. More comparative study of these measures is clearly required.

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**Authors' contribution:** TN and TP designed the experiment, analyzed the data, and wrote the manuscript; MC, CB-C, and TP conducted the spindle analyses, analyzed the data, and edited the manuscript; all other authors conducted PSG recordings, completed neurocognitive testing, performed artifact rejection, collected dream reports, and entered/checked the data.

**Conflict of interest:** The authors declare no conflict of interest.

**Ethics:** This study was approved by Research Ethics Committee of the Hôpital du Sacré-Coeur de Montréal (#2012-749).

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