Contribution of REM sleep and N2 sleep spindles to procedural memory consolidation in Vipassana meditators and non-meditating controls.

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Abstract

Study objectives Rapid eye movement (REM) sleep, non-rapid eye movement (NREM) sleep, and sleep spindles are all implicated in the consolidation of procedural memories. The relative contributions of sleep stages and sleep spindles was previously shown to depend on individual differences in task processing. Experience with Vipassana meditation is one such individual difference that has not been investigated in relation to sleep. Vipassana meditation is a form of mental training that enhances proprioceptive and somatic awareness and alters attentional style. The

goal was thus to examine a potential moderating role for Vipassana meditation experience on sleep-dependent procedural memory consolidation.

Methods Groups of Vipassana meditation practitioners (N=20) and matched meditation-naïve controls (N=20) slept for a single daytime nap in the laboratory. Before and after the nap they completed a procedural task on the Wii Fit balance platform.

Results Meditators performed slightly better on the task before the nap, but the two groups improved similarly after sleep. The groups showed different patterns of sleep-dependent procedural memory consolidation: in meditators task learning was negatively correlated with density of fast and positively correlated with density of slow occipital spindles, while in controls task improvement was associated with increases in REM sleep. Meditation practitioners had a lower density of sleep spindles, especially in occipital regions.

Conclusions Results suggest that neuroplastic changes associated with sustained meditation practice may alter overall sleep architecture and reorganize sleep-dependent patterns of memory consolidation. The lower density of spindles in meditators may mean that meditation practice compensates for some of the memory functions of sleep.

Keywords: Procedural memory; Vipassana meditation; REM sleep; sleep spindles; body awareness

Introduction

Recent cognitive science and philosophy of mind theories have seen an important shift of focus from inquiry focused predominantly on the role of the brain in subjective experience to the view that the brain is a part of a whole body and is intimately rooted in the physical and social world [1-4]. From this perspective, much current research focuses on relationships between awareness of one's body and physical and mental health. Mindfulness interventions, including sitting meditation

practices and movement-based practices such as yoga or t'ai chi [5], all include an element of cultivating access to and awareness of increasingly subtle bodily sensations [6, 7]. Meditation practitioners, therefore, may represent an 'expert' group of healthy individuals who intentionally cultivate attention to bodily states, and are better able to access and employ them [8]. Meditators may embody cognitive processes differently than do non-meditators; in particular, they may rely more upon awareness of kinesthetic and other types of endogenous information to encode memories. The term *body awareness* captures this characteristic, referring to an ability to focus on, and become familiar with, one's bodily sensations; it is defined as a subjective, explicitly available aspect of proprioception and interoception [9]. Critically, while some individuals may be naturally more attuned to body awareness than others, it is a trainable skill that can be enhanced by contemplative practices [10, 11].

The main research goal of the current study is to investigate whether meditation practice, by virtue of increasing body awareness, also changes the neurobiological and phenomenological qualities of sleep-dependent memory consolidation. Specifically, we chose a full body procedural memory task and a daytime nap protocol to test whether: 1) meditation practitioners and meditation-naïve controls differ in performance and improvement on a procedural balance task; 2) the two groups differ in their patterns of sleep stage and sleep microarchitecture in reaction to the task; and 3) daytime nap sleep characteristics (sleep stages and sleep spindles) in meditation practitioners are similar in quality to nighttime sleep.

Memory and sleep

Traditionally, human long-term memory has been divided into the two broad categories of explicit/declarative and implicit/non-declarative memory [12, 13]. Explicit memory deals with autobiographical events, is characterized by self-awareness and autonoetic consciousness or the ability to "mentally time travel" through past experience, and is responsible for accumulating semantic knowledge, or facts about the world [14]. Crucially, explicit memory is accessible to

conscious retrieval [15]. Implicit memory, on the other hand, concerns procedural knowledge, the learning of skills, behavioral conditioning and priming effects and is largely inaccessible to conscious report [16].

Consolidation of procedural memory in sleep has been studied using a number of tasks, including sequential finger tapping [17-24]; serial-reaction time task [25-27]; motor sequence task [28, 29]; mirror-tracing task [30-33]; button-box sequence [34]; visuomotor adaptation task [23]; texture discrimination task [35, 36]; visual discrimination task [37], and others. These tasks usually involve either fine motor skills using the fingers or hand-eye coordination, but do not typically involve balance or bodily displacements.

Tasks involving balance skills or full-body learning have only rarely been used in memory consolidation research [38] [39, 40]. One example specific to sleep research is the Alpine Racer arcade game used in a study of memory incorporation into dream content [41].

Sleep and memory consolidation

A wealth of research supports a role for sleep in memory consolidation [for reviews see 42, 43, 44]. Sleep is thought to strengthen information learned during the day, to select which experiences are best remembered and which best forgotten, and to assimilate new knowledge into existing autobiographical networks [45-48]. While most research has focused on the effects of a full night of sleep, an increasing number of studies report that daytime naps have similar effects to nighttime sleep on memory processes [49-56].

A number of studies link procedural memory to rapid-eye-movement (REM) sleep processes; these include a variety of tasks: mirror-tracing [57], Corsi block tapping, Tower of Hanoi [33, 58] and others. For example, among obstructive sleep apnea patients, reduced rate of REM eye movements (REM density) was associated with poor mirror-tracing performance [59]. Similarly, selective REM sleep deprivation disrupted visual discrimination learning [60]. Yet other studies suggest an important role for NREM sleep in procedural memory consolidation. NREM sleep

duration [61] as well as NREM electrophysiological events, such as sleep spindles [62, 63], have been associated with post-sleep task improvement.

Sleep's role in memory consolidation is not only influenced by task type and sleep stage/sleep microarchitecture, but also by individual differences in learning abilities and cognitive styles. In one study, for example [64], the ability to bring a motor task into explicit awareness improved post-sleep performance on the task, suggesting that training a particular attentional engagement with the learning task may change the neurocognitive style of offline memory processing.

In sum, mounting evidence now links both REM and NREM sleep to procedural memory consolidation. In fact, the same procedural task has been shown to be related, in different contexts, to both REM and NREM sleep. While it is not yet clear why task performance may be associated with one or the other sleep stage—or both—some authors have proposed 2-stage or sleep organization models to account for the findings, i.e., that both stages are necessary for successful consolidation and integration of newly encoded information [65, 66], including procedural skills [67]. However, such models do not explain how the same task may be associated with different sleep stages. The present study assesses trained meditating participants who are known to differ on a key factor that may be critical for procedural learning—body awareness—and compares sleep-related changes of this group with a matched, meditation-naïve, control group.

Sleep spindles

One reliable index of memory consolidation in NREM sleep is the sleep spindle, a phasic event (.5- to 3.0-sec duration) characterized by bursts of 11-16 Hz EEG activity occurring predominantly during stage 2 NREM (N2) sleep. Converging evidence points to possible different neural mechanisms implicated in fast and slow sleep spindles [68], but few studies to date have examined the combined contribution of slow and fast sleep spindles to memory consolidation. In one recent study, fast (but not slow) sleep spindles were involved in transfer or implicit knowledge to more explicit awareness [69]. In another study, consolidation of face memory, which can be considered

as having both explicit and implicit components, was associated with both fast and slow sleep spindles [70]. In this case, fast spindles showed a positive correlation with post-sleep face recognition, and slow spindles showed a negative correlation.

The current study focuses on procedural memory, specifically on motor skill acquisition of a balance-oriented task. Procedural memory is thought to be acquired through repetition of a skilled activity that is stabilized over time [71]. However, little is known about the effect of sleep on balance. Sleep deprivation was reported to negatively affect postural stability [72-74], but no study to our knowledge has assessed relative contributions of sleep stages and sleep spindles on a postural task.

Meditation and heightened body awareness

Recent years have seen a significant increase in research on the effects of various meditation practices, often grouped under the umbrella of “mindfulness” practices, on neuroplasticity, attention, and emotion regulation processes among others. While all contemplative practices share some elements such as attention training, body awareness [7] and emphasis on insight and self-regulation [75], different meditation practices are characterized by different kinds of subjective experiences, recruit different neural networks and may have different effects on cognitive and physical functions, including well-being [76, 77].

Vipassana meditation is characterized by developing a sustained and systematic practice of being aware of one’s bodily sensations in order to ultimately gain insight into the nature of reality [78-80]. Practitioners typically start with a focused attention practice, specifically with mindfulness of breathing or *anapana*. The main part of the practice consists of the body scanning technique, where practitioners are instructed to mentally examine their bodily states to become aware of subtle sensations and, ultimately, to approach them with equanimity and nonjudgementally. We hypothesize that this contemplative tradition may change the practitioner’s cognitive style in a

global way, including changing processes of attention, memory encoding, consolidation and retrieval.

Recent research showed that Vipassana practice is similar to other contemplative practices in having the beneficial effects of decreasing stress and improving subjective feelings of well-being [81], helping generate greater perceptual clarity and decrease automated reactivity to stimuli [82-84], and decreasing anger, hostility and depressive symptoms [85]. Other studies report improved psychological well-being [86] and cognitive flexibility [85] and increased heart rate variability [87]. Other effects of Vipassana training include increased somatosensory awareness, e.g., increased awareness of pain, more spontaneous body movements, increased mindfulness, and development of equanimity, or the ability to adapt to extreme changes in lived experience [88].

Sleep architecture changes of Vipassana practitioners are few, but include longer REM sleep periods when compared to controls and yoga practitioners [89]. Longer-term practitioners (over 7 years of daily practice) have more N3 sleep, less N2 sleep, fewer awakenings from sleep and an altered pattern of REM sleep microarchitecture [90].

While the idea that meditation practice, by virtue of enhancing specific cognitive and attentional skills [91-93], should have an effect on learning and memory seems intuitive, very few studies to date have directly addressed the effect of meditation on memory consolidation. And existing results are mixed. One study reports very few differences between long-term meditation practitioners (including Vipassana meditators) and non-meditating controls; meditators showed better performance on short-term and free recall long-term memory [94]. Some studies report improvements in working memory in meditation practitioners [95], including a military cohort [96], and adolescents [97].

With respect to procedural motor memory, only one study to our knowledge assessed contribution of post-training meditation practice to memory consolidation [98]; experienced yoga *nidra* meditation practitioners showed post-training memory benefits on a sequence tapping task.

In sum, Vipassana meditation may produce changes in body awareness, which in turn may influence not only health and well-being but the effectiveness of memory. While studies of procedural memory are lacking, the preceding review suggests that increased body awareness may help meditators excel at procedural tasks. Critically, there are as yet no studies of sleep-dependent learning in meditators.

Objectives and hypotheses:

The primary objective of the present study was to investigate the relationship between Vipassana meditation practice and sleep-dependent processes of memory consolidation. Specifically, we tested the idea that training in a meditation technique which enhances introspective accuracy and increases body awareness will influence sleep characteristics and style of sleep-dependent learning of a procedural full-body task.

- 1) following a daytime nap Vipassana meditators (MED group) will show more improvement on a procedural task than will meditation-naïve controls (CTL group).
- 2) the MED and CTL groups will express two distinct neurobiological learning patterns:
 - a. the MED group will show a NREM-dependent pattern, reflecting a more explicit learning process. fast sleep spindles in particular will correlate with task improvement
 - b. the CTL group will show a REM-dependent pattern, consistent with previous research on non-declarative learning.

Methods

Participants

Forty-two male ($n = 21$) and female ($n = 21$) participants between the ages of 18 and 35 y ($M = 25.4 \pm 4.4$) were recruited for a daytime nap study via online advertisements and through contact with Vipassana Quebec and subsequently screened via phone or online questionnaire. In the

Vipassana meditation practitioners group (MED) there were 22 participants (M age = 25.8 ± 4.1 , 11 men, 11 women) and in the non-meditating control group (CTL) there were 20 participants (M age = 25.0 ± 4.8 , 10 men, 10 women). Inclusion criteria for both groups were: 18-35 years of age, high dream recall (3+ per week), good self-reported physical/mental health, no sleep disturbances (e.g., shift work or jet lag). To be included in the MED group, Vipassana practitioners had to have taken part in at least one 10-day retreat, which consists of approximately 100 hours of practice, and to be currently practicing Vipassana meditation on at least a weekly basis. Participants completed an informed consent form approved by the Hôpital du Sacré-Coeur de Montréal ethics board. They were financially compensated for the time spent in the laboratory, parking or public transit, and lunch expenses.

Body Awareness

Body awareness was measured using the Scale of Body Connection (SBC) questionnaire [99], which consists of 20 items each scored on 0-4 scales and which produces two independent subscales: body awareness (12 items) with items that assess awareness of, e.g., tension, bodily stress, breath, and emotional state, and bodily dissociation (8 items) with items that assess e.g., feeling frozen/numb, separated from the body, and difficulty in expressing emotions. Subscale scores consist of the average ratings of constituent items (0-4). The questionnaire has been validated on studies of bodily awareness in women with substance abuse disorder [100], of exercise and body awareness therapy in major depression [101], of body therapy for survivors of childhood sexual abuse [102], and of interoceptive awareness of breathing in experienced meditation practitioners [103]. This and the following questionnaires were completed at home and sent back to the laboratory by mail: short versions of the Beck Depression Inventory, Beck Anxiety Inventory, and Boundary Questionnaire; full versions of the Dream Experience Questionnaire; Mirror Behaviour Questionnaire; Dream Enactment Behaviour; Toronto Alexithymia Scale; Other Experiences Questionnaire. Results from these questionnaires are not discussed further in this paper.

Procedure

Participants arrived in the laboratory at 9:00 am and completed a consent form and a battery of questionnaires which included the Scale of Body Connection. They then completed the procedural task and had the PSG setup installed. Immediately before lights-out, the MED group meditated in bed for 10 minutes and the CTL group simply relaxed for the same amount of time. All participants were then given a window of opportunity to sleep of approximately 90 minutes. They were awakened twice with a non-stressful, 80 dB, 500 Hz, once at sleep onset and once at the end of the nap. At these times, spontaneous dream reports and dream questionnaires were completed. Following the second awakening, electrodes were removed and participants repeated the procedural task.

Procedural memory (balance) task

Participants performed a procedural memory task requiring whole body balance, i.e., a video game entitled "Balance bubble" for the Nintendo Wii Fit Balance Board. In this task, participants control a virtual character that moves along a river in a bubble by shifting their weight on the Balance Board. The objective is to complete the river path as quickly as possible without touching the river's edges and thus bursting the bubble. Bursting the bubble required the participant to start again from the beginning of the path. The task was performed on a 42-in. television screen. All participants were assessed for any vision correction and instructed to wear their glasses or contact lenses if needed. Participants had a 2-minute period to acquaint themselves with the task, and to ask questions of the experimenter, who ensured that participants clearly understood the requirements of the game. The total maximum game time was 90 seconds, and participants were allowed to repeat the task until a total of 5 minutes of gameplay had elapsed. Participants were instructed to attempt to complete the task as many times as possible during the 5-minute period. The task was performed once before lights-out (T1) and once after awakening (T2).

The following variables were calculated to assess performance on the task: HiScore (highest score on all attempts averaged); #Wins (the number of times participants completed the task by arriving at the end of the “river”); GameScore (average score in game “meters” over all attempts at the game) and Time (average time spent correctly balanced in the bubble averaged over all attempts). Two measures of improvement on the task were used: T2-T1GameScore (Score after nap minus score before nap), and T2-T1Time (Time after nap minus TimeBalance before nap).

Polysomnography

Participants slept in a quiet bedroom under continuous audio-visual monitoring with a two-way intercom. A standard polysomnographic montage was used: 6 EEG channels (F3, F4, C3, C4, O1, O2) referenced to A1 and re-referenced to A1+A2 offline; four electrooculography (EOG) channels (horizontal and vertical), and three electromyography (EMG) channels (chin, wrist, leg). Acquisition of EEG signals was done using an M15 Grass Acquisition System (–6 dB filters with cut-offs at 0.30 and 100 Hz) and Harmonie v6.2b software (Natus Medical Incorporated, Pleasanton, CA, USA). Sleep stages were scored according to standard criteria [104] by an experienced technician and standard sleep variables were calculated using in-house software.

Sleep spindles were detected on artifact-free sleep epochs recorded from F3, F4, C3, C4, O1 and O2 derivations by an in-house detector. The full detection algorithm is described by Nielsen et al [105] and by O’Reilly and Nielsen [106]. Spindles were separated into slow (10.00-12.99 Hz) and fast (13.00-16.00 Hz) types and densities calculated as the number of spindles of each type divided by time elapsed in N2 sleep.

Results

Body awareness and dissociation

32 participants (15 MED and 17 CTL; 80%) returned questionnaires by mail. Independent samples t-tests on the SBC score and Body Awareness and Bodily Dissociation subscales revealed, as predicted, that the MED group scored significantly higher on Body Awareness than did the CTL

group ($M(\text{MED})=.243\pm.060$; $M(\text{CTL})=.194\pm.061$; $t(30)=2.289$; $p=.029$, 2-tailed) but did not differ on Bodily Dissociation.

Body Awareness and Bodily Dissociation scores were not correlated in the MED group ($r=.182$, $p=.517$) but tended to be inversely correlated ($r=-.475$, $p=.054$) in the CTL group. Body Awareness and Bodily Dissociation were not correlated with years of meditation experience in the MED group (Body Awareness: $r=-.471$, $p=.077$; Bodily Dissociation: $r=.079$, $p=.779$).

The MED group showed positive correlations between Body Awareness and average time ($r=.580$; $p<.05$) and score ($r=.518$; $p<.05$) on the task at T1, and a strong negative correlation between Bodily Dissociation and task improvement ($r=-.546$; $p<.05$). In contrast, CTL participants showed a different pattern: no significant correlations were observed between Body Awareness scores and task performance measures but strong positive correlations were seen between Bodily Dissociation and several task measures: average time in balance at T2 ($r=.681$; $p<.01$); average score at T2 ($r=.530$; $p<.05$); average time improvement ($r=.592$; $p<.05$); and average score improvement ($r=.619$; $p<.01$).

Task performance

Separate paired samples t-tests were used to evaluate whether groups improved on the task following the nap. Scores on average time spent balanced on the board (T2-T1Time), average (GameScore) and highest score (HiScore) before nap (T1) and after nap (T2) served as improvement measures. Both MED and CTL groups significantly improved on all three measures (see Table 1/Figure 1).

Insert Figure 1 about here

Insert Table 1 about here

No group differences were observed on post-nap measures of task improvement. However, meditators finished the game more often (more #Wins), especially after the nap: 2 (10%) of CTL participants finished the task at least once before the nap (T1), compared with 5 (25%) of MED participants ($\chi^2=0.693$, $p=.405$, 2-tailed, Yates corrected) whereas 6 (30%) of CTL participants finished the task after the nap (T2) compared with 12 (60%) of MED participants ($\chi^2=3.636$, $p=.057$) (Figure 2).

Insert Figure 2 about here

Similarly, the HiScore at T1 was significantly higher in MED than in CTL ($M(\text{MED})=1028.4\pm142.21$; $M(\text{CTL})=913.3\pm187.54$; $t(38)=2.188$; $p=.035$). For a comparison of complete results on task performance between the two groups see Table 1.

Insert Table 2 about here

Sleep structure

Two MED participants were dropped from spindle analyses due to insufficient sleep duration. No statistically significant differences between MED and CTL groups were observed for

any sleep characteristic, except for a non-significant trend ($p=.09$) for the MED group to have lower total sleep duration (See Table 3 for complete results).

Insert Table 3 about here

Relationship between sleep and meditation experience

For the MED group, Spearman correlations revealed a strong negative correlation between lifetime meditation experience (in hours) and time in NREM2 sleep ($r_s=-.546$, $p=.015$) but no other relationships with sleep measures.

Sleep spindles

A total of 20 CTL and 20 MED subjects were compared (Figure 3 for group comparisons of spindle density). There were no group differences in total spindle density or fast spindle density. However, the MED group showed lower slow spindle densities in occipital derivations, specifically: a lower spindle density in O1 ($M(\text{MED})=1.074\pm.797$; $M(\text{CTL})=1.754\pm.100$; $t(38)=2.385$; $p=.022$) and a marginally lower slow spindle density in O2 ($M(\text{MED})=1.264\pm.838$; $M(\text{CTL})=1.848\pm 1.035$; $t(38)=1.963$; $p=.057$).

Insert Figure 3 about here

Sleep and procedural memory consolidation

To assess sleep relationships with improvement on the balance task, the two most sensitive task measures were used: change in average time spent in balance ($T2-T1$) and change in average score ($T2-T1$). Spearman correlations were calculated to evaluate dose-response relationships between change in sleep stages, task performance, and slow and fast spindle density.

Sleep stages

For the MED group there were no statistically significant relationships between task improvement scores (average time and average score) and sleep stages. For CTL group,

improvement on average time spent balanced correlated negatively with Stage 1 NREM duration ($r = -.465$, $p = .007$) and positively with REM sleep duration ($r = .592$, $p = .006$). Further, improvement on average score correlated negatively with Stage 1 NREM duration ($r = -.470$, $p = .037$); and positively with REM sleep duration ($r = .536$, $p = .015$). Improvement on average score also correlated with several other sleep measures which were not predicted, i.e., negatively with sleep latency ($r = -.475$, $p = .034$); positively with sleep efficacy ($r = .451$, $p = .046$); and negatively with wake duration ($r = -.498$, $p = .025$). See Table 4 for complete results.

Insert Table 4 about here

Sleep spindles

Pearson correlations between measures of task improvement (T2-T1Time and T2-T1GameScore) and sleep spindle densities revealed significant relationships for the MED group, but not the CTL group (Figure 4). T2-T1Time correlated positively with density of slow sleep spindles in O1 ($r = .515$, $p = .024$) and marginally in O2 ($r = .421$; $p = .072$). T2-T1GameScore correlated positively with density of slow sleep spindles in O1 ($r = .539$, $p = .017$); negatively with density of fast sleep spindles in O1 ($r = -.551$, $p = .014$); and negatively with density of fast sleep spindles in O2 ($r = -.520$, $p = .022$).

Insert Figure 4 about here

Discussion

This study is the first to examine sleep-dependent memory consolidation in meditation practitioners. Although meditators were found to perform slightly better on the balance task at first testing than were controls, both groups improved to a similar extent after a morning nap. However, distinct patterns of relationships between task improvement and sleep structure were observed for the two groups: meditators showed a relationship between task improvement and occipital NREM sleep spindles while controls showed a relationship between task improvement and REM sleep time. Additionally, there were marked differences in spindle density between meditators and controls, with meditators having significantly lower spindle density, especially in occipital regions.

These results together suggest that meditation experience may contribute to large-scale changes in the electrophysiological indicators of neuroplasticity during sleep.

Different sleep-dependent memory consolidation styles in meditators and controls

Results support the study's main hypothesis that Vipassana meditation practitioners, by virtue of training in attending to bodily states and stimuli, may rely upon a different neurobiological learning style, one that manifests in distinct changes in sleep microarchitecture.

Specifically, meditation practitioners showed relationships between the density of slow and fast occipital spindles in N2 sleep and task improvement. While slow occipital spindle density correlated positively with task improvement, fast occipital spindle density showed the opposite. Meditators did not, however, show any links between duration of REM or NREM sleep stages and task improvement. On the other hand, non-meditating controls did show a strong positive correlation between time in REM sleep and task improvement. This is consistent with previous research where in a series of studies a novel motor skill, in this case jumping on a trampoline, was associated with increased REM sleep [39, 40]. Our results partially replicate these findings to the extent that improvement on our procedural balance task was associated with length of REM sleep during the daytime nap for control participants only. They did not, however, show any links between sleep spindles, especially fast sleep spindles, and task improvement. Both of these findings have been reported in previous studies. To illustrate, for the N2 spindle finding among meditators, we previously reported similarly perpendicular relationships between fast and slow spindles in relation to learning: fast N2 spindles correlated positively and slow spindles correlated negatively with face recognition [70]. For the REM sleep finding in controls, earlier research similarly linked duration of REM sleep with implicit memory consolidation [60].

In sum, post-task sleep architecture of meditators was distinctly different from that of non-meditating controls; it was correlated with occipital spindle density in N2 sleep but not with the duration of any sleep stages whereas in controls task improvement was associated with increased time in REM sleep, but not with N2 sleep spindles. Both patterns of sleep changes have been

observed in prior research although never linked differentially to meditation experience as in the present study.

Different styles of post-task sleep-dependent processing?

One interpretation of these findings is that meditation practitioners approach a procedural full-body balance task in a more “explicit” manner, in the sense that they are able to bring to awareness elements of their somatic and bodily experience that usually remain unconscious among untrained individuals. Their greater familiarity with bodily sensations may thus have allowed them to perform somewhat better on some, but not all, aspects of the task. They performed slightly better than the control group on the task overall, achieving higher maximum scores both before and after the nap. This advantage may reflect a shift in the neuroplasticity mechanisms that were brought to bear on the task during sleep. This idea is consistent with the suggestion (Smith, Aubrey and Peters [107] that REM sleep is associated with processing of complex tasks while Stage 2 sleep benefits the consolidation of simpler tasks. Smith et al (2004) propose that the involvement of REM or Stage 2 sleep in consolidation of a motor task depends on perceived complexity of the task; participants who are less skillful at the outset will show a dependence on REM sleep and those who find the task easier will show a N2 dependence. Because our meditators scored higher in body awareness and possibly found the task slightly easier, they may have needed only N2 spindle mechanisms to refine their learning. In contrast, if control participants found the task more complex or novel they may have had a greater need for REM sleep control mechanisms.

Despite the feasibility of this explanation, the significance of several additional findings from the current study remain unclear. One is the question of why meditators had a lower overall rate of spindles when sleep spindle density was associated with task improvement.

A second outstanding question is why slow rather than fast sleep spindle densities were associated with task improvement. Many previous studies [63, 108, 109] report that fast spindle density is preferentially correlated with improvement on procedural tasks. However, a growing body of evidence supports the notion that slow spindles are also a reliable correlate of procedural

learning in some contexts. Nishida and colleagues [110] showed a negative association between slow spindle power and a finger-tapping motor tracing task in depressed but not in healthy participants. A second group [30] showed a positive correlation between slow spindle activity (sigma: 12-14 Hz) in NREM sleep and improvement on a mirror tracing task. Third, some studies have shown that slow spindles are associated with explicit memory consolidation on tasks such as word-lists [30] and auditory verbal learning and declarative learning in epileptic patients [111]. Fourth, in children slow sleep spindle activity was found to be associated with declarative learning efficiency [112]. Finally, in a study using daytime naps [113], participants learning difficult and easy word-pairs showed evidence of slow spindle associations with improvement only on the difficult pairs. Such converging evidence links slow spindles to procedural learning and is consistent with our finding that meditators reacted to the balance task as a procedural task requiring N2 sleep mediation.

Possible napping profile

A second possible explanation of our group differences in sleep-dependent effects is that meditators are conforming to a profile known to characterize habitual nappers, either because they are used to taking frequent naps or because periods of daytime meditation may confer advantages similar to those provided by sleep, especially theta-rich Stage 1 NREM sleep [114]. Unfortunately, our findings do not further clarify the first point because we did not collect information about habitual napping practices. Yet, there is evidence [115] that individuals habitually taking daytime naps show a relationship between motor task improvement and sleep spindles whereas non-habitual nappers do not. Such findings, together with evidence that meditation practitioners commonly fall asleep during meditation sessions [116], provides some support for the notion that meditation confers either sleep-dependent or sleep-like advantages in memory consolidation. However, more research taking into account the habitual napping practices of participants is clearly needed for this explanation to be considered probable.

To summarize, our finding of different patterns of sleep-dependent memory consolidation for meditating and non-meditating controls can be accounted for by at least two explanations. On the one hand, the body-focused practices of meditation may contribute to large-scale changes in learning, including changes in sleep microarchitecture and sleep-dependent memory consolidation. On the other hand, similarities between meditation practice and habitual napping may confer additional sleep-related or sleep-like advantages to meditators. At present, more research supports the former possibility as an explanation for the present findings.

The notion that meditation practice leads to a different style of learning is consistent with both the philosophy of meditation approaches and a growing body of research. Indeed, the underlying goal of most traditional meditation practices, including Vipassana meditation, is not simple training of attentional acuity, but rather development of insight into one's own patterns of reactivity in order to decrease unwholesome traits and increase wholesome traits and behaviours [79, 80]. Ultimately, the goal is not to improve at meditation, but to improve at life skills more generally. Thus, neuroplastic changes and acquired mental skills associated with meditation practices may have an important effect on changing one's cognitive, emotional and memory patterns more broadly [117]. This idea is consistent with previous findings, including those from a study wherein mindfulness training led to increased somatosensory awareness of the experience of sadness, which in turn was related to decreased depression [118]. Neurophysiologically, meditation training may change the functional connectivity associated with bodily representation and thereby recruit the interoceptive skills that underlie several perceptual and cognitive tasks [119]. Our findings are thus consistent with the notion that Vipassana practice, through increased interoception and body awareness, facilitates the development of cognitive skills and thereby differentially influences sleep's reactions to new procedural learning tasks.

Task performance, body awareness and bodily dissociation

Both meditators and non-meditating controls improved their performance on the balance task following a daytime nap. Contrary to our predictions, meditators performed only marginally better

on the task than did controls: they did not improve more than controls overall, but they had higher scores before the nap and they completed the task more often after the nap.

As predicted, however, meditators scored higher than controls on the Body Awareness subscale of the Scale of Body Connection and that these scores were related in a graded fashion to task performance (time and score) before the nap. These findings are consistent with studies suggesting that sustained meditation practice contributes to higher levels of somatic awareness [8] and confirms our rationale for choosing a full-body balance task to examine patterns of sleep-dependent memory consolidation. In this case, one required skill for learning the task quickly is a heightened level of attunement to one's own bodily/somatic states.

Sleep and spindle differences between meditators and controls

Sleep architecture

In contrast to existing literature, we did not find longer REM sleep or SWS periods in meditation practitioners or differences in sleep efficiency or #awakenings, but meditators did show a tendency for a lower overall sleep time. For instance, in one study on Mindfulness-Based Cognitive Therapy, meditation practitioners showed more cortical arousal and more awakenings during nighttime sleep than did controls [120]. On the other hand, experienced long-term Buddhist practitioners [121] had a lower total sleep time like the trend in our study but also more awakenings—unlike our sample.

The fact that we found no associations between meditation experience and sleep latencies, sleep efficiency or duration/proportion of individual sleep stages may be due to the fact that our sample contained no expert meditation practitioners, typically quantified as having more than 10 000 hours of meditation practice [122]. Because all our participants can be considered meditation novices or at best intermediate practitioners, it is possible that the short daytime naps taken were insufficiently sensitive to reveal subtle group differences. Future studies might require all-night recordings or protocols that unmask subtle group differences by augmenting homeostatic pressure or REM sleep propensity.

Sleep spindles

We found sleep spindle density differences between meditators and controls, with meditators unexpectedly showing reduced sleep spindle density, especially in occipital derivations. Reduced spindle density has been suggested as a marker of neurodegeneration [123, 124] and psychopathological conditions such as schizophrenia [18, 125]. Our finding is unexpected because practice of meditation has been associated with increased neuroplasticity [126-128], and is thought to have neuroprotective effects against cognitive decline [129] and psychopathology [130]. For instance, in one study [131] Vipassana practitioners showed no age-related decline in slow-wave sleep and REM sleep compared to controls, suggesting that Vipassana practice may protect against age-related neurodegeneration.

Sleep spindles have also been suggested to play a role in maintaining sleep in face of environmental stressors, especially noise [132-135]. Reduced sleep spindles, in addition to other markers of physiological arousal during sleep in meditation practitioners may represent a general developed trait of increased alertness/awareness of the environment during sleep. While in normal populations sleep fragmentation may represent a pathological hyper-vigilance that may lead to insomnia and increased stress levels [136, 137] in meditation practitioners, it may not have the same negative effect due to practices that emphasize non-reactive awareness, an active monitoring of the contents of awareness, and a general increase in alertness [138]. These effects, however, tend to depend on proficiency in meditation practice: meditators in early stages of practice report more fatigue and sleepiness, while more experienced practitioners report greater alertness [139].

Brain synchronization mechanisms have been proposed to be a marker of neuroplasticity, reflecting processes of strengthening of neuronal connections and creation of new, experience-dependent, networks [140]. These processes were shown to have a strong top-down attentional component [141]. Long-term meditation practitioners generate long-distance phase-synchrony during a compassion meditation practice, and express EEG signatures different from those of controls during both active practice and the resting state [142]. This long-distance synchrony has been proposed to be a marker of cognitive integration [143, 144], and alterations in neural

synchrony patterns can be seen as markers of psychopathology [145]. Sleep spindles involve synchronization on the level of thalamo-cortical communication in NREM sleep [146]. Recently, slow spindles were reported to be associated with brain synchrony over longer circuits, and faster spindles with more local connectivity [147]. Thus, involvement of slow sleep spindles in procedural memory consolidation in meditation practitioners may reflect large-scale reorganization of brain connectivity—perhaps an increased efficiency of these networks—which may positively affect many cognitive skills, including memory.

Meditation practitioners, therefore, may develop a trait-like neurophysiological profile that involves both daytime and sleep changes. This trait may be similar to that of individuals with high dream recall: in a recent study we showed that increased fast but decreased slow sleep spindles correlate with dream recall frequency [105]. The latter is a measure previously linked with higher reactivity to auditory stimuli both in wake and during sleep [148], and with increased activity in the temporoparietal junction and medial prefrontal cortex – areas typically associated with attention and memory [149]. This finding is consistent with observations in our current study: all our participants had high dream recall, and meditators had fewer slow sleep spindles than did non-meditating controls, possibly reflecting their increased alertness in sleep.

Another possible explanation of our group difference in slow spindles is that some effects of meditation practice overlap with the function of sleep spindles, thus reducing the processing load on sleep-dependent processes. For instance, sleep spindles are associated with intelligence [150-153], and pharmacologically induced sleep spindles correlate with memory for emotionally negative memory, suggesting an emotion regulation function [154]. Analogously, meditation practice may contribute to the slowing of age-related decline in fluid intelligence [155], to improvement in cognitive function [93] and to enhanced emotion regulation [156].

Finally, it is possible that meditation subsumes some of the beneficial functions of sleep. While meditation practice is generally associated with increased self-reported well-being, health and life quality, during intensive meditation practice e.g., a meditation retreat, meditators require less sleep

[88], and exhibit physiological arousal signs, such as increased gamma coherence during slow wave sleep [121]. And while sleep plays an important role in memory consolidation, restful wakefulness (as opposed to active wakefulness) also promotes learning [157]. It is possible, therefore, that daytime meditation practice is sleep-like in nature and thus reduces sleep pressure and alter subsequent sleep architecture.

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Author contributions

ES and TN designed the study, interpreted the results and wrote the manuscript and ES, TN, SD, AS-R, CB-C, MC, TP collected data and analyzed results.

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Figure 1. Performance on procedural balance task in meditators (MED) and non-meditating controls (CTL) before nap (T1) and after nap (T2). * $p < .05$

Table 1. Paired samples t-tests: comparison of task scores before and after the nap in meditators (MED) and non-meditating controls (CTL).

MED					
	Mean $\pm$ SD	Mean $\pm$ SD	Paired sample correlations		Paired t-test
	Before nap	After nap	R	<i>p</i>	<i>p</i>
Time	31.31 $\pm$ 10.98	36.85 $\pm$ 11.35	0.71	0.000	0.009
GameScore	708.43 $\pm$ 184.71	852.35 $\pm$ 170.19	0.75	0.000	0.000
HiScore	1028.40 $\pm$ 142.21	1120.15 $\pm$ 106.44	0.48	0.034	0.006
CTL					
	Mean $\pm$ SEM	Mean $\pm$ SEM	Paired sample correlations		Paired t-test
	Before nap	After nap	R	<i>p</i>	<i>p</i>
Time	31.20 $\pm$ 12.66	40.38 $\pm$ 16.11	0.68	0.001	0.003
GameScore	656.87 $\pm$ 199.14	827.98 $\pm$ 186.02	0.78	0.000	0.000
HiScore	913.25 $\pm$ 187.54	1061.95 $\pm$ 141.42	0.63	0.003	0.000

Figure 2. Proportion of meditators (MED) and controls (CTL) who did (Finished) and did not (Unfinished) complete the procedural task at least once before and after the daytime nap

Table 2. Scores on procedural task for Vipassana meditators (MED) and non-meditating controls (CTL). *p<.05; †p<.10

Task variable	Mean MED ± SD	Mean CTL ± SD	t	df	p	
T1 HiScore**	1028.40 ± 142.21	913.25 ± 187.54	2.19	38.00	0.04	*
T1 Time	31.31 ± 10.97	31.20 ± 12.66	0.03	38.00	0.98	
T1 GameScore	708.43 ± 184.71	656.87 ± 199.16	0.85	38.00	0.40	
T1 #Wins	0.30 ± 0.57	0.10 ± 0.31	1.38	29.18	0.18	
T2 HiScore	1120.15 ± 106.44	1061.95 ± 141.42	1.47	35.30	0.15	
T2 Time	36.85 ± 11.35	40.38 ± 16.11	- 0.80	38.00	0.43	
T2 GameScore	852.35 ± 170.19	827.98 ± 186.02	0.43	38.00	0.67	
T2 TotScore	7322.75 ± 1631.78	6458.45 ± 1806.54	1.59	38.00	0.12	
T2 #Wins*	0.95 ± 0.10	0.45 ± 0.83	1.73	38.00	0.09	†
T2-T1Time	5.54 ± 8.46	9.18 ± 11.97	- 1.11	38.00	0.28	
T2-T1Score	143.93 ± 126.76	171.12 ± 129.26	- 0.67	38.00	0.51	

T1 refers to procedural task completed before the daytime nap; T2 refers to the same task completed after the nap. Score was calculated in “meters” according to the gameplay distance measure. Time was measured in seconds. Game completion was measured as a number of times participants arrived at the end of the virtual river. Improvement on task was measured as the difference between post-nap and pre-nap performance (T2-T1).

Table 3. Sleep measures for Vipassana meditators (MED: N=20) and non-meditating controls (CTL: N=20). †p <.10

Sleep characteristic	Mean MED ± SD^a	Mean CTL ± SD	t	df	p
Total sleep duration (min)	65.98 ± 25.27	78.30 ± 19.32	-1.73	38.00	0.09†
Sleep latency (min)	8.78 ± 6.75	14.35 ± 20.08	0.20	38.00	0.84
REM latency (min)	16.35 ± 22.35	20.74 ± 31.23	-0.47	32.00	0.64
Sleep efficiency	73.66 ± 23.10	81.70 ± 13.31	-1.31	29.68	0.20
N1 duration (min)	7.13 ± 7.67	7.03 ± 3.81	0.05	38.00	0.96
N2 duration (min)	32.83 ± 16.47	36.05 ± 15.05	-0.65	38.00	0.52
N3 duration (min)	15.05 ± 13.38	22.53 ± 18.99	-1.44	38.00	0.16
Total NREM duration (min)	55.00 ± 23.28	65.60 ± 22.37	-1.47	38.00	0.15
REM duration (min)	10.98 ± 6.12	12.70 ± 9.99	-0.66	38.00	0.51
Wake duration (min)	24.75 ± 24.71	17.45 ± 12.33	1.18	27.91	0.24
N1%	13.31 ± 16.30	10.45 ± 8.94	0.69	38.00	0.50
N2%	50.55 ± 17.18	45.10 ± 15.68	-0.90	38.00	0.50
N3%	19.46 ± 15.95	26.45 ± 20.43	-1.21	38.00	0.24
NREM%	83.32 ± 10.68	82.90 ± 15.17	0.10	38.00	0.92
REM%	16.69 ± 10.68	17.11 ± 15.17	-0.10	38.00	0.92
Wake%	26.29 ± 24.02	18.30 ± 13.31	1.30	29.66	0.20
N awakenings	5.65 ± 3.84	6.70 ± 4.18	-0.83	38.00	0.41

Figure 3. Sleep spindle densities ($M \pm SEM$) for Vipassana meditators (MED; $N=20$) and non-meditating controls (CTL; $N=20$). Spindle density calculated as the number of sleep spindles/time in NREM2 sleep. * $p < .05$; † $p < .06$

Figure 4. Pearson correlations between fast and slow sleep spindle densities and post-nap improvement on the balance task (average time and score) in meditators (MED) and controls (CTL). * $p < .05$; ** $p < .01$

Table 4. Pearson correlation coefficients between sleep characteristics and post-nap improvement in performance on a procedural task in meditators (MED) and controls (CTL). Average improvement in time and in score is reported.
 *=p<.05; **=p<.01; ***=p<.001 (Conservative error rate adjustment for 32 correlations per group=32/.05=.002).

Sleep variable	MED		CTL		
	Time	Score	Time	Score	
total sleep duration	0.31	0.06	-0.10	0.01	
sleep latency	0.16	0.20	-0.20	-0.48	**
REM latency	-0.02	0.18	0.28	0.26	
Sleep efficiency	0.20	0.04	0.29	0.45	**
N1 duration	0.01	-0.09	-0.47	-0.47	**
N2 duration	0.22	0.14	-0.39	-0.23	*
N3 duration*	0.20	-0.01	-0.01	0.01	
Total NREM duration*	0.30	0.06	-0.35	-0.23	
REM duration	0.11	0.00	0.59	0.54	**
Wake duration	-0.15	-0.02	-0.32	-0.50	**
N1%	-0.11	-0.14	-0.41	-0.42	*
N2%	0.02	0.20	-0.42	-0.33	
N3%	0.12	-0.07	-0.01	0.00	
NREM%	0.05	-0.01	-0.66	-0.57	***
REM%	-0.05	0.01	0.66	0.57	***
Wake%	-0.20	-0.04	-0.29	-0.45	**