

How to become an expert: A new perspective on the role of sleep in the mastery of procedural skills



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ABSTRACT

How do you get to Carnegie Hall? Practice, sleep, practice. With enough practice – and sleep – we adopt new strategies that eventually become automatic, and subsequently require only the refinement of the existing skill to become an “expert”. It is not known whether sleep is involved in the mastery and refinement of new skills that lead to expertise, nor is it known whether this may be primarily dependent on rapid eye movement (REM), non-REM stage 2 (NREM2) or slow wave sleep (SWS). Here, we employed behavioural and scalp-recorded electroencephalography (EEG) techniques to investigate the post-learning changes in the architecture (e.g., REM, NREM2 and SWS duration) and the electrophysiological features (e.g., rapid eye movements, sleep spindles and slow wave activity) that characterize these sleep states as individuals progress from night to night, from “Novice” to “Experts” on a cognitive procedural task (e.g., the Tower of Hanoi task). Here, we demonstrate that speed of movements improves over the course of training irrespective of whether sleep or wake intervenes training sessions, whereas accuracy improves gradually, but only significantly over a night of sleep immediately prior to mastery of the task. On the night that subjects are first exposed to the task, the density of fast spindles increased significantly during both NREM2 and SWS accompanied by increased NREM2 sigma power and SWS delta power, whereas, on the night that subjects become experts on the task, they show increased REM sleep duration and spindles became larger in terms of amplitude and duration during SWS. Re-exposure to the task one-week after it had already been mastered resulted in increased NREM sleep duration, and again, increased spindle density of fast spindles during SWS and NREM2 and increased NREM2 sigma power and SWS delta power. Importantly, increased spindle density was correlated with overnight improvement in speed and accuracy. Taken together, these results help to elucidate how REM and NREM sleep are uniquely involved in memory consolidation over the course of the mastery of a new cognitively complex skill, and help to resolve controversies regarding sequential nature of memory processing during sleep in humans, for which consistent evidence is currently lacking.

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1. Introduction

A good night of sleep is necessary for the optimal transformation of new learning into long-term memory, leading to enhanced performance (i.e., reflecting *memory consolidation*) for a variety of memory types (for reviews see: Albouy, King, Maquet, & Doyon, 2013; Born & Wilhelm, 2012; Peigneux, Fogel, & Smith, 2015; Stickgold, 2013; Walker, 2005). Evidence employing various techniques (e.g., sleep deprivation, sleep recording, sleep enhancement studies) in both humans and animals has provided compelling

convergent evidence that sleep is necessary for optimal memory consolidation. Support from a wealth of total and selective sleep deprivation studies in animals (Beaulieu & Godbout, 2000; Datta, Mavanji, Ulloor, & Patterson, 2004; Fishbein & Gutwein, 1977; Graves, Heller, Pack, & Abel, 2003; Hagerwoud et al., 2010; Legault, Smith, & Beninger, 2004; Rolls et al., 2011; Smith, 2003; Smith & Butler, 1982; Smith & Kelly, 1988; Smith & Rose, 1996) and studies in humans (Barrett & Ekstrand, 1972; Deliens, Gilson, Schmitz, & Peigneux, 2013; Deliens, Neu, & Peigneux, 2013; Deliens & Peigneux, 2014; Ekstrand, 1967; Gais, Plihal, Wagner, & Born, 2000; Hu, Stylos-Allan, & Walker, 2006; Jenkins & Dallenbach, 1924; Maquet, Schwartz, Passingham, & Frith, 2003; Orban et al., 2006; Plihal & Born, 1997, 1999; Rauchs et al., 2008; Smith & MacNeill, 1994; Sterpenich et al., 2007; Yaroush,

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Sullivan, & Ekstrand, 1971) have suggested that dissociable types of memory (e.g., declarative vs. non-declarative) depend on particular stages of sleep (rapid eye movement (REM) sleep vs. non-REM (NREM) sleep). Sleep recording paradigms have identified the learning-dependent changes in sleep architecture (e.g., increased REM: Buchegger, Fritsch, Meier-Koll, & Riehle, 1991; Buchegger & Meier-Koll, 1988; De Koninck, Lorrain, Christ, Proulx, & Coulombe, 1989; Goerke et al., 2013; Mandai, Guerrien, Sockeel, Dujardin, & Leconte, 1989; Smith & Lapp, 1991; Smith, Nixon, & Nader, 2004; Stickgold, Whidbee, Schirmer, Patel, & Hobson, 2000; and NREM sleep: Fogel & Smith, 2006; Fogel, Smith, & Cote, 2007; Meier-Koll, Bussmann, Schmidt, & Neuschwander, 1999; Stickgold et al., 2000) and the respective characteristic changes in the electrophysiological features of REM and NREM sleep, e.g., rapid eye movements (Fogel, Smith, et al., 2007; Freixa i Baqué et al., 1983; Smith & Lapp, 1991; Smith, Nixon, et al., 2004) and spindles (Albouy, Fogel, et al., 2013; Fogel & Smith, 2006, 2011; Fogel, Smith, et al., 2007; Gais, Mölle, Helms, & Born, 2002; Meier-Koll et al., 1999; Morin et al., 2008; Peters, Ray, Smith, & Smith, 2008; Schabus et al., 2004) that take place following new learning. Neuroimaging studies have revealed the brain regions (e.g., striatum, hippocampus) where sleep-dependent consolidation enhances activation and learning-dependent reactivation during sleep (Albouy, Fogel, et al., 2013; Bergmann, Mölle, Diedrichs, Born, & Siebner, 2011; Fogel et al., 2013; Laureys et al., 2001; Maquet et al., 2000; Orban et al., 2006; Peigneux et al., 2004). Finally, targeted cueing (Antony, Gobel, O'Hare, Reber, & Paller, 2012; Hoedlmoser et al., 2008; Oudiette, Antony, Creery, & Paller, 2013; Rasch, Büchel, Gais, & Born, 2007; Schönauer, Geisler, & Gais, 2014; Smith & Weeden, 1990; Sterpenich, Schmidt, & Albouy, 2014), pharmacological enhancement (Mednick et al., 2013; Rasch, Pommer, Diekelmann, & Born, 2009; Wamsley et al., 2013), and brain stimulation (Huber et al., 2008; Marshall, Helgadóttir, Mölle, & Born, 2006; Marshall, Kirov, Brade, Mölle, & Born, 2011; Massimini, Tononi, & Huber, 2009) during post-training sleep have demonstrated that sleep has a modulating effect on memory consolidation. Together, this body of evidence shows that sleep is crucial for the optimal consolidation of memory. This benefit does not occur simply as a factor of the passage of time (Debarnot, Castellani, Valenza, Sebastiani, & Guillot, 2011; Doyon et al., 2009; Fischer, Drosopoulos, Tsen, & Born, 2006; Korman et al., 2007; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002; Walker, Brakefield, Seidman, et al., 2003) or reduced interference, but rather, studies convincingly show that sleep actively contributes to the consolidation of memories. The *active system consolidation hypothesis* (Born & Wilhelm, 2012; Diekelmann & Born, 2010; McClelland, McNaughton, & O'Reilly, 1995) proposes that sleep is required for the effective and optimal transformation of new memories to be actively consolidated, relying on a dialogue between the hippocampus and the neocortex, as reflected (or possibly, actively induced) by the features of sleep (e.g., slow waves, sleep spindles and sharp wave ripples), ultimately stabilizing and integrating labile memory traces into long-term memory via repeated reactivation.

Sleep however, is not a unitary phenomena, and in humans, consists of both REM and NREM sleep. The distinct role that each sleep stage (and the electrophysiological events that define them) plays in memory consolidation remains controversial (for insightful reviews on the topic see: Ackermann & Rasch, 2014; Rasch & Born, 2013; Stickgold, 2005, 2013). REM sleep is paradoxically characterized by wake-like, low amplitude, high frequency desynchronized electroencephalographic (EEG) activity, rapid eye movements and muscle atonia, and occurs predominantly at the end of the night. By contrast, slow wave sleep (SWS) is characterized by large amplitude, highly synchronized slow wave activity, occurring

predominantly at the beginning of the night, and the lighter NREM stage 2 (NREM2) sleep is characterized by synchronized, low amplitude EEG, k-complexes and sleep spindles and occurs rather evenly interspersed throughout the night. Accounting for these categorically different types of sleep, the *dual process hypothesis* (Gais & Born, 2004; Maquet, 2001; Smith, 2001) proposes that declarative memories, including semantic facts and figures, episodic experiences, and events are consolidated primarily during SWS. Alternatively, non-declarative memories including procedural skills, particularly those that are cognitively complex in nature are consolidated during REM sleep (Fogel, Smith, et al., 2007; Peters, Smith, & Smith, 2007; Plihal & Born, 1997; Smith, 2001; Smith, Aubrey, & Peters, 2004). As well, emotional memory consolidation also appears to rely on REM sleep (Groch, Wilhelm, Diekelmann, & Born, 2013; Payne, Chambers, & Kensinger, 2012; Sterpenich et al., 2007; Wagner, Gais, & Born, 2001).

Much of the evidence for the role of REM sleep in memory consolidation comes from animal studies employing selective REM sleep deprivation (for review see: Smith, 1985, 1996, 2003) and typically employ tasks that have an emotional component in some way (e.g., stress, pain, novelty, reward). Recording studies in animals suggest that REM sleep may not be exclusively involved; rather, both REM and NREM sleep appear to play a role in the consolidation of memories (Binder et al., 2012; Fogel, Smith, & Beninger, 2009; Giuditta, Mandile, Montagnese, Piscopo, & Vescia, 2003; Giuditta et al., 1995). However, with the exception of emotional memory consolidation, the precise role for REM sleep is less clear in humans (for an excellent review of the recent literature addressing this issue see: Ackermann & Rasch, 2014). A recent study has shown that NREM2 may be correlated with the ability to perform cognitive procedural tasks classically employed (Cohen, Eichenbaum, Deacedo, & Corkin, 1985; Milner, 1971) to investigate the relationship between REM sleep, dreaming and task aptitude to perform this task (Nielsen et al., 2014). In their study, participants were administered a cognitively complex procedural task (the Tower of Hanoi) and a spatial memory span test (the Corsi Block Tapping task). Higher REM sleep duration was associated with improved performance on the Corsi Block Tapping task, whereas higher NREM2 sleep duration was associated with improved performance on the Tower of Hanoi task. In addition, sleep spindle density and amplitude were associated with the Tower of Hanoi and the Corsi Block Tapping tasks, respectively. However, it is not known whether the associations between sleep and task performance were related to learning and memory, or to inter-individual traits in aptitude for these tasks. Thus, the distinct roles that REM and NREM sleep play in memory consolidation remain to be fully elucidated. It may be that both NREM and REM play a role in the consolidation memories; either over several nights (Fogel et al., 2009) or within the same night as sequential hypotheses (Giuditta, 1985; Giuditta et al., 1995, 2003) have suggested.

Another complementary hypothesis (Smith, Aubrey, et al., 2004), proposes that the acquisition of procedural skills which are novel, require REM sleep to be consolidated. By contrast, practice on procedural tasks which are already well-learned, require non-REM sleep for the further refinement of performance. This hypothesis is compelling because it may resolve controversy over the role of REM sleep in memory consolidation, but it remains to be fully investigated, and there is currently limited support for this hypothesis. One study (Peters et al., 2007) found that the increase in REM density from a baseline night to a post-training test night and the improvement in Pursuit Rotor performance were positively correlated in a low skill group, but not in a high skill group. Conversely, the increase in sleep spindle density and Pursuit Rotor performance improvement was positively correlated in the high skill group, but not in the low skill group. These results suggest that

an individual's initial skill level is an important factor to consider when investigating post-learning changes in sleep, and may even interact. Thus, according to this perspective, the sleep spindle appears to be related to the refinement of existing motor skills, but not necessarily to the initial acquisition of completely novel and newly learned skills.

Importantly, it is not known how the learning-related changes in sleep architecture (e.g., duration of NREM2, SWS and REM sleep) and the learning-related changes of the characteristic electrophysiological features (e.g., spindles, slow wave activity, rapid eye movements) of these states occur over the course of the acquisition of a novel procedural skill, leading to the refinement and mastery of the skill. In addition, it remains unclear which of the aforementioned hypotheses might best explain the time course of skill learning. Here, using behavioural and scalp-recorded EEG techniques, we sought to identify the electrophysiological correlates of the development of expertise of a cognitively complex procedural task (the Tower of Hanoi) by examining the changes in the sleep EEG that accompanied the mastery of performance on that task over repeated training sessions until expertise was acquired. By using a procedural task that requires the acquisition of a new cognitive strategy to reach perfect performance, and comparing post-learning changes in sleep to a control condition, we were able to characterize the learning-dependent changes in sleep involved in the acquisition of expertise of a novel task. After continued practice, following mastery of the new strategy, improvement requires only the refinement of existing skills, thus, we were able to test whether refinement of already mastered skills is uniquely associated with dissociable changes in post-learning sleep. In line with Peters et al. (2007), we predicted that learning-dependent changes in REM sleep (including increased REM sleep duration and REM density and amplitude) will take place immediately prior to mastery of a new procedural skill. However, once the task is mastered, and no further improvement in accuracy is possible, continued training and re-testing on the same task will result in refinement of performance and learning-dependent changes in NREM sleep (including changes in sleep spindle characteristics such as duration and amplitude). We also explored whether learning-related changes in slow wave activity would coincide with spindles, as previous studies have shown that these temporally-related features of NREM sleep may work in concert for memory consolidation (Möller, Bergmann, Marshall, & Born, 2011; Möller, Eschenko, Gais, Sara, & Born, 2009).

2. Materials and methods

2.1. Participants

Fifteen healthy young adults (10 female; mean age = 21.80 ± 2.86 years; age range: 19–29 years) participated in this study. Participants were recruited via posters displayed around Western University campus. All potential participants underwent an initial telephone screening interview and were excluded if they reported they were not in good health, left-handed, considered themselves poor sleepers, had irregular sleep schedules (outside of approximately 11 PM to 9 AM), a body mass index >30, were diagnosed with a sleep disorder, were shift workers, took medications known to interfere with sleep, or had a history of head injury or seizure. To be included, interested participants had to score <10 on the Beck Depression Inventory and the Beck Anxiety Inventory, and have no signs of sleep disorders indicated by the Sleep Disorders Questionnaire. In addition, the first night of polysomnographic (PSG) recording served as an acclimatization/sleep disorder screening night. The screening night included EEG recordings (via electrodes placed on the face and

scalp including EEG channels Fz, Cz, Pz and Oz), respiration (via thorax and abdomen belts), electrocardiographic activity (via electrodes placed below each clavicle), leg muscle activity (via electrodes placed on the outer, anterior tibialis muscle of each leg) and blood oxygen saturation (via a finger probe placed on the index finger of the right hand). Screening night recordings were scored by a single, expert Registered Polysomnographic Technologist in accordance with clinical scoring guidelines established by the American Academy of Sleep Medicine (Iber, Ancoli-Israel, Chesson, & Quan, 2007). Participants were excluded from further participation in the study if the results of their screening night identified greater than 5 respiratory events per hour of sleep or greater than 10 periodic leg movements per hour of sleep. Participants were also asked to wear an 'Actiwatch' (Philips-Respironics Inc., Andover, MA, U.S.A.; a wrist-worn accelerometer, to measure sleep-wake-related limb movements) and to complete a log of their daily activities and sleep habits, to verify that they maintained a regular sleep schedule for the length of their participation in the study. Participants were excluded from further participation in the study if the results of their Actiwatch or sleep diary identified variability in their sleep schedule outside of the aforementioned exclusion criteria, or non-compliance with the study protocol prior to the in-laboratory sleep recordings.

2.2. Ethics statement

All participants were given a letter of information, provided informed written consent prior to participation and were financially compensated for their participation. This research was approved by the Western University Health Science Research Ethics Board.

2.3. Polysomnographic recording and analysis

Embla Titanium (Natus, San Carlos, CA, USA) PSG systems were used to perform in-laboratory sleep recordings. Physiological data were recorded at a sampling rate of 512 Hz, with a high pass filter = 0.1 Hz and low pass filter = 220 Hz. EEG, electrooculogram (EOG), and electromyogram (EMG) recordings were taken using gold-plated electrodes applied to the skin. The EEG (F3, Fz, F4, C3, Cz, C4, P3, Pz, P4 and Oz) and EOG (from the left and right outer canthus of the eye) were recorded and re-referenced offline to the contralateral mastoid derivations (M1 and M2). The EMG (submental chin muscles) channel was recorded as a bipolar derivation. Sleep stages were scored in accordance with standard criteria (Iber et al., 2007) using RemLogic analysis software (Natus, San Carlos, CA, USA).

Spindle detection was carried out using in-house EEGlab (Delorme & Makeig, 2004) compatible software written for Matlab R2014a (Mathworks Inc, Natick, MA, USA). The EEG data was initially down-sampled to 128 Hz. The detection was performed at Fz, Cz and Pz derivations. The spindle data was extracted from movement artifact-free, NREM sleep epochs (NREM2 and SWS separately). The detection method (Fogel et al., 2013; Ray et al., 2015), used a complex demodulation transformation of the EEG signal with a bandwidth of 5 Hz centered about a carrier frequency of 13.5 Hz. Each data point was transformed into z-scores using the mean and the standard deviation derived from a 60 s sliding window. Events (spindle onsets, peaks and offsets) were then detected on the transformed signal with a z-score threshold of $z = 2.33$. The variables of interest extracted from this method include spindle peak amplitude, spindle duration, peak frequency and spindle density (number of spindles per-minute of NREM sleep), for each subject and at each derivation (Fz, Cz and Pz). Spindles less than 0.25 s were removed from further analyses. Spindles were categorized as slow spindles (11–13.5 Hz) at Fz, fast spindles (13.5–16 Hz) at Pz and total bandwidth spindles (11–16 Hz) at Cz.

REM detection was carried out using in-house software written for Matlab R2014a (Mathworks Inc, Natick, MA, USA). The EOG data was initially down-sampled to 128 Hz. The detection was performed on the left and right EOG channels. The REM data was extracted from movement artifact-free, REM sleep epochs. The detection used the same approach as for sleep spindles, but instead was applied to the EOG signals with a bandwidth of 4 Hz centered about a carrier frequency of 3 Hz.

Power spectral analysis of movement artifact-free epochs of EEG scored as NREM2, SWS and REM sleep from all EEG derivations was conducted using Fast Fourier Transform (FFT) using the “spectopo” EEGLab function that employs the “pwelch” function from the Matlab Signal Processing Toolbox. Power spectral estimates (amplitude, μV^2) were extracted with a frequency resolution of 0.2 Hz, by using a 5 s window with no overlap, averaged over 6 windows to provide a power spectrum density for each 30-s epoch of sleep, from 0.2 to 20 Hz.

2.4. Behavioural testing

2.4.1. Tower of Hanoi task

The Tower of Hanoi task (invented by a French mathematician, Édouard Lucas in 1883, first marketed in 1889 as “*Dots and Boxes*”) was used as a measure of complex cognitive procedural motor learning. The computerized version of the task, coded in Matlab 2014a (Mathworks Inc, Natick, MA, USA), consisted of three vertical pegs, equally spaced, and five disks of different sizes that could be moved from one peg to another (Fig. 1). The start configuration of the task had all disks located in a stack, in increasing size from top to bottom and all on the furthest left-most peg. The objective of the task was to move the stack to the furthest right-hand peg, obeying the following rules: (1) only one disk could be moved at a time, (2) each move could consist of taking the upper disk from one of the stacks and placing it on another peg, and (3) no disk could be placed on top of a smaller disk. The optimal solution to the task could be obtained using an iterative solution (i.e., alternate moves between the smallest and non-smallest disk), a recursive solution (i.e., breaking the problem down into smaller problems) or a non-recursive solution (i.e., move the smallest disk to the location it did not previously come from, and make the only possible remaining legal move), any of which cognitive strategies arrive at the same pattern of movements to solve the puzzle in the minimum number of moves = $2^N - 1 = 31$, where N = the number of disks. Importantly, these logical strategies all result in the identical pattern of movements, learned through extensive practice.

Each PM training and AM testing session consisted of the subjects performing the task 5 times. Training and testing sessions were repeated until they reached criterion performance (e.g., perfect performance in 3 of 5 trials). The main variables of interest for the Tower of Hanoi were speed (inter-move-interval for correct responses) and accuracy (Mean Absolute Percentage Error; MAPE), which can be interpreted as the percentage of perfect performance (e.g., 100% reflects perfect performance, whereas 50% reflects making twice as many errors as perfect performance and 0% represents an infinite number of moves). Increased speed would not be expected to necessarily increase with the development of learning the underlying logical strategy, rather reflect more generally processing speed and motor performance. Accuracy is particularly appropriate for the Tower of Hanoi task given that there is only one optimal solution. We are interested here in how close performance was to the optimal solution (in this case, representing “expertise”), and where making an infinite number of moves is theoretically possible (if the correct solution is never achieved). Increased accuracy would only occur with acquisition of the underlying logical strategy required to reach the optimal solution.

2.4.2. Control task

The control task was identical to the Tower of Hanoi task, except that there were only two disks and each move was prompted, from one random location to another within the constraints of the rules. Each control session consisted of the subjects performing the control task a total of 5 times, matched for the approximate average total duration to solve the Tower of Hanoi task.

2.5. Procedure

All participants were initially screened to verify that they met the inclusion criteria (see Section 2.1 for details). Each participant underwent several PSG recordings including an initial acclimatization/screening night one week prior to the training nights, followed by up to three consecutive training nights, a re-test night recording one week later (Fig. 2) and a control night either the night prior to the first training night or the night after the retest night (counter-balanced across subjects). Subjects were trained until they reached criterion (e.g., perfect performance = 31 moves, in 3 of 5 trials).¹ For each recording night, the participant would arrive at the sleep lab in the evening where they were prepared for overnight PSG recording. On the training and re-test nights, the subjects performed the Tower of Hanoi task (see Section 2.4.1 for details) in the evening prior to electrode application (PM training session) and then again in the morning following electrode removal (AM testing session). On the control night, the subjects performed the Tower of Hanoi control task (see Section 2.4.2 for details) in the evening prior to electrode application and then again in the morning following electrode removal.

2.6. Statistical analyses

All statistical analyses were carried out using SPSS Statistics version 22 (IBM, Armonk, New York, U.S.). Changes in speed and accuracy over the course of training (Training, Criterion, Retest PM and AM sessions) were analyzed using within subjects ANOVAs, and follow-up paired *t*-tests were used to test for changes from evening training to morning testing over each consecutive sleep interval (PM vs. AM) and from morning testing to evening training over each consecutive wake interval (AM vs. PM).

Post-learning changes in sleep architecture, REMs, sleep spindles and spectral power over the course of the: (1) control night, (2) the post-training sleep from the first training session when the task was novel to the subjects (i.e., “Novice”), (3) the night that subjects reached criterion (i.e., “Expert”) and (4) the retest night were analyzed using within subjects ANOVAs. Repeated measures ANOVAs on spectral power were used to identify the frequency bin where the effect of training session was maximal across derivations in the delta (0–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), sigma (12–16 Hz) and beta (16–20 Hz) bands. Follow-up paired *t*-tests were used to test for changes from the control night to the other nights. Pearson’s correlation coefficients were used to follow-up the relationship between Tower of Hanoi speed and accuracy, with significant changes in sleep architecture, REMs, spindles and spectral power (at the site and frequency bin where the effect of training was maximal) from the control night.

Although 15 subjects met the inclusion criteria and were enrolled in the study, one participant dropped out of the study

¹ All subjects included in the statistical analyses ($N = 12$, see Section 2.6) required at least two training sessions to reach this level of performance. $N = 4$ subjects reached criterion in two sessions, and $N = 8$ reached criterion after three sessions. No subjects included in the statistical analysis failed to reach criterion by the third session. The first training session was considered the “Novice” session and the last training session, when subjects reached criterion was considered the “Expert” session.

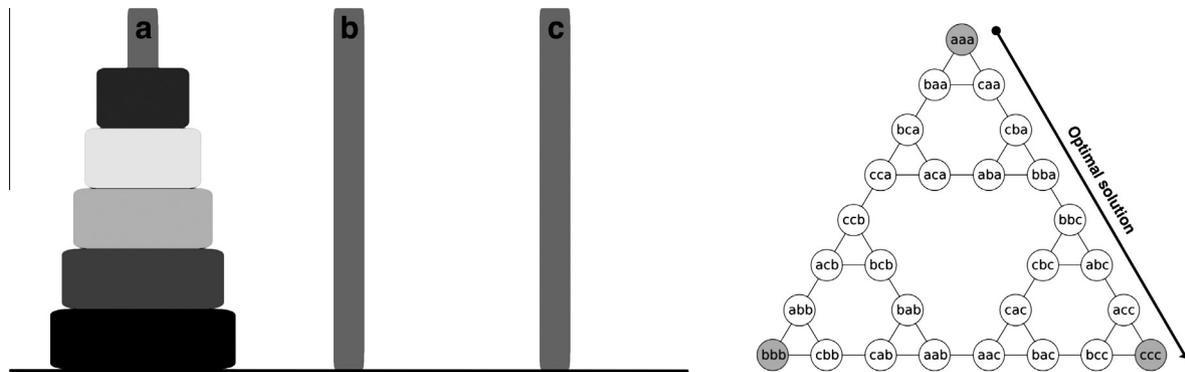


Fig. 1. Tower of Hanoi task (left). The goal of the task is to move all five disks from the left-most location (a) to the right-most location (c), moving one disk at a time, moving the uppermost disk, without placing a larger disk on a smaller disk and in the minimum number of moves. The solution (right), represented by a graph where the nodes represent the distribution of disks and the edges represent moves. For the sake of simplicity, the graph for the 3-disk puzzle is shown. The 5-disk solution would have nine interconnected graphs as shown. The nodes at the vertices represent distributions with all disks on the same peg. There is only one unique and perfect solution, in this case, for 3 disks, number of moves = $2^N - 1 = 7$, where N = the number of disks, or in the case of the 5 disk puzzle, 31 moves.



Fig. 2. Experimental protocol. Participants were screened for sleep quality and sleep disorders from overnight PSG recordings (see Section 2.3), from ~11:00 PM to 7:00 AM. This also served as an opportunity to acclimatize subjects to sleeping in the laboratory environment. Either one or two weeks later (counterbalanced over subjects), participants were trained on the control task (see Section 2.4.2) in the evening (Control PM), followed by a full night of PSG recording and subsequent testing in the morning (Control AM). Subjects were also trained for up to 3 consecutive nights on the Tower of Hanoi task in the evening (Tower 1–3 PM), followed by a full night of PSG recording and subsequent testing in the morning (Tower 1–3 AM), until they reached criterion. Finally, subjects were retested on the Tower of Hanoi task one week later in the evening (Tower RT PM), followed by overnight PSG and a morning retest (Tower RT AM).

before completing the protocol, one subject did not comply with the sleep-wake schedule, and one subject was excluded due to medical complications. Thus, the final number of participants included in the statistical analyses was $N = 12$.

3. Results

3.1. Tower of Hanoi behavioural results

To investigate the acquisition of expertise on the Tower of Hanoi task (Fig. 3), a within subjects ANOVA revealed significant improvements in performance over the practice sessions (Training, Criterion, Retest PM and AM sessions) for speed ($F(5,55) = 21.02$, $p < 0.001$) and accuracy ($F(5,55) = 15.72$, $p < 0.001$). Post-hoc paired t -tests revealed that speed increased over the first sleep (Training PM to AM) interval ($t(11) = 2.55$, $p = 0.027$), the first wake (Training AM to Criterion PM) interval ($t(11) = 3.51$, $p = 0.005$) and the last sleep (Criterion PM to AM) interval ($t(11) = 2.95$, $p = 0.013$), but not over the retest sleep (Retest PM to AM) interval ($t(11) = 0.72$, $p = 0.49$). Thereby indicating that speed increased incrementally over the practice sessions, regardless of whether the interval contained sleep or wake, and then leveled off at retest after reaching criterion. On the other hand, accuracy did not increase significantly until the last sleep (Criterion PM to AM) interval ($t(11) = 2.60$, $p = 0.25$), suggesting that rule learning did not significantly improve until after several practice sessions, and only when the interval contained sleep.

3.2. Sleep architecture results

To investigate post-learning-related changes in sleep architecture (Table 1) over the course of acquiring expertise on the Tower

of Hanoi task, within subjects ANOVAs for each stage of sleep revealed significant changes in NREM2 (min: $F(3,33) = 4.79$, $p = 0.007$; % TST: $F(3,33) = 6.00$, $p = 0.002$) and REM (min: $F(3,33) = 6.94$, $p = 0.001$; % TST: $F(3,33) = 8.73$, $p < 0.0001$) sleep at dissociable times. Post-hoc paired t -tests revealed that first, increased REM sleep duration was observed on the night that subjects reached Expert performance as compared to the control night (min: $t(11) = 3.40$, $p = 0.006$; % TST $t(11) = 3.66$, $p = 0.004$). A significant increase in NREM2 sleep duration was observed one-week later on the retest night as compared to the control night (min: $t(11) = 2.21$, $p = 0.049$; % TST: $t(11) = 1.93$, $p = 0.08$). Thus suggesting that REM sleep may be involved in the increased accuracy observed that night, and NREM2 sleep may be involved once expertise has been acquired, but when no overt signs of improvement are detectable.

3.3. Rapid eye movement results

Within subjects ANOVAs were used to test if there was a change in REMs from baseline over the course of the training to Novice, to Expert and at Retest. Surprisingly, no significant changes in REMs over the course of training were found for eye movement amplitude, duration or density.

3.4. Sleep spindle results

3.4.1. NREM2 sleep spindles

Within subjects ANOVAs revealed post-learning-related changes in fast spindles (13.5–16 Hz) during NREM2 sleep at Pz over the course of acquiring expertise on the Tower of Hanoi task (Fig. 4A and B) for density ($F(3,33) = 13.35$, $p < 0.001$), and peak frequency ($F(3,33) = 11.54$, $p < 0.001$). Post-hoc paired t -tests

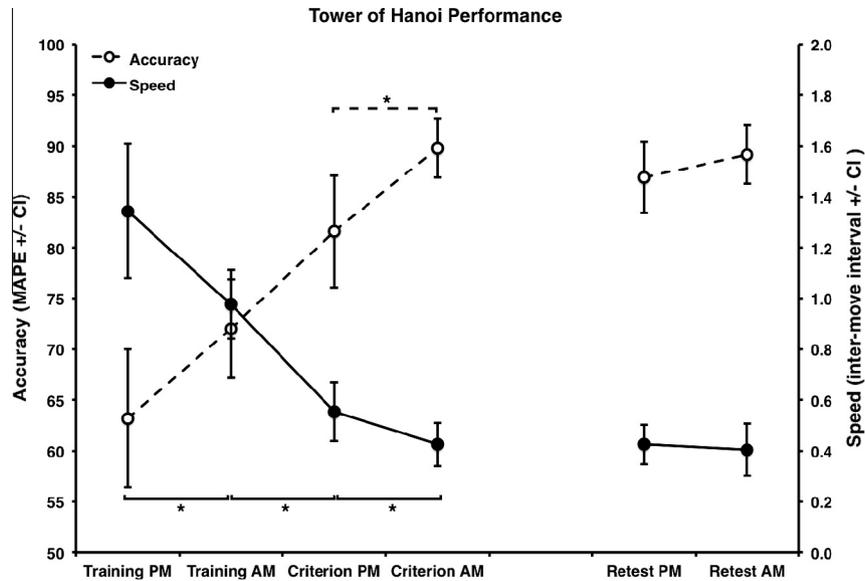


Fig. 3. Mean ($\pm 95\%$ confidence interval) speed and accuracy performance improvements on the Tower of Hanoi task over the course of Training and Criterion practice sessions, and at Retest one week later. Speed improved over the Training night sleep interval, the following intervening wake interval and over the Criterion night sleep interval, whereas accuracy significantly increased only over the Criterion night sleep interval.

Table 1

Sleep architecture results. Mean (standard deviation) duration in minutes and percent total sleep time for NREM1, NREM2, SWS, REM and total sleep time (TST). REM sleep was significantly elevated on the night that subjects performed at an Expert level, whereas NREM2 was significantly elevated on the Retest night.

Stage of sleep		Control	Novice	Expert	Retest
NREM1	min	14.41(5.27)	16.71(6.46)	15.92(3.50)	15.38(7.83)
	% TST	3.33(1.30)	3.75(1.54)	3.67(0.78)	3.42(1.98)
NREM2	min	174.19(26.47) [#]	182.95(30.81) [#]	162.53(33.79)	195.94(31.84) [*]
	% TST	39.83(4.97) ⁺	41.42(7.15)	36.50(5.23) [#]	43.42(5.30) [*]
SWS	min	148.16(21.48)	154.87(29.97)	148.79(17.00)	143.29(28.32)
	% TST	34.17(5.70)	35.00(5.51)	34.00(4.49)	31.75(6.43)
REM	min	100.84(30.69) [#]	88.15(16.47) [#]	115.98(23.50) [*]	93.07(24.69) [#]
	% TST	22.58(4.89) [#]	19.92(3.40) [#]	26.08(3.78) [*]	20.50(5.14) [#]
Total sleep time	min	437.61(48.25)	442.72(26.59)	443.22(46.44)	451.88(30.68)

Note: * indicates significantly higher than [#] at $p < 0.05$, and a trend at ⁺ $p < 0.10$.

revealed that spindle density and spindle frequency were increased on the first post-training night (density: $t(11) = 5.26$, $p < 0.001$; frequency: $t(11) = 5.64$, $p < 0.001$) and at retest (density: $t(11) = 3.45$, $p = 0.005$; frequency: $t(11) = 2.38$, $p = 0.037$) as compared to the control night (Fig. 4A and B), suggesting that there were more faster spindles during NREM2 sleep on the night when subjects were still novices and also after they had mastered the Tower of Hanoi task. There were no learning-related changes in slow spindles (11–13.5 Hz) at Fz or total bandwidth spindles (11–16 Hz) at Cz, thus suggesting that the effect of learning was specific to fast spindles.

3.4.2. SWS sleep spindles

Within subjects ANOVAs revealed post-learning-related changes in fast spindles (13.5–16 Hz) during SWS at Pz over the course of acquiring expertise on the Tower of Hanoi task (Fig. 4E–H) for density ($F(3,33) = 10.66$, $p < 0.001$), frequency ($F(3,33) = 5.88$, $p = 0.002$), duration ($F(3,33) = 12.04$, $p < 0.001$) and amplitude ($F(3,33) = 6.07$, $p = 0.002$). Similar to spindles in NREM2 sleep, post hoc paired t -tests revealed that spindle density and spindle frequency were increased on the first post-training night (density: $t(11) = 4.56$, $p = 0.001$; frequency: $t(11) = 3.10$, $p = 0.010$) and also at retest (density: $t(11) = 2.37$, $p = 0.037$; frequency: $t(11) = 2.35$, $p = 0.038$) as compared to the control night

(Fig. 4E and F), suggesting that the learning-dependent changes in spindles on the Novice night and Retest night were consistent across NREM2 and SWS. In addition, there was an increase in the average size of spindles in terms of duration ($t(11) = 6.03$, $p < 0.001$) and amplitude ($t(11) = 3.06$, $p = 0.011$) on the night that subjects reached Expert performance as compared to the control night (Fig. 4G and H), suggesting that while spindles were no more numerous than control on the night that Expert performance was reached, spindle size was increased during SWS. There were no learning-related changes in slow spindles (11–13.5 Hz) at Fz or total bandwidth spindles (11–16 Hz) at Cz, thus suggesting that similar to NREM2 spindles, the effect of training was also specifically related to fast spindles during SWS.

3.4.3. Correlations with performance improvements

Bivariate correlation coefficients were used to further follow-up the significant results of the post hoc t -tests, to determine if the observed post-training changes in spindle characteristics from the control night were correlated with overnight performance improvements. Importantly, the change in NREM2 spindle density from the control night to the retest night was correlated with the overnight change in accuracy ($r(10) = 0.79$, $p = 0.002$; Fig. 5A) and speed ($r(10) = -0.62$, $p = 0.032$; Fig. 5B). No other significant correlations were observed (all $p > 0.2$).

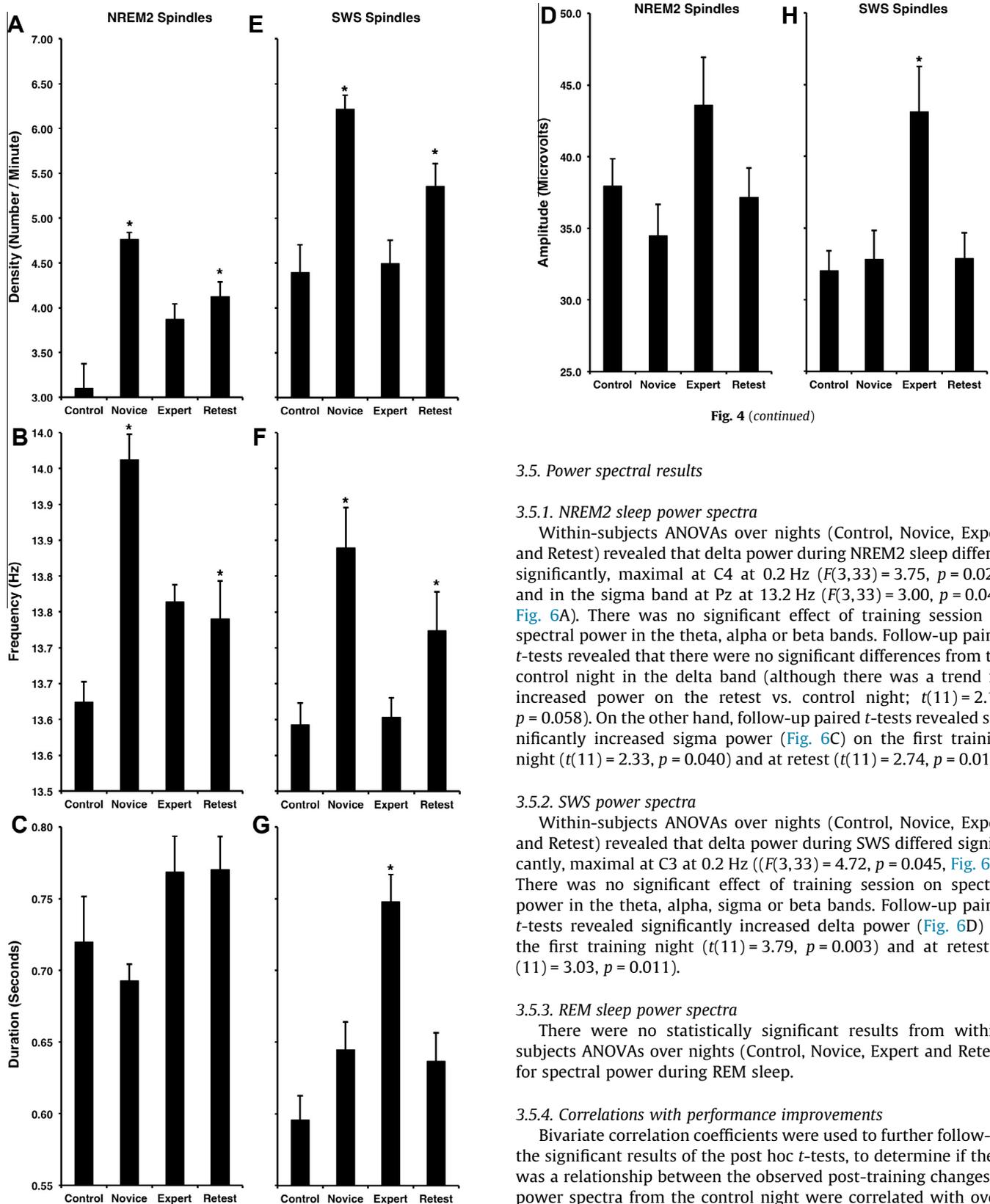


Fig. 4 (continued)

3.5. Power spectral results

3.5.1. NREM2 sleep power spectra

Within-subjects ANOVAs over nights (Control, Novice, Expert and Retest) revealed that delta power during NREM2 sleep differed significantly, maximal at C4 at 0.2 Hz ($F(3,33) = 3.75, p = 0.020$) and in the sigma band at Pz at 13.2 Hz ($F(3,33) = 3.00, p = 0.045$, Fig. 6A). There was no significant effect of training session on spectral power in the theta, alpha or beta bands. Follow-up paired *t*-tests revealed that there were no significant differences from the control night in the delta band (although there was a trend for increased power on the retest vs. control night; $t(11) = 2.11, p = 0.058$). On the other hand, follow-up paired *t*-tests revealed significantly increased sigma power (Fig. 6C) on the first training night ($t(11) = 2.33, p = 0.040$) and at retest ($t(11) = 2.74, p = 0.019$).

3.5.2. SWS power spectra

Within-subjects ANOVAs over nights (Control, Novice, Expert and Retest) revealed that delta power during SWS differed significantly, maximal at C3 at 0.2 Hz ($F(3,33) = 4.72, p = 0.045$, Fig. 6B). There was no significant effect of training session on spectral power in the theta, alpha, sigma or beta bands. Follow-up paired *t*-tests revealed significantly increased delta power (Fig. 6D) on the first training night ($t(11) = 3.79, p = 0.003$) and at retest ($t(11) = 3.03, p = 0.011$).

3.5.3. REM sleep power spectra

There were no statistically significant results from within-subjects ANOVAs over nights (Control, Novice, Expert and Retest) for spectral power during REM sleep.

3.5.4. Correlations with performance improvements

Bivariate correlation coefficients were used to further follow-up the significant results of the post hoc *t*-tests, to determine if there was a relationship between the observed post-training changes in power spectra from the control night were correlated with overnight performance improvements. However, no significant correlations were observed (all $p > 0.05$).

4. Discussion

The study of the role of sleep in memory consolidation in humans has largely been limited to single, brief laboratory training

Fig. 4. Mean (+ standard error) NREM2 fast (13.5–16 Hz) spindle density (A), peak frequency (B), duration (C) and amplitude (D), and SWS fast spindle density (E), peak frequency (F), duration (G) and amplitude (H) at Pz. Increased spindle density was observed on the night when participants were first exposed to the Tower of Hanoi task (Novice), and these spindles were faster in terms of peak frequency during NREM2 and SWS. Spindles were larger in terms of duration and amplitude on the night when subjects reached Expert performance in SWS only. * indicates significantly different from Control night.

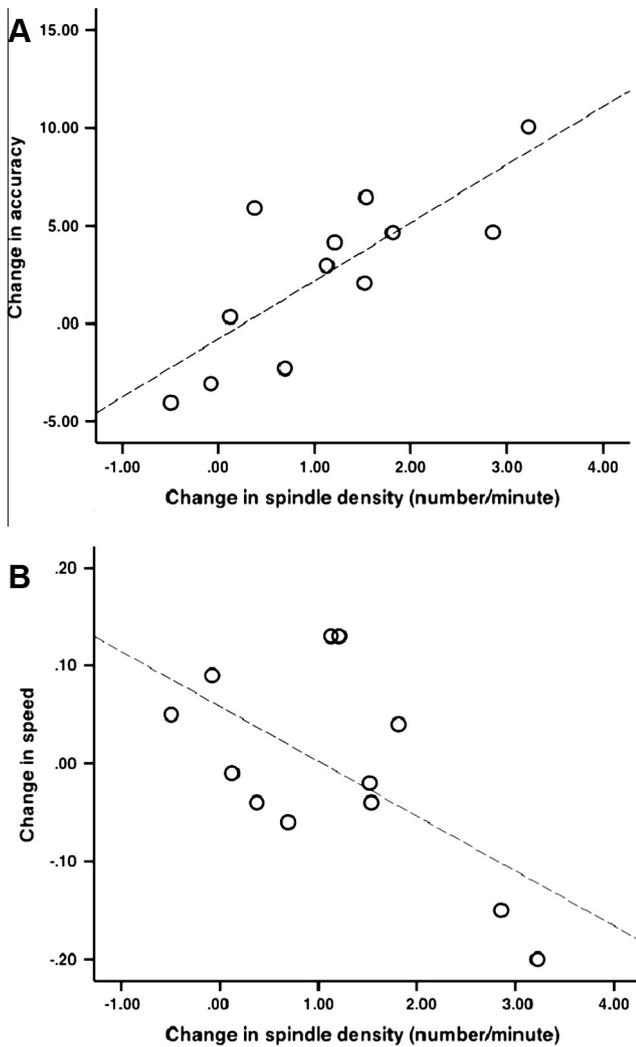


Fig. 5. The relationship between the change in spindle density (Retest–Control) and the overnight change (PM–AM) in accuracy and speed on the Tower of Hanoi task. The increase in spindle density from the Control to the Retest night was positively correlated with the overnight improvement in both accuracy (A) and speed (B) on the Tower of Hanoi task.

sessions, with the aim of: (1) investigating the types of sleep that support overnight memory consolidation by identifying the impact of post-learning sleep deprivation on subsequent performance, (2) characterizing the nature of the learning-dependent changes in post-learning sleep in order to identify what happens during sleep that supports memory consolidation processes, and (3) causally manipulating post-training sleep (e.g., using cueing, stimulation and pharmacological manipulation) to enhance sleep-dependent memory consolidation. For certain tasks (e.g., motor procedural learning), this has led to the notion that sleep is involved in memory consolidation, perhaps only, on the first post-learning night (Fogel & Smith, 2006; Gais et al., 2000; Maquet et al., 2003; Walker, Brakefield, Hobson, & Stickgold, 2003). However, outside the laboratory, humans rarely set out to learn a new skill without the intention of reaching a certain level of expertise or, perhaps even with the aim of mastering a skill over the course of a lifetime (e.g., the mastery of a musical instrument, a sport, or games such as chess). Certain cognitively complex or novel skills require repeated practice until we acquire a *new set of rules*, or a *new way of thinking*. This is a challenge to study in the laboratory, as this process can take a great deal of time and practice, and thus for practical reasons, most sleep and memory studies have limited their recordings

to only one post-training night. As a result, it is not known whether sleep is involved in the mastery and refinement of new skills that lead to expertise (e.g., playing Carnegie Hall, winning Olympic gold, or beating IBM's "Deep Blue" at chess). Here, using behavioural and scalp-recorded EEG techniques, across repeated overnight sessions, we have identified the EEG correlates of new cognitive/procedural skill learning that accompany the mastery and refinement of a newly acquired skill with repeated practice. In terms of sleep architecture, our results show that on the night that subjects become experts on the task, they have increased REM sleep duration. Re-exposure to the task one-week after it has already been mastered resulted in increased NREM2 sleep. Based on the sleep architecture results alone, in line with the hypothesis proposed by Smith, Aubrey, et al. (2004), these results demonstrate that REM sleep is important for the acquisition of expertise of a new skill, but NREM sleep is involved in the subsequent refinement of an already mastered skill. This hypothesis puts forward the idea that REM sleep is involved in the consolidation of procedural learning that is novel and requires the acquisition of new strategies and rules to be acquired before performance improves. On the other hand, NREM sleep is hypothesized to support the refinement of already existing, or cognitively simple tasks for which there is already some pre-existing related skills to rely on to perform the task (Peters et al., 2007).

However, sleep architecture alone does not pinpoint the specific characteristic features of the sleep EEG that reflect the physiological activity related to the consolidation process. While the learning-dependent changes in the macrostructure of sleep in the present study support the hypothesis put forward by Peters et al. (2007), a closer look at the phasic features (e.g., spindles and eye movements) and tonic EEG activity (e.g., sigma and delta power) that characterize these sleep stages revealed a different, and more complex pattern of results. While we did observe increases in the duration of REM sleep immediately prior to the night when the strategy required to perform the task perfectly was achieved (i.e., the "Expert" night), surprisingly, there were no changes in rapid eye movements themselves as compared to the control night. It is possible that learning-related changes in sleep architecture manifest themselves in multiple ways; either by increasing the amount of a particular stage, or in terms of intensity, indicated by increases in specific types of phasic or tonic activity reflected by events such as REMs or EEG activity, respectively. Given that there were no changes in the intensity of REMs or EEG spectral power during REM sleep, the current approach may not be sufficient to identify the specific neural activity involved in REM sleep-dependent memory consolidation. In addition to increased REM sleep, the characteristics (e.g., spindle duration and amplitude, but not the density) of spindles during SWS appear to have been modulated by new learning on the night when subjects approached perfect performance. Thus suggesting that both REM and NREM sleep (and perhaps SWS in particular) may play a role in the realization of the optimal strategy required to solve the task.

In addition to the learning-related changes in REM sleep duration and spindle size during SWS on the night prior to reaching maximal performance, there were, learning-related increases in the features of NREM sleep (spindle density and spindle peak frequency) that occurred on the first post-training night during both NREM2 and SWS when the task was still novel, and at retest when the underlying strategy to perform the task had already been mastered. This pattern was consistent with the results of the power spectral analysis of the EEG, which revealed that sigma activity (13.2 Hz) was elevated at parietal sites (maximal at Pz) during NREM2 sleep. In addition, delta activity (0.2 Hz) was elevated at central sites (maximal at C3) during SWS (and a non-significant trend during NREM2) when the task was novel and at retest, as compared to the control night. Importantly, the overnight

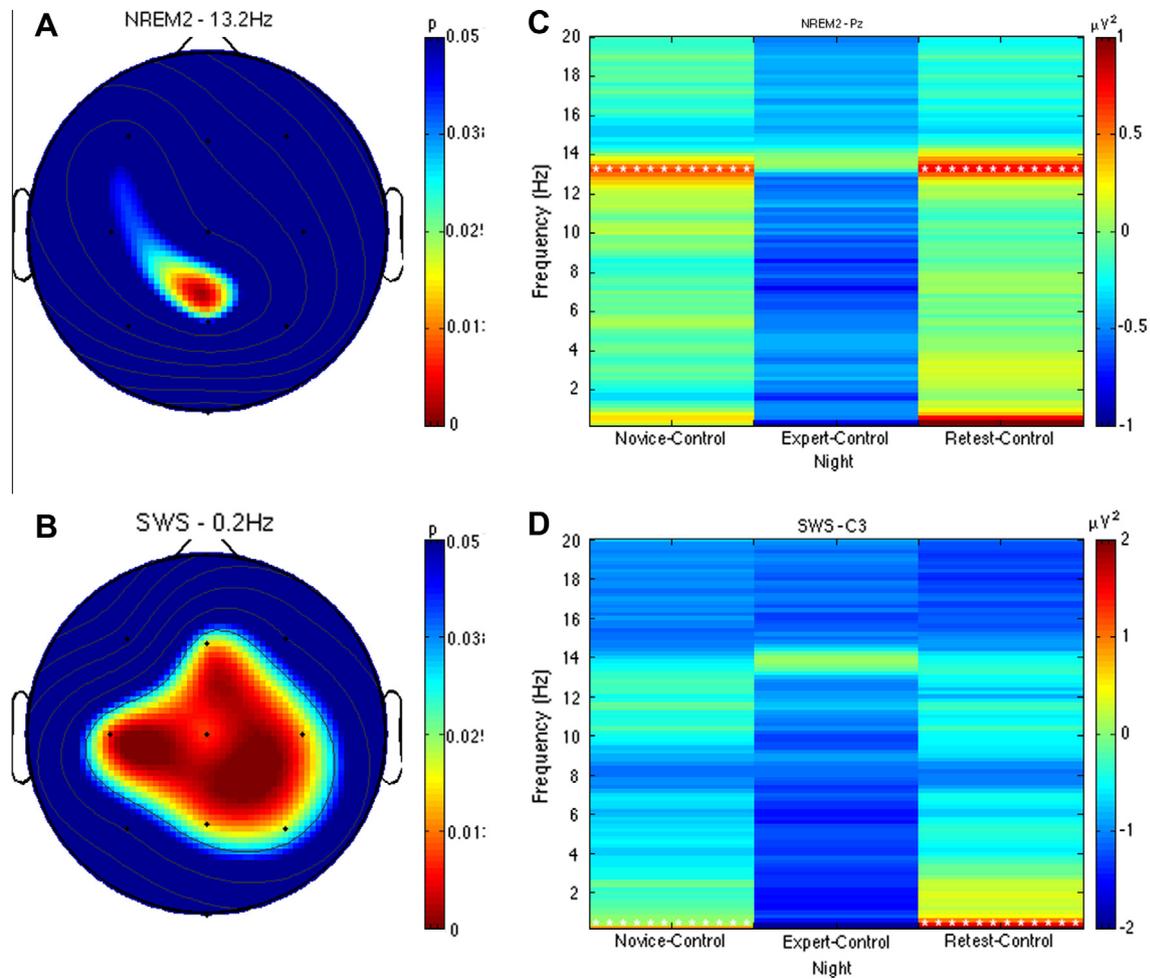


Fig. 6. Power spectral analysis. Statistical p -value maps from within subjects ANOVAs illustrating the distribution of significant results across the scalp for sigma power in NREM2 sleep at 13.2 Hz, maximal and highly localized at Pz (A), and for delta power in SWS at 0.2 Hz, maximal at C3, but distributed about central derivations (B). Follow-up paired t -tests revealed: (1) significantly increased sigma power at Pz during NREM2 sleep (C) on the first training night vs. the control night (Novice-Control) and on the retest vs. the control night (Retest-Control), and, (2) significantly increased delta power at C3 during SWS sleep on the first training night vs. the control night (Novice-Control) and on the retest vs. the control night (Retest-Control). *** indicates significant paired t -test.

improvement in accuracy and speed was significantly correlated with the increase in spindle density during NREM2 as compared to the control night. Thus, these results suggest that sleep spindles and slow wave activity are involved at an early stage when the strategy to perform the task was only starting to be acquired, and again for the subsequent refinement of task performance, after the underlying strategy had already been mastered. It is possible that spindles and slow waves serve a complimentary function for memory consolidation, as both have been implicated in memory consolidation and synaptic plasticity in humans and animals (Eschenko, Mölle, Born, & Sara, 2006; Fogel & Smith, 2006, 2011; Fogel et al., 2009; Gais et al., 2002; Marshall et al., 2006; Rosanova & Ulrich, 2005; Tononi & Cirelli, 2006). Evidence from animals has shown that spindles are grouped by slow oscillations (Steriade & Amzica, 1998), and these coupled events are associated with depolarization of cortical neurons during up states (Steriade, 1999; Steriade & Amzica, 1998) and shifts in scalp-recorded potential in humans (Marshall, Mölle, & Born, 2003). More recently, these spindle-slow wave complexes have been linked to memory processing (Möller et al., 2009, 2011), particularly for fast spindles. However, it is unclear from the present study, whether the underlying processes reflected by changes in spindles and slow wave activity are the same at these different stages of learning, or whether they serve dissociable functions. Future neuroimaging

studies may reveal dissociable cerebral activation related to these EEG events (e.g., spindles, slow waves) along the time-course of skill acquisition.

Taken together, NREM sleep neural oscillations such as sleep spindles and slow waves appear to be involved in both the gradual refinement of skills (when the task is novel) and are involved in the acquisition of expertise for a new cognitive strategy (when expert performance is achieved). REM sleep on the other hand, is involved only when performance accuracy improves to the point where expertise is attained and the optimal strategy can be consistently performed. Taken together, our results suggest that both REM and NREM sleep have a role to play in memory consolidation, particularly for tasks that are novel and require the acquisition of new rules in order to improve performance to the point where they have mastered the new skill. These findings go beyond previous explanations such as the dual process hypothesis, suggesting that both REM and NREM sleep (and the electrophysiological features and associated neural activation which characterize these states) play a role to enhance certain aspects (rule-learning vs. refinement) or at certain stages (Novice vs. Expert) of the mastery of a new cognitively demanding and novel task. More specifically, both REM and NREM sleep may be required for the acquisition of new rules, and over the course of the mastery and refinement of a novel and cognitively complex skill.

These results are consistent with the influential work of Giuditta et al. who proposed the sequential hypothesis (Giuditta, 1985; Giuditta et al., 1995, 2003). The sequential hypothesis proposes that both REM and NREM sleep are involved in the sequential processing of memory during sleep. It is the repetitive cyclic trains of transitions between sleep stages initially from NREM sleep to REM that relate to learning (Langella, Colarieti, Ambrosini, & Giuditta, 1992). In particular, transitions that include the “transition sleep” (an intermediate stage of sleep characterized by enhanced theta activity, immediately prior to REM sleep), are related to processing of novel responses (Datta et al., 2004; Vescia et al., 1996). At present, there is only limited evidence that a similar process may take place in humans (Stickgold et al., 2000), but the present study suggests that all stages of sleep may contribute over the course of learning, consolidation, and perhaps re-consolidation (Stickgold & Walker, 2007). In addition, there are other interesting parallels with the existing animal literature investigating the role of post-learning sleep periods over repeated training sessions, distributed over several days. A great deal of experimental evidence in rats supports the hypothesis that REM sleep is crucial for memory consolidation (for review see: Smith, 1985, 1996, 2003). Short and discrete post-training periods termed “REM sleep windows” have been identified where REM sleep is necessary for sleep-dependent gains in performance to occur. These windows are characterized by a marked increase in REM sleep duration (Fishbein & Gutwein, 1977; Fishbein, Kastaniotis, & Chattman, 1974; Fogel, Smith, & Beninger, 2010; Fogel, Smith, Higginson, & Beninger, 2010; Fogel et al., 2009; Smith, Kitahama, Valatx, & Jouvet, 1974; Smith & Lapp, 1986; Smith & Rose, 1997), which lasts for a period of about 4 h. REM sleep deprivation during, but not outside, the REM sleep window blocks consolidation (Fogel, Smith, & Beninger, 2010; Smith & Butler, 1982; Smith, Conway, & Rose, 1998; Smith & Kelly, 1988; Smith & Rose, 1996). Remarkably, even when sleep is severely restricted only to the window and prevented at all times outside the window, sleep-dependent memory consolidation takes place equally well as compared to normally rested controls (Smith & Butler, 1982). REM sleep windows vary in terms of their timing, depending primarily on the type of task and the intensity of the training regime (for review see: Smith, 1985, 2003). When practice is intense (100 trials in one session), the REM window occurred immediately after training. However, similar to the present study, when the same amount of training was protracted over several days (20 trials over 5 days), the REM window occurred immediately prior to the maximal increase in performance (Smith, Young, & Young, 1980). When an intermediate training regime was used (50 trials over 2 days), post-training changes in REM sleep and theta activity were observed from 13 to 20 h after training, whereas increased spindle density was observed from 20 to 24 h after training (Fogel et al., 2009). In humans, previous studies investigating the role of sleep in complex cognitive procedural memory consolidation have found that REM sleep deprivation impairs performance (Plihal & Born, 1997; Smith, 1993), as well, increased post-learning REM sleep duration (Smith, Nixon, et al., 2004) and rapid eye movements (Fogel, Smith, et al., 2007; Peters et al., 2007; Smith & Lapp, 1991; Smith, Nixon, et al., 2004) were associated with improved performance on the first post-training night. Here, when training was protracted over several days, similar to the aforementioned results in rats, the timing of the learning related changes in REM sleep duration take place on the night of the maximal improvement in performance. Although speculative, it is tempting to suggest that REM sleep windows may also exist in humans. However, given that this was not the goal of the current study, future research is required to directly test this hypothesis.

A recent study (Nielsen et al., 2014) has revealed that NREM sleep, but not REM sleep, was related to inter-individual

differences in task performance (speed) on the Tower of Hanoi task, and spindle density was correlated with overnight changes in accuracy and speed. Another task (Corsi Block Tapping task) performed on the same night, was on the other hand, related to REM sleep duration in those that improved on the task overnight. However the relationship between task performance and sleep could be interpreted akin to studies that investigated the relationship between sleep and cognitive abilities, normally assessed by IQ tests (for review see: Fogel & Smith, 2011), rather than pre vs. post learning-dependent changes in sleep compared to a baseline or control night of sleep. Similarly, previous studies have shown that sleep spindles were correlated to Performance IQ (which taps similar reasoning abilities as the Tower of Hanoi task), but not Verbal IQ (Fogel, Nader, Cote, & Smith, 2007), particularly for individuals with a high IQ. By contrast, the number of rapid eye movements were correlated with Verbal IQ, but not Performance IQ. Taken together, these studies suggest that individuals with a greater aptitude for tasks that require the acquisition of complex rule learning, reasoning and cognitive strategies are related to inter-individual differences in sleep spindles.

Learning on the Tower of Hanoi task has been considered to be implicit in nature (Beauchamp, Dagher, Panisset, & Doyon, 2008; Danion et al., 1992; Gras-Vincendon et al., 1994; Hömberg, Bickmann, & Müller, 1993; Vakil et al., 2000); a reasonable assumption considering that the length of the optimal solution (in this case, a sequence of 31 correct moves) is beyond the normal capacity of working memory, and also given that the strategy is novel, and cannot be arrived at simply by knowing the constraints of the task (i.e., the task instructions). Thus, subjects are obligated to learn the underlying rule that governs the pattern of moves required to solve the puzzle using the optimal strategy through practice, and possibly trial-and-error. However, consistent with literature investigating the neural correlates of planning in a similar task (Owen, Doyon, Petrides, & Evans, 1996), it may not be safe to assume the learning is purely implicit in nature, and may involve conscious planning and perhaps the development of explicit knowledge of a strategy. While it is tempting to speculate about potential insight into the strategy needed to perform the task (as sleep has been reported to be involved in this process, e.g., Wagner, Gais, Haider, Verleger, & Born, 2004), in the current study, we do not have any direct measure of implicit/explicit knowledge of the underlying strategy required to solve the task, and thus do not have any data to support such a conclusion. This intriguing unresolved issue would require further research to investigate the role of sleep in the acquisition of explicit knowledge of the underlying strategy. In addition, there was variability in the number of training nights required to reach expert performance. This may reflect two distinct profiles of skill acquisition; in both slow and fast learners. Future studies could also investigate whether learning-related changes in sleep follow dissociable patterns depending on how quickly the task is mastered.

5. Conclusions

In conclusion, by employing a task that requires repeated practice over several days in order to acquire a novel strategy (e.g., recursive logic) in order to master a complex motor procedural skill, the present findings lend new support for the role of both REM and NREM sleep in the acquisition of expertise. Initially, performance improves gradually in terms of speed over the course of several sleep and wake episodes, and eventually, significant improvements in accuracy are observed prior to mastery of the strategy. When the task is novel, increased spindles during NREM2 and SWS, and slow wave activity during SWS are involved in the early stages when the task is novel during the acquisition of the

optimal strategy to solve the task. Once expert performance is attained at retest, both spindles and slow wave activity are again involved in when given the opportunity to rehearse the optimal solution, suggesting a role for both SWS and NREM2 sleep in the refinement of the skill. These results, taken together suggest that REM, NREM2 and SWS sleep are sequentially involved in the mastery of a new skill. This study may help to provide insight into some of the inconsistencies and unresolved questions in the extant literature on the sleep states that support procedural learning. These findings have implications not only for understanding the role of sleep in memory consolidation, but also in furthering our understanding of the neural mechanisms which underlie the acquisition of new strategies and refinement of existing skills. These processes combined, ultimately support our ability to become highly specialized in areas of expertise, such as our ability to become for example, world-class professional athletes, musicians, or computer programmers.

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