The role of sleep in the realization of solutions to problems: Impact of age

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I. Abstract

Unlike other domains of cognition, the acquisition of procedural skills (*e.g.*, the "*how to*" of memory) is spared by age. However, the consolidation (*i.e.*, the transformation from labile memory to long-term storage) of this type of memory is compromised by age. Optimal memory consolidation for procedural skills is dependent on sleep. Sleep is also negatively impacted by normal, healthy aging. Recent research has identified the neural markers of the lost benefit of sleep for reduced memory consolidation with age. While this is relatively well-established for procedural memory, and for cognitively simple motor skills, the impact of age-related changes in sleep on cognitively complex procedural memory consolidation (*i.e.*, novel cognitive strategies required for "*problem-solving skills*") remains to be investigated. Furthermore, reduced capacity to solve problems with age has serious mental health-related consequences, including increased depression and suicide attempts, as well as disability in depressed, cognitively impaired older adults. Moreover, problem-solving therapy has been found to improve quality of life in older adults.

As such, the aims of these series of studies were to investigate: 1) the behavioural consequences of age on sleep-dependent memory consolidation, 2) identify the electrophysiological markers during sleep of the lost benefit of sleep, 3) identify the age-related changes in brain structure and how this relates to and behavioural outcomes and sleep, and, 4) identify the impact of age on sleep-dependent consolidation of the memory trace for problem-solving skills. Using an innovative combination of EEG, MRI, and behavioural testing in healthy young and older adults, these series of studies revealed novel insights into the breakdown of the normal processes that occur during sleep that support memory. The main objective of this thesis is to identify the neural markers of the very earliest signs under optimal conditions of age-related cognitive decline for problem-solving skills. Investigating the neurophysiological and behavioral consequences of age-related changes in sleep, and their impact on problem-solving skills, will help reveal therapeutic targets for future research that will improve quality of life for seniors. Furthermore, this research will ultimately lead to the development of early interventions targeting sleep that could delay or lessen the severity of the onset of clinically significant cognitive impairment; as those who sleep better, may also age better cognitively.

Keywords: Memory consolidation, aging, procedural memory, sleep, fMRI, EEG.

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III. Abbreviations

EEG	Electroencephalography
EMG	Electromyography
EOG	Electrooculogram
fMRI	Functional magnetic resonance imaging
HPC	Hippocampus
MSL	Motor sequence learning
NREM	Non-rapid eye movement sleep
NREM1	Non-rapid eye movement sleep stage 1
NREM2	Non-rapid eye movement sleep stage 2
NREM3	Non-rapid eye movement sleep stage 3
PSG	Polysomnography
PVT	Psychomotor vigilance task
REM	Rapid eye movement sleep
Rapid EMs	Rapid eye movements
SO	Slow-Oscillation
SLL	Second language learning
SMA	Supplementary motor area
SWA	Slow wave activity
SWS	Slow-wave sleep
TMR	Targeted Memory Reactivation
ToH	Tower of Hanoi
WASO	Wake after sleep onset

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Toor, B., Baena Pérez, D, van den Berg, N. H, Ray, L. B., & Fogel, S. M. (in production). Sleep spindles and slow-wave coupling and cognitively complex learning: Impact of age.

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VIII. Other publications and manuscripts related to this thesis

van den berg, N.H., Smith, D., Fang, Z., Pozzobon, A., **Toor, B**., Al-Kuwatli, J., Ray, L., Fogel, S. M. (2023). Sleep Strengthens resting-state functional communication between brain areas involved in the consolidation of problem-solving skills. *Learning and Memory.*

Gibbings, A., Ray, L.B., Smith, D., van den Berg, N., **Toor, B**., Sergeeva, V., Viczko, J., Owen, A.M., and Fogel, S.M. (2022). Does the early bird really get the worm? How circadian chronotype relates to human abilities. *Current Research in Behavioral Health.*

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Chapter 1

Overview of Sleep, Memory, and Aging

1.1 The Characteristics of Sleep

Sleep is a homeostatically regulated (Borbély & Achermann, 1999), naturally recurring altered state of consciousness characterized by reduced responsiveness to external stimuli and relative inactivity (Rasch & Born, 2013). However, sleep is not simply a state of quiescence, it is a dynamic state which supports an array of physical and mental functions, including healthy cognitive aging (Scullin, 2017). Sleep is also known to have important links to cognition and memory, and in recent years the relationship between sleep and memory has become a contentious and highly intensive area of research (for a review, see; Rasch & Born, 2013).

The following sections will provide a general overview of sleep architecture, including a detailed description of the various stages of sleep, their importance and how they change across the lifespan. This will be followed by a discussion of the functions of sleep.

1.2 Architecture of sleep

Sleep is divided into two categories: rapid eye movement (REM), and non-rapid eye movement (NREM) sleep. NREM sleep is further subdivided into NREM stage 1 (NREM1), NREM stage 2 (NREM2), and NREM stage 3 (NREM3) sleep or slow wave sleep (SWS). In addition to electromyography (EMG) and electrooculogram (EOG) changes, the different sleep stages are characterized by distinct electroencephalogram (EEG) activity. A full sleep cycle encompasses all stages of sleep and lasts approximately 90 minutes. Throughout a night of sleep, healthy adults will complete four to five sleep cycles.

1.2.1 NREM1

NREM1 sleep marks the onset of sleep and is the lightest sleep stage with the lowest arousal threshold of all the stages of sleep. It is characterized by less than 50% alpha activity, presenting with sharp EEG vertex waves and low voltage, mixed frequency EEG. During NREM1 sleep, there is little to no EOG activity as one drifts in and out of sleep, creating effortless awakenings and decreases in amplitude of EEG as the brain falls asleep (Carskadon & Dement, 2011; Sergeeva et al., 2020). NREM1 accounts for approximately 2-5% of the night's total sleep time (Colten & Altevogt, 2006), and can contain vivid visual hypnogogic imagery (Rowley et al., 1998).

1.2.2 NREM2

NREM2 sleep is also considered a light stage of sleep, but compared to NREM1, requires a more intense stimulus to produce arousal (Sergeeva et al., 2020). It is characterized by primarily theta waves, which are relatively low in voltage and contain mixed frequency EEG. NREM2 occupies approximately half (45-55%) of the night's total sleep time (Carskadon & Dement, 2011). EMG activity and conscious awareness of the external environment are further decreased (Sergeeva et al., 2020). In this stage, theta waves dominate but are interrupted by brief waxing-and-waning bursts of thalamocortical oscillations in the sigma frequency range, called sleep spindles. Sleep spindles are short (~0.5–3 seconds) (Sergeeva et al., 2020), low amplitude (Iber et al., 2007) bursts of neural activity (11-16 Hz), which occur repeatedly during NREM sleep. It has been proposed that two types of sleep spindles exist: fast and slow spindles (De Gennaro & Ferrara, 2003). Slow spindles are thought to be generated in the frontal regions of the brain and occur at a frequency of ~11-13.5Hz, while fast spindles are maximal at central and parietal regions of the brain and occur at a frequency of ~13.5-16 Hz (Werth et al., 1997). Sleep spindles act to block external sensory processing during sleep (Dang-Vu et al., 2010), as well as play a role in cognitive function, and brain plasticity (Fang et al., 2019; Fogel & Smith, 2011; Schönauer & Pöhlchen, 2018; Smith et al., 2020). More specifically, sleep spindles are thought to be important for memory consolidation (for reviews, see; Fogel & Smith, 2011; Rasch & Born, 2013). Briefly, sleep spindles appear to be actively involved in the strengthening and stabilizing of new memories (for reviews, see; Fogel & Smith, 2011; Ulrich, 2016), a process called memory consolidation.

In addition to sleep spindles, K-complexes also characterize NREM2 sleep (Iber et al., 2007; Williams et al., 1964). K-complexes comprise short (~0.5 sec), high amplitude slow waves of positive polarity, followed by a sharp negative wave (Iber et al., 2007). K-complexes are thought to be generated in the frontal regions of the brain and can occur in response to environmental stimuli. They consist of a negative sharp wave, followed by a slower positive component occurring ~350-550 ms later, terminating with a final negative peak approximately 900 ms after the first negative peak (Colrain, 2005). To date, there is no clear consensus on the function of the K-complex (for a review, see; Colrain, 2005), however, evidence suggests that they might serve as a ‘night watch’ or ‘sentinel.’ They can process the relevance or importance of external stimuli, to judge whether to alert the sleeper (Bastien et al., 2000).

NREM3 sleep, also referred to as SWS, is the deepest stage of sleep, and compared to all other sleep stages requires the most intense stimulus to produce arousal (Rechtschaffen & Kales, 1968). NREM3 is characterized by an abundance of high amplitude, cortically generated, low-frequency delta waves. Delta waves have a frequency of ~0.5-2 Hz (often defined as up to 4 Hz) and a large peak-to-peak amplitude of at least 75 μV. SWS generally lasts 20-40 minutes, and accounts for between 15-25% of a night’s total sleep time (Carskadon & Dement, 2011). NREM3 has important restorative functions, as slow waves play a central role in sleep homeostasis (Achermann & Borbély, 2003; Borbély et al., 1999). Slow wave activity (SWA) is prominent during the early portions of the sleep period, with the proportion spent in SWS reducing as the night progresses (Carskadon & Dement, 2011).

More recently, the coupled interaction between slow waves and sleep spindles during NREM sleep has been proposed to support memory consolidation (Helfrich et al., 2018; Muehlroth et al., 2019). Temporal interactions between slow waves, spindles, and hippocampal ripples are temporally coupled in a hierarchy that allows for information transformation into long-term memory and retention (Clemens et al., 2007; Helfrich et al., 2018; Latchoumane et al., 2017; Rasch & Born, 2013; Staresina et al., 2015). However, most of the research to date has focused on declarative memory and motor sequence learning tasks. The effects on procedural memory, particularly problem-solving abilities, remains to be investigated as a function of age.

1.2.3 REM

REM sleep is also considered a paradoxically light stage of sleep, and compared to SWS, requires a less intense stimulus to produce an arousal (Carskadon & Dement, 2011). REM sleep is characterized by high-frequency sawtooth or theta waves, rapid eye movements (Rapid EMs), muscle atonia (Iber et al., 2007; McCarley, 2007), and vivid dreams (Aserinsky & Kleitman, 1953). The first REM period usually occurs 90 minutes after sleep onset. It occupies approximately 20-25% of a night's total sleep time. REM sleep cyclically occurs throughout the night, alternating with NREM sleep. This cyclicity which occurs approximately every 90 minutes, is consistent throughout a night of sleep, with the duration of the REM portion tending to increase later in the night (Carskadon & Dement, 2011).

1.3 Sleep Across the Lifespan

Sleep systematically changes across the lifespan **(see Figure 1.1).** Newborns and infants sleep approximately 12-16 hours each day, half of which is spent in REM sleep. During childhood, total sleep time decreases to 10-12 hours, along with spent in REM sleep, however, time spent in SWS increases. In adolescence, total sleep time continues to decrease to 8-10 hours, and similarly, time spent in SWS decreases. During adulthood and older age, total sleep time decreases to between 6 and 8 hours, with time spent in REM and SWS decreasing linearly with age. In addition, with age, sleep becomes lighter, and more fragmented, awakenings during sleep become longer, and sleep onset latency (SOL) increases (for a review, see; Ohayon et al., 2004). Given the focus of this thesis, a much more in-depth review of the impact of age on sleep is presented in section 1.8.

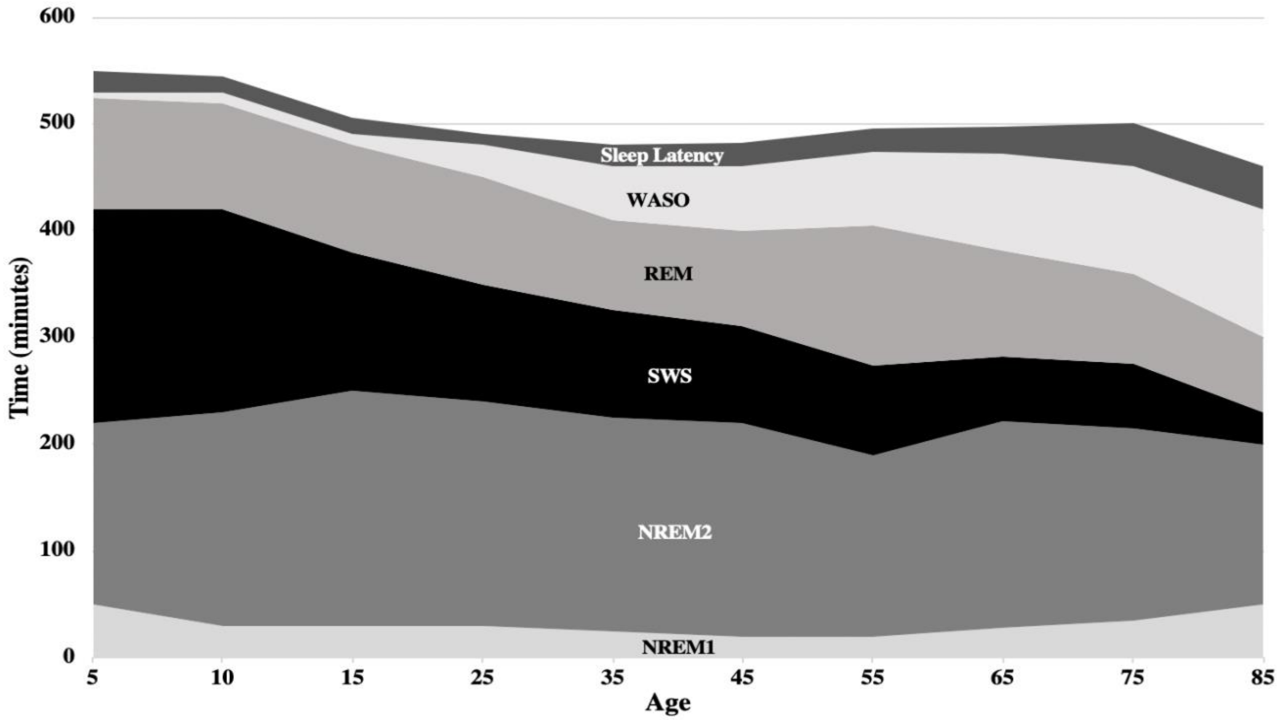

Figure 1.1. Age-related changes in NREM1, NREM2, SWS, REM, wake after sleep onset (WASO), and SOL (in minutes) across the lifespan. Adapted from (Ohayon et al., 2004).

1.4 The Functions of Sleep

Sleep is regulated at both the molecular and cellular levels. It has been hypothesized to impact a wide variety of biological and psychological functions, making it impossible to ascribe a singular function to sleep. Considering the necessity of sleep for survival (Grandner, 2017), many theories regarding the functions of sleep have been proposed, including; energy conservation

(Berger & Phillips, 1995); brain waste clearance (Fultz et al., 2019; Xie et al., 2013); modulation of immune responses (Besedovsky et al., 2012; Zielinski & Krueger, 2011); cognition and memory (Doyon, Korman, et al., 2009; Fogel & Smith, 2011; Maquet, 2001; Rasch & Born, 2013; Smith, 2001; Stickgold & Walker, 2013; Tononi & Cirelli, 2014); daytime performance (Alhola & Polo-Kantola, 2007); vigilance (Dinges et al., 1997); disease (Besedovsky et al., 2012); and mental health (Weissman et al., 1997).

Theories supporting an energy saving, and thermoregulation function for sleep posit that one of the primary functions of sleep is to reduce an individual's energy demand and expenditure during part of the day or night, especially at times when it is efficient to do so (Berger & Phillips, 1995). Most recently, a novel function of sleep has been proposed for brain waste clearance, suggesting that during sleep, intercellular space is increased allowing cerebrospinal fluid to clear toxins from the brain, serving to get rid of accumulated metabolic 'trash' (Fultz et al., 2019). Sleep has also been implicated in regulating immune functioning. A causal link has been found between lack of sleep and weakening of the immune system's ability to fight off diseases (Besedovsky et al., 2012). Briefly, sleep loss alters immune functioning, and immune challenges alter sleep.

With a lack of sleep, there is a decrease in performance levels on tasks that require fast reaction times, along with a decrease in vigilance and subjective sleepiness (Dinges et al., 1997). Sleep deprivation can also impact psychological states and mental health in a bidirectional manner, with poor psychological health also affecting a person's ability to sleep well (Weissman et al., 1997). Finally, sleep also plays a vital role in supporting memory and cognition (Doyon et al., 2009; Fogel & Smith, 2011; Rasch & Born, 2013; Smith, 2001; Stickgold & Walker, 2013; Tononi & Cirelli, 2014), with different stages of sleep playing a unique role in the consolidation process.

Given the focus of the current thesis, this topic will be reviewed in greater detail after introducing memory systems.

1.5 Memory Systems

The formation of long-term memories takes place over time and in distinct stages. The stages of memory processing include encoding, consolidation, and retrieval. During encoding, information from sensory inputs is changed into a form of memory that can be stored to prevent its loss. During consolidation, the memory trace begins to stabilize, going through many stages of either long-term (e.g., system level) or short-term (e.g., synaptic and molecular level) consolidation processes (McGaugh, 2000). During retrieval, the stored memory is accessed and recalled. Memories that are newly acquired tend to be in a labile state, and the process of stabilizing the memory into a long-term form can take hours, days or even years; depending on the type of memory being consolidated (for a review, see; Rasch & Born, 2013).

1.5.1 Declarative Memory

Declarative memory includes memory for facts, figures, places, and events, and is normally acquired through rehearsal and rote memorization. It is considered memory for knowing "*what*", as opposed to "*how*" (for a review, see; Smith, 2001). A classic task used to assess declarative memory is the paired associates learning task. Paired associate learning involves the ability of a person to learn and retrieve formed associations between two unrelated word pairs (Sakai & Miyashita, 1991). This task is commonly used to study hippocampal-dependent declarative memory which is explicitly learned, and typically assessed through recognition or recollection. Declarative memory primarily depends on the hippocampus (HPC) (for a review, see; Squire, 1992), the prefrontal cortex (PFC) (Kapur et al., 1995; Nyberg et al., 1996; Schacter et al., 1996), and the medial temporal lobe (Davachi et al., 2003; Douville et al., 2005). Consolidation of this memory type takes place via a hippocampal-neocortical dialogue which slowly transfers the memory trace from the HPC to the neocortex for more permanent storage (for a review, see; Rasch & Born, 2013)

1.5.2 Procedural Memory

Non-declarative or procedural memory, which is memory for skills and habits, tends to be acquired and assessed through performance rather than recognition or recollection, and is considered memory for learning and knowing "*how*" as opposed to "*what*." Procedural memory can be further subdivided into cognitively simple motor skills and cognitively complex procedural skills (for a review, see; Smith, 2001). Cognitively simple procedural memory tasks, which are usually motor in nature involve the refinement of skills for which there is already a pre-existing set of skills to use to learn the task. Classic examples of simple procedural memory tasks include the pursuit rotor (Adams, 1952; Ammons, 1955), which is a visual-motor tracking task that requires hand–eye coordination; and the finger tapping task (Karni, 1995), which is a motor-sequence learning task.

In contrast, and the main focus of this thesis, cognitively complex procedural memory involves the learning of new rules, or acquiring a new skill set to solve or improve performance on a task (for a review, see; Smith, 2001) that typically involves strategy, problem-solving or grammatically complex learning. Classic examples of complex procedural memory tasks include the artificial grammar task (Cleeremans & McClelland, 1991; Fischer et al., 2006), which tests a subject's ability to learn made-up grammar; the Tower of Hanoi (Simon, 1975), and the mirror tracing task (Starch, 1910), all of which involve learning a new cognitive strategy to complete the task successfully.

Procedural memory is dependent on a variety of brain structures (for reviews, see; Doyon et al., 2003; Schacter, 1997; Unterrainer & Owen, 2006). More specifically, evidence from neuroimaging and neuropsychological studies implicate the PFC, HPC, anterior cingulate cortex, and the striatum—particularly the caudate (Albouy et al., 2008; Albouy, King, et al., 2013; Albouy, Sterpenich, et al., 2013; Baker et al., 1996; Laventure et al., 2016; Morris et al., 1993; Owen et al., 1996; Poldrack, Prabhakaran, et al., 1999; Poldrack, Wagner, et al., 1999; van den Berg et al., 2021).

1.6 Sleep and Memory

1.6.1 Sleep and Declarative Memory

The consolidation of declarative memories is thought to be dependent on both NREM (Fowler et al., 1973; Gais et al., 2000; Plihal & Born, 1997; Smith, 1995; Yaroush et al., 1971), and REM sleep (Fogel, Smith, et al., 2007; Groch et al., 2013; Hutchison & Rathore, 2015). Sleep deprivation (Empson & Clarke, 1970; Plihal & Born, 1997; Smith, 1993), behavioural (Berner et al., 2006; Clemens et al., 2005; Fogel, Smith, et al., 2007; Gais et al., 2002; Lau et al., 2010; Ruch et al., 2012; Schabus et al., 2004; Schmidt et al., 2006; Tucker et al., 2006; Tucker & Fishbein, 2008), and targeted memory reactivation (TMR) (Fuentemilla et al., 2013; Rasch, Büchel, et al., 2007) studies indicate that NREM sleep is necessary for optimal consolidation to take place and enhances declarative memory consolidation. Studies examining the EEG features of NREM sleep related to declarative memory consolidation reveal an increase in sleep spindle activity following declarative learning, suggesting that declarative learning influences post-learning sleep and that sleep spindles play a role in the consolidation process (Clemens et al., 2005; Fogel, Nader, et al., 2007; Gais et al., 2002; Ruch et al., 2012; Schabus et al., 2004).

More recently, simultaneous EEG-fMRI studies in humans (Bergmann et al., 2012; Dang-Vu et al., 2011) have shown that memory trace reactivation of brain regions recruited during declarative learning (*e.g.*, the HPC) were reactivated during subsequent sleep. Importantly, these reactivations were time-locked to spindle events (Bergmann et al., 2012), which in turn are nested in SOs within SWS (Marshall, Helgadóttir, et al., 2006; Staresina et al., 2015), supporting hippocampal-cortical memory transfer through repeated reactivation of the newly formed memories (for a review, see; Dudai et al., 2015). It is possible that both SOs and sleep spindles, which are temporally related events, work together, whereby spindles reflect synaptic strengthening (Rosanova & Ulrich, 2005; Werk et al., 2005), which act in coordination with SWA for synaptic downscaling (for a review, see; Massimini et al., 2009) to consolidate and optimize declarative memory.

TMR is another more recent, but now common technique that allows for the manipulation of sleep-dependent consolidation through cueing the replay of specific memories in sleep (for a review, see; Oudiette & Paller, 2013). TMR studies have provided compelling evidence that sleep-dependent declarative memory consolidation can be causally enhanced by triggering reactivation externally using auditory or olfactory reminder cues during sleep (Cairney et al., 2014; Fuentemilla et al., 2013; Göldi et al., 2019; Lehmann et al., 2016; Oyarzún et al., 2017; Schreiner et al., 2018; Schreiner & Rasch, 2015; van Dongen et al., 2012; Wang et al., 2018). These findings support an active and potentially causal role for NREM sleep in the consolidation of declarative memories.

REM sleep has also been implicated in the consolidation of declarative memories following new language learning (De Koninck, 1995; De Koninck et al., 1989; De Koninck et al., 1990), or if the memories include an emotional context (Marshall & Born, 2007; Wagner et al., 2006). This is especially important to note in conditions where memory strengthening can be problematic or maladaptive, such as in post-traumatic stress disorder (PTSD) (for a review, see; Murkar & De Koninck, 2018).

In a series of pioneering investigations (De Koninck et al., 1989; De Koninck et al., 1990), researchers investigated the consolidation of newly acquired declarative memories. Specifically, studies were conducted investigating the sleep architecture of English-speaking subjects over a 6-week intensive French immersion course. Increases in REM sleep were found immediately preceding French language performance improvements. This was also associated with the first REM-based dreaming in French. These ground-breaking studies were the first to present evidence that reprocessing newly learned declarative information occurs during REM sleep and in dream content (De Koninck et al., 1989; De Koninck et al., 1990). However, second language acquisition is not purely declarative and does involve the learning of new grammatical rules. As such, a more recent study from our group (Thompson et al., 2021) re-investigated this phenomenon by examining if the shift from declarative to procedural memory in early learning (learning that depends at first on declarative memory) vs. late second language learning (learning that is shifted to procedural memory) was a process supported by sleep. Interestingly, improvements in French proficiency were associated with changes in spindles during early second language, while increased event-related theta power time-locked to Rapid EMs were reported during late second language learning compared with early second language learning. Thus, sleep spindles were involved in early second language learning when grammar depended on declarative memory, whereas cortical theta activity time-locked to Rapid EMs was involved in late second language learning when grammar depended on procedural memory, further supporting the notion that procedural grammatical learning requires both declarative and procedural memory consolidation processes.

1.6.2 Sleep and Procedural Memory

Early sleep deprivation studies found NREM sleep to be involved in memory consolidation for motor procedural skills (Smith & MacNeill, 1994; Tweed et al., 1999). Specifically, when NREM2 sleep was selectively disrupted, individuals performed worse on tasks such as the finger tapping and pursuit rotor, compared to non-sleep deprived individuals (Smith & MacNeill, 1994; Tweed et al., 1999). Interestingly, the difference in performance following NREM2 deprivation was the same as the difference in performance following all-night sleep deprivation, suggesting that NREM2 was the important component for this type of memory from a whole night of sleep. However, when REM sleep was selectively deprived, performance was not affected (Smith & MacNeill, 1994; Tweed et al., 1999). In addition, studies have also identified that the amount of NREM2 sleep increases following motor skill learning (Fogel, Smith, et al., 2007; Fogel & Smith, 2006). Taken together, this suggests that NREM sleep, specifically NREM2 sleep, but not REM sleep, is involved in the consolidation of motor procedural memories.

Sleep spindles play an important role in the consolidation of procedural memory (Barakat et al., 2013; Fogel, Smith, et al., 2007; Fogel & Smith, 2006; Laventure et al., 2016; Morin et al., 2008; Nishida & Walker, 2007; Peters et al., 2007). Morin et al. (2008) trained subjects on either a motor sequence learning (MSL), or a control task in the evening, recorded their sleep via PSG overnight, and retested them the following morning. After performing the MSL task, subjects exhibited an increase in the number and duration of spindles. Thus, suggesting that sleep spindles are actively involved in the offline consolidation of a new sequence of finger movements known to be sleep dependent. Additionally, performance improvements for MSL have been observed after a daytime nap (Korman et al., 2007; Milner et al., 2006; Nishida & Walker, 2007), demonstrating that a daytime nap affords a similar benefit to memory consolidation as a night of nocturnal sleep. However, the role of REM sleep in daytime napping is less clear.

TMR sleep studies provide further behavioural evidence that reactivation supports the consolidation of motor procedural memory in humans (Antony et al., 2012; Cousins et al., 2014; Diekelmann et al., 2016; Schönauer et al., 2014). TMR studies have identified that motor sequence memory is consolidated after cueing in both NREM2 (Schönauer et al., 2014) and SWS (Cousins et al., 2014; Diekelmann et al., 2016; Schönauer et al., 2014), but not in REM sleep (Laventure et al., 2016). Taken together, this suggests that NREM sleep is actively involved in the consolidation of motor skill memory and that spindles may mediate the transformation from a labile to a stronger and consolidated memory trace (for a review, see; Fogel & Smith, 2011).

Most recently, studies have used functional magnetic resonance imaging (fMRI) to investigate the neural correlates of sleep-dependent memory consolidation for procedural skills. It is well-established that the striatum, thalamus, and motor cortical regions (*e.g.* the supplementary motor areas (SMA), premotor cortex, and primary motor cortex) are recruited during motor sequence learning (Albouy, King, et al., 2013; Albouy, Sterpenich, et al., 2013; Debas et al., 2014; Doyon et al., 1996; Doyon & Benali, 2005; Grafton et al., 1992, 1994; Lehéricy et al., 2005). Furthermore, activity in the striatum is enhanced when there is a period of sleep between training and retest on a motor task, relative to a period of wake (Debas et al., 2010). Thus, suggesting that sleep enhances/strengthens the memory trace as compared to an equivalent period of wake. This remains to be investigated for problem-solving skills (the focus of Study 2). Simultaneous EEG-fMRI recordings have shown that functional connectivity within the network of brain regions recruited during training is restored after a period of sleep and that the memory trace is transformed and strengthened in neocortical areas during sleep (Vahdat, Albouy, et al., 2017). Interestingly, Fogel, Albouy et al. (2017) found that the brain areas that were activated during motor skill learning, were also reactivated during subsequent NREM sleep, and that these reactivations were time-locked to sleep spindle events. In addition, the magnitude of spindle-related reactivations was related to the degree of offline gains in performance. Taken together, this suggests that sleep spindles are actively involved in the consolidation of motor skill memory through the process of memory trace reactivation, ultimately leading to a transformed and strengthened memory that is associated with improved performance.

Various studies (Maquet et al., 2000; for a review, see; Smith, Aubrey et al., 2004) that utilized tasks with a motor procedural component have reported increases in REM sleep following motor procedural learning. However, and importantly, these studies employed tasks that involve both a motor component, *as well as a cognitively complex component*, which requires the acquisition of a new rule or strategy to improve on the task, which is REM-dependent. Human studies have revealed that REM sleep is necessary for the consolidation of newly acquired procedural memories that have an underlying cognitive strategy (for reviews, see; Rasch & Born, 2013; van den Berg, Benoit, et al., 2019), with Rapid EMs during REM sleep being an important marker of this process (Fogel, Smith, et al., 2007; Mandai et al., 1989; Smith, Nixon, et al., 2004; Smith & Lapp, 1991). Amongst the first studies to test the notion that REM sleep is important for the processing of new information was that of Zimmerman et al. (1970), where visual inversion was utilized, which involves complex psychomotor learning. He observed that subjects wearing inverting prisms during daytime experienced a significant increase in REM sleep during adjacent nights compared to pre and post experimental nights. Furthermore, it appears that learning is one of the few activities which can have enhancing effects on REM sleep while using visual inversion, which is also reflected in subsequent REM sleep dream activity (De Koninck et al., 1996; De Koninck & Prévost, 1991).

Further support for this notion comes from sleep deprivation (Karni et al., 1994; Lewin & Glaubman, 1975; Plihal & Born, 1999), behavioural (Buchegger et al., 1991; Buchegger & Meier-Koll, 1988; De Koninck & Prévost, 1991; Fogel et al., 2015; Mandai et al., 1989; Peters et al., 2007), and TMR studies (Guerrien et al., 1989; Smith & Weeden, 1990) that utilized tasks that were more cognitive in nature, reflecting novel rule/skill learning. Sleep deprivation studies have found that participants who consumed alcohol immediately before sleep (which suppresses REM sleep and Rapid EMs during REM sleep performed worse on the ToH after the period of sleep, compared to those who consumed alcohol early in the afternoon. Consuming alcohol early in the afternoon allowed time for the alcohol effects on REM sleep to dissipate before sleep. In addition, there was a reduction in the Rapid EMs themselves, and the number of minutes in REM in the first half of the night, suggesting that Rapid EMs may play a role in the off-line processing of memory (Smith & Smith, 2003).

Behavioural studies, including overnight EEG recordings, have observed post-learning increases in REM sleep following cognitive procedural learning on the mirror tracing and ToH tasks (Smith, Nixon et al., 2004). REM sleep duration was also increased following novel complex motor skill learning (Buchegger et al., 1991; Buchegger & Meier-Koll, 1988). In addition, increases in frontal delta activity during REM sleep (reflecting an increase in the intensity of the Rapid EMs) on a post-training night, immediately before the acquisition of the cognitive strategy required to solve the ToH have also been noted (Fogel et al., 2015). Lastly, TMR studies where auditory stimuli or odor cues are presented during training, and again during post-learning REM sleep, reveal an increase in post-sleep memory performance on cognitively complex problem-solving skills (Guerrien et al., 1989; Smith & Weeden, 1990). Together, these studies suggest that REM sleep plays a role in improving performance on cognitive procedural tasks. Interestingly, it has been recently shown that NREM sleep might "fine tune" existing skills previously enhanced by REM sleep (Fogel et al., 2015; Nielsen, Reilly, et al., 2015). More specifically, Fogel et al. (2015) utilized the Tower of Hanoi task to investigate 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.” Interestingly, on the night that subjects were 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. By contrast, on the night that subjects became experts on the task, they showed increased REM sleep duration and spindles became larger in terms of amplitude and duration during SWS. More importantly, when subjects were re-exposed to the task one-week later, 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 were observed. Thus, suggesting that REM and NREM sleep may be involved in distinct stages of consolidation for cognitively complex procedural skills.

1.7 Theories of Sleep and Memory Consolidation

A large body of accumulating evidence supports the notion that one of the primary functions of sleep is to support memory consolidation. Several theories have emerged to explain how sleep supports memory including the passive protection, dual-process, sequential, and the active systems consolidation hypotheses.

1.7.1 Passive Protection Hypothesis

The first formal study into the role of sleep in memory consolidation was conducted by Jenkins & Dallenbach. (1924). Their seminal research demonstrated two main findings: firstly, sleep provided only modest protection against memory deterioration, as participants displayed slightly better recall of words learned after sleep than after wake conditions, secondly, sleep, but not wake protected remembered words from future interference. This was the first study to establish that sleep acts by passively protecting newly acquired memories from interference that occurs during wake but does not actively consolidate memory. However, now, sleep is widely considered to play a rather active and vital role in the consolidation of memories (for reviews, see; Diekelmann et al., 2009; Rasch & Born, 2013). For example, (1) if learning takes place directly before sleep, rather than earlier in the day, post-sleep recall is improved (Gais et al., 2006; Payne et al., 2012); (2) if learning is hindered post-sleep, memories are still less likely to be forgotten, compared to if the interference, especially retroactive word pair interference, occurred before post-learning sleep (Ellenbogen et al., 2006, 2009).

1.7.2 Dual-Process Hypothesis

The Dual-Process Hypothesis assumes that different sleep stages support the consolidation of different types of memories (for a review, see; Fogel & Smith, 2011). Specifically, NREM sleep serves to support declarative memories, and REM sleep supports the consolidation of procedural memory (for reviews, see; Gais & Born, 2004; Peigneux et al., 2001; Smith, 2001). The following sections provide a more specific account of the most pertinent findings.

Post-learning changes in sleep architecture provide the most direct support for this hypothesis. For example, cognitively complex procedural learning on such tasks as The Tower of Hanoi (Brand et al., 2010; Fogel et al., 2015; Nielsen, Reilly, et al., 2015; Smith, 1995; Smith, Aubrey, et al., 2004), mirror tracing (Plihal & Born, 1997; for a review, see; Smith, Aubrey et al., 2004), the weather prediction task (Djonlagic et al., 2009) and the artificial grammar learning task (Batterink et al., 2014) have also implicated REM sleep in procedural memory consolidation. Thus, these studies provide evidence that REM sleep may play an important role in the consolidation in cognitively complex procedural learning.

In contrast, SWS has been implicated in memory consolidation for word-pair list memorization and paired-stimuli association (Plihal & Born, 1997; Yaroush et al., 1971). In addition, NREM2 sleep, particularly sleep spindles are related to declarative memory improvements (Clemens et al., 2005; Fogel, Nader, et al., 2007; Ruch et al., 2012; Schabus et al., 2004). Interestingly, Marshall et al. (2006) employed direct current brain stimulation to potentiate slow wave activity during SWS, which resulted in subsequent enhancement of word-pair memory recall. This enhancement was not observed on a procedural finger sequencing task, further emphasizing the importance of NREM sleep for declarative, but not procedural memory.

While the literature provides convincing support for the Dural-Process Model, recent work suggests this hypothesis may provide an oversimplified account of the nuanced relationship between sleep and memory consolidation. A more complex understanding beyond—NREM for Declarative, and REM sleep for procedural memory has begun to emerge. A more recent hypothesis, *The Active System Consolidation Hypothesis* cuts across these domains.

1.7.3 Sequential Hypothesis

The sequential hypothesis takes into consideration the importance of the cyclic alterations of NREM sleep and REM sleep for memory formation, with sleep stages serving complimentary functions (for a review, see; Rasch & Born, 2013). The sequential hypothesis posits that during SWS nonadaptive memories are weakened and adaptive responses are strengthened; during REM sleep the adaptive memories are then integrated and stored into pre-existing knowledge networks

(Ambrosini et al., 1992, 1995; Ambrosini & Giuditta, 2001; Giuditta et al., 1995; Langella et al., 1992).

Animal studies (Ambrosini et al., 1988, 1992, 1995) provide early seminal support for this theory. For example, Langella et al. (1992) reported high positive correlations between the number of SWS periods followed by REM sleep with memory performance on a two-way active avoidance task. In contrast, the number of SWS periods, followed by wakening correlated negatively with performance providing indirect support for a weakening of memories during SWS if not followed by REM sleep. Interestingly, it was later suggested that SWS led to a global depotentiation of synaptic connections due to the slow EEG frequency. However, during subsequent REM sleep, the high-frequency EEG and hippocampal theta activity acted by supporting the strengthening of synaptic connections (Giuditta et al., 1995).

Additional support for the sequential hypothesis also comes from human research. Overnight improvement on a visual texture discrimination task was best predicted by the time in SWS in the first quarter, and the time in REM sleep in the last quarter of the night (Stickgold et al., 2000). Furthermore, disruption of the cyclic structure of a night of sleep impaired overnight retention of words, whereas the same degree of fragmentation did not impair word recall when the sleep cycles were preserved (Ficca et al., 2000). Interestingly, sleep-dependent consolidation of the texture discrimination task can also be accomplished in humans by brief (60-90 min) naps containing both SWS and REM sleep, providing evidence that a nap is as good as a night of sleep (Mednick et al., 2003). Thus, suggesting that there is a restorative phase that NREM sleep is initially responsible for, followed by the role of REM sleep to actively process and store memories. Although, the Sequential Hypothesis highlights the complexities of how sleep sequentially processes memories, more recent functional evidence suggests that while NREM and REM are complementary, they both have very distinctive and specific roles in consolidating both declarative and procedural memories.

1.7.4 Active Systems Consolidation Hypothesis

The Active System Consolidation Hypothesis proposes that sleep is actively involved in the overnight consolidation of newly acquired memories via memory replay and reactivation (for a review, see; Rasch & Born, 2013). This theory proposes that reactivations which occur during NREM sleep, potentiate memory representations, whereas REM sleep acts to integrate, or transform, acquired memories into a long-term storage system (i.e., actively, memory traces are transferred between short and long-term memory brain systems). Furthermore, the HPC is thought to be the primary structure in the immediate acquisition and short-term storage of memories (for reviews, see; Peigneux et al., 2001; Rasch & Born, 2013; Schwindel & McNaughton, 2011; Steriade & Timofeev, 2003), whereas the neocortex is where long-term memories are integrated and stored across existing distributed networks (Dudai et al., 2015; McClelland et al., 1995; Squire & Zola-Morgan, 1996; Takashima et al., 2009). Ample evidence supports this hypothesis, not only via sleep architecture (see Dual-Process Hypothesis), but also neuroanatomically through memory replay, and reactivation after post-learning sleep.

The active systems hypothesis further supports the notion that memories are selectively tagged for sleep-dependent consolidation based on factors such as emotional salience (Hu et al., 2006; Nishida et al., 2009), task difficulty (Kuriyama et al., 2004), motivation (Fischer & Born, 2009), self-relevance (Wilhelm et al., 2011), and how intentional encoding of the memory trace was (Robertson et al., 2004).

One of the primary mechanisms thought to promote consolidation in this hypothesis is through active replay within the hippocampus and the cortex (for a review, see; Dragoi, 2020). As mentioned previously, hippocampal sharp-wave ripples occur in phase together with NREM sleep spindles and SW up-states (Siapas & Wilson, 1998; Sirota et al., 2003), and are believed to reflect the HPC-neocortical dialogue involved in memory consolidation (Diekelmann & Born, 2010; Dudai et al., 2015; Siapas & Wilson, 1998). Across multiple studies, spindle activity has been associated with a wide array of sleep-dependent improvements in both declarative and procedural tasks (see sections 1.6.1 and 1.6.2), acting by selectively tagging important information for consolidation. In addition, SWA has also been implicated in memory reactivation and selection during the consolidation process (Wilhelm et al., 2011). In a study conducted by Rasch et al. (2007), an odor cue was presented during a card matching game and was re-presented during subsequent SWS or REM sleep. When the odor was presented during SWS, gains in post-sleep memory performance were observed. It was suggested that the cue further enhanced the underlying reactivation of the memory traces during sleep, which was not observed during REM sleep. Functionally, the same neuroanatomical regions that are activated when learning a task (*i.e.* putamen and HPC), are reactivated during post-learning sleep, time-locked to sleep spindles (Bergmann et al., 2012; Boutin et al., 2018; Fogel, Albouy, et al., 2017). Thus, suggesting that spindles are actively involved in memory consolidation via reactivation of the memory traces acquired during initial learning.

1.8 Aging, Sleep and Memory

Sleep changes dramatically throughout the lifespan. With aging, the neural oscillations of sleep provide insight into the physiological changes that accompany aging and help to explain functional changes in daytime performance, learning, and memory. As one ages, their sleep changes, and these changes impact the consolidation of memories during sleep. Thus, suggesting that as we age the benefit of sleep for memory consolidation is heavily compromised. The following sections will discuss the complex relationships between aging, memory and sleep, and finally, the interaction between sleep, memory, and aging.

1.8.1 Memory and Healthy Aging

As we age, there are well-known negative consequences in terms of memory deficits (Lupien, & Wan, 2004). Interestingly, the negative impact of age is not uniform across all domains of cognition. Interestingly, some aspects of memory are preserved, and some are even enhanced as aging progresses. In the following sections, I will discuss theories of aging and memory, followed by how aging affects cognition, both positively and negatively, and lastly discuss 'successful cognitive aging'.

In the last 50-years there has been a shift from early single-mechanism perspectives explaining memory to more multifactorial models to account for commonly observed age-related deficits in memory function (for a review, see; Park & Festini, 2017). These mechanistic theories of processing speed, limited resources, and inhibitory deficits are especially important constructs for understanding age-related memory decline.

Slowing Account

The initial theory on cognitive speed was developed by James Birren (Birren, 1965). According to the "slowing account", aging is accompanied by a general reduction in processing speed that in turn leads to a decline in a broad range of cognitive functions, including memory performance (Luo & Craik, 2008). Processing speed plays a critical role in many cognitive functions, and it is plausible that complex tasks involving multiple types of processing suffer more from slowing, showing greater age-related decline. There is consistent evidence showing that performance is slower on motor sequence learning tasks for older vs. younger adults (for a review, see; Voelcker-Rehage, 2008). However, this does not account for age-related changes in tasks that involve free recall, where speed is less involved (Luo & Craik, 2008). Overall, this hypothesis posits that cognitive performance is degraded when processing is slow because relevant operations cannot be efficiently executed in part because the products of early stages of information processing may no longer be available when later stages of information processing occur (Salthouse, 1996).

Limited Resources

The limited processing resources hypothesis proposes that the amount of attentional resources available for cognitive processing declines with age (Luo & Craik, 2008). As a consequence of reduced processing resources, older adults are less likely to carry out memory processes associated with good performance in the same way as younger adults (Salthouse, 1996). While there is much evidence to support this hypothesis (Craik, 2012), it has been criticized for the circularity of the theory, with no real evidence indicating processing resources are in fact independently exhausted (Light, 1988).

Inhibitory Deficits

Originally proposed by Lynn Hasher and Rose Zacks in 1988 (Hasher & Zacks, 1988), this hypothesis posits that older adults exhibit working memory deficits caused by less efficient inhibitory mechanisms. According to their view, inhibition serves two primary functions: preventing irrelevant information from entering working memory and removing no-longer relevant information from working memory. There is considerable support for this hypothesis from studies that show that older adults often have difficulty handling interference and distraction. Interference studies have shown that older adults are more vulnerable to interference for verbal working memory (Zeintl & Kliegl, 2010), visuospatial working memory (Cornoldi et al., 2007), implicit memory (Ikier et al., 2008), and paired-associated memory (Winocur & Moscovitch, 1983).

Aging Effects on Cognition and the Brain

The impact of age cognition is not uniform across domains. For example, Cognitive abilities and aptitudes that comprise Crystallized Intelligence, which refers to the ability to use and remember facts, figures, events, and places, tend to be preserved, and even continually improve as we age. Notably, vocabulary and general knowledge, tend to gradually improve at a rate of 0.02 to 0.003 standard deviations per year through the sixth and seventh decades of life (Salthouse, 2012). In contrast, Fluid Intelligence refers to abilities involving reasoning, problem-solving skills, the ability to employ logic and to identify complex patterns. Executive function, processing speed, memory, and psychomotor ability are a part of Fluid Intelligence. Notably, psychomotor and processing speed, peak in the third decade of life and then decline at an estimated rate of −0.02 standard deviations per year (Salthouse, 2012). Attention and short-term memory are other cognitive domains that displays a gradual decline later in life, specifically, selective and divided attention (Salthouse et al., 1995).

In terms of long-term memory, there are two major subtypes: declarative and procedural memory (see sections 1.51 & 1.52). Various aspects of declarative memory are not all uniformly impacted by age. Episodic memory shows a lifelong decline starting around the age of 30 (Park et al., 2002), while semantic memory shows a decline later in life (Rönnlund et al., 2005). Other aspects of declarative memory such as language abilities remain relatively intact with age, especially vocabulary. Visuospatial abilities remain intact as well, whereas concentration abilities decline with increasing age (Howieson et al., 1993). Lastly, executive functioning, including working memory and problem-solving abilities tend to see a decline with age (Hultsch et al., 1992; Nyberg et al., 2012).

Advancements in the field of neuroscience, via neuroimaging, have provided insight into the structural and functional brain changes that accompany the aging process that have implications for memory. Specifically, and discussed in more detail in Chapter 4, gray matter volume tends to decrease after the age of 20, specifically in the prefrontal cortex, possibly due to both reduction in neuron size and synaptic densities (Terry & Katzman, 2001) and in neuronal death, in general. In addition, there are white matter volume decreases noticed as well as one ages (Salat et al., 2006).

Reductions in brain volume and weight are the most significant changes that are observed with aging, with the decrease happening at a rate of around 5% per decade after 40 years of age (Peters, 2006). One study (Scahill et al., 2003) utilized two MRI scans separated by about one-two years, and found that the first area of the brain to display decreases in grey matter volume was the prefrontal cortex. The striatum was the next-most affected region, followed by the temporal lobe, cerebellar vermis, cerebellar hemispheres, and finally, the hippocampus. Interestingly, the striatum, frontal lobe and hippocampus are all critical structures that support higher-order cognitive functioning, and support several distinct, yet overlapping memory systems (see sections 1.5.1 & 1.5.2) (Peters, 2006; Raz et al., 2005).

However, some areas of the brain are generally spared in the aging process such as the entorhinal cortex, regions of the inferior frontal gyrus, and the primary visual cortex (Feng et al., 2020; Raz et al., 2005). The entorhinal cortex is responsible for information flowing in and out of the hippocampal formation (for a review, see; Garcia & Buffalo, 2020), which may suggest that aspects of encoding of information into the hippocampus may be spared by age. The inferior frontal gyrus is a key region for language comprehension and production (Ishkhanyan et al., 2020), which is consistent with preserved verbal abilities later in life. Lastly, the primary visual cortex receives, integrates, and processes visual information (Huff et al., 2023), suggesting the preservation of sensory visuo-spatial abilities. Taken together, this research suggests that brain regions which support certain aspects of memory visuospatial abilities, verbal abilities, language and semantic memory are relatively well-preserved with age as compared to other specialized brain areas such as the frontal lobe, hippocampus and striatum.

Successful Aging

This hypothesis posits that maintaining an active lifestyle and engaging in certain activities during one's life may help prevent age-associated cognitive decline and dementia (Harada et al., 2013). Older adults with preserved cognitive function participate in activities that include intellectually engaging activities (*i.e.* puzzles, discussion groups, board games, musical instruments), physical activities (*i.e.* exercise, gardening), and social engagements (Marioni et al., 2012). Lastly, the 'cognitive reserve' hypothesis posits that certain individuals have a greater ability to withstand pathologic changes to the brain due to sources of cognitive reserve that they can rely on to compensate for cognitive decline. Factors related to cognitive reserve include level of education, participation in intellectually and physically stimulating activities, sleep and higher socioeconomic status (for a review, see; Stern, 2002).

Overall, the aging process is associated with both negative and positive changes in terms of cognition. Participation in certain activities, building cognitive reserve, engaging in cognitive training, exercise and getting sufficient and good quality sleep may result in successful cognitive aging.

1.8.2 Sleep and Aging

With increasing age, complaints of difficulties initiating and maintaining sleep become common (for a review, see; Sergeeva et al., 2020). Moreover, the physiology of sleep, in terms of neural oscillations that characterize REM and NREM sleep is reduced or disorganized in older adults. Although sleep-related changes in aging populations are well documented, the neural mechanisms that underlie these changes are just starting to be uncovered.

Sleep is altered both at the micro (*e.g.*, quantity, and quality of sleep, and sleep oscillations), and the macro level (*e.g.*, sleep duration, and sleep stages). At the macro level, with increasing age, earlier bed and rise times are observed (Bliwise et al., 2005; Klerman & Dijk, 2008), it takes longer to fall asleep (*i.e.*, SOL) (Sergeeva et al., 2020), sleep fragmentation increases due to more frequent awakenings, arousals, and transitions into lighter stages of sleep. This is in part due to more fragile sleep and heightened sensitivity to external stimuli. A shorter overall sleep duration, with an increase in time spent in wake through the night, is observed. Furthermore, there is a reduction in the amount of time spent in SWS, and an increase is seen in time spent in lighter stages of sleep (NREM1 and NREM2), with shorter, and less frequent NREM-REM sleep cycles (for a review, see; Mander et al., 2017). In addition, older adults also engage more frequently in daytime naps (compared to younger adults), with 10% of adults aged 55-64, and 35% aged 75-84, reporting the occurrence of regular daytime naps (Foley et al., 2007). Importantly, Foley et al. (2007) found that 1 in 4 older adults report experiencing daytime fatigue interfering with day-to-day activities.

1.8.2.1 NREM1

The amount of time spent in NREM1 is significantly increased between young and middle-aged adults and between middle-aged and elderly individuals. A well-versed meta-analysis revealed that there is about a 5% increase in the time spent in NREM1 between the second and seventh decade of life (for a review, see; Ohayon et al., 2004). This increase in NREM1 stems from an increase in SOL to deeper stages of sleep, as well as a failure to maintain sleep with a significant increase in number of arousals throughout the night (Dijk et al., 2001; Mander et al., 2017). SOL has been shown to increase with age, increasing in the sixth decade of life and beyond (for a review, see; Ohayon et al., 2004). Importantly, the mean amount of time spent awake, after lights off, is nearly double for older adult participants (approximately 30 minutes) as compared to young adults (Ohayon et al., 2001). Furthermore, differences in SOL are in part associated with changes in circadian rhythms (for a review, see; Hofman & Swaab, 2006).

With increasing age, a greater number of arousals after sleep onset occur (for a review, see; Mander et al., 2017). Arousals are discrete bursts of synchronized alpha activity intruding lighter stages of sleep, specifically in NREM2 in older adults (Dijk et al., 2001), lasting longer than three seconds (Iber et al., 2007). Interestingly, Halász et al. (2004) characterized arousals into three types: (1) behavioral arousals, associated with movement, (2) cortical arousals, which is a shift in desynchronized EEG activity occurring independently of other behavioral, muscular, or autonomic events, and (3) subcortical arousals, EEG patterns that are associated with an autonomic event. The functional consequences of increased sleep fragmentation and arousal in older adults, include, but are not limited to; excessive daytime sleepiness, increased daytime naps (Foley et al., 2007), nocturnal insomnia (Gaillard, 1978; Ohayon et al., 2001), and cognitive decline (for a review, see; Crowley, 2011).

1.8.2.2 NREM2

As we age, NREM2 sleep increases in middle age and continues to increase into old age (for a review, see; Ohayon et al., 2004). Furthermore, with increasing age, the duration, amplitude, and density of spindles decrease, in contrast to spindle frequency, which has been shown to increase in older adults, which is consistent with an overall reduction of frontal slow frequency EEG that is observed with age (for reviews, see; Mander et al., 2017; Sergeeva et al., 2020). Interestingly, Nicolas et al. (2001) found that the consistency of spindles also changes with age, where the interval between spindles, and the duration of a series of spindles decreases. Fewer spindles with age may contribute to the fragmented sleep older adults face, as sleep spindles have been suggested to play a role in protection from external stimuli (for a review, see; Sergeeva et al., 2020).

K-complexes are another marker of NREM2 sleep and are also affected through the aging process, whereas K-complex density is practically half the amount for ages 50 and up, relative to adults 30 years and younger (Kubicki et al., 1989).

1.8.2.3 SWS

Decreased SWS is one of the most dramatic changes seen in older adults (ages 55 and up) (for reviews, see; Mander et al., 2017; Ohayon et al., 2004; Sergeeva et al., 2020). Interestingly, a meta-analytic study conducted by Ohayon et al. (2004) found that there is a 2% linear decrease in the amount of time individuals spend in SWS, and in SWA in general, per decade of increasing age. Furthermore, older adults tend to have smaller and less frequent slow waves compared to young adults (for a review, see; Sergeeva et al., 2020). Since older adults tend to take longer to fall asleep, it then takes considerably longer to enter the deeper stages of sleep, such as SWS.

1.8.2.4 REM

A meta-analytic review by Ohayon et al. (2004) reported a slight decrease (about 4%) of REM sleep in older adults compared to young, with the amount of REM sleep remaining fairly stable into late adulthood. Another prominent metanalytic study Floyd et al. (2007), reported that REM sleep tends to be stable until the 9th decade of life, where the amount of REM sleep drops off below 10% of the night. Even though it takes older adults much longer to fall asleep, latency to their first REM period displays only a small decrease across adulthood (for a review, see; Ohayon et al., 2004). Interestingly, from middle age to old age, signal irregularity increases, which indicates a change in spectral power favoring faster activity with increasing age, as faster frequency EEG is associated with a more “active/busy brain,” resembling more wake-like information processing (Bruce et al., 2009).

1.9 The Impact of Aging on Sleep and Memory

Depending on the explicit or implicit nature of learning, sleep-related consolidation of motor skills differs for procedural memory in older adults (for a review, see; Song, 2009). Explicit learning refers to the learner’s conscious and purposeful attempt to solve a problem, whereas implicit learning involves acquiring new skills and knowledge without conscious awareness to solve a problem. Through the use of the serial reaction time test, Spencer et al. (2007) had both young and older adults perform the task and were reassessed again after a 12-hour interval with either a period of sleep or wakefulness. Older and young adults showed similar degrees of initial learning. However, performance in older adults did not improve following sleep, indicating that sleep-dependent consolidation is impaired with age. This study was then replicated by Wilson et al. (2012), where they also reported reduced sleep-dependent changes in performance in older adults. As such, the benefit of sleep for memory consolidation appears to be lost in older adults.

Sequence learning is intact in older subjects for cognitively simple skills (for a review, see; King et al., 2013), and cognitively complex procedural skills, although the execution of individual movements is slower overall (Fogel, Albouy, Vien, et al., 2014). However, older adults seem to benefit less from retention intervals between learning sessions compared to younger adults, suggesting age-related deficits in latent learning processes (Raz et al., 2000; Wright & Payne, 1985). Remarkably, when age-realted changes in REM sleep are normalized pharmacologically by administering an acetylcholinesterase inhibitor, cognitive procedural memory consolidation in older adults is improved (Hornung et al., 2007). Thus, suggesting that age-realted changes in sleep may result in a reduced benefit to memory consolidation for cognitively complex procedural tasks.

As previously mentioned, age-related reduction in spindles and SWA may explain age-related and sleep-dependent deficits in memory consolidation and may serve as novel biomarkers for the age-related changes in cognitive procedural memory (the focus of Study 1). Neuroimaging studies provide additional support for this notion. Recently, Fogel et al. (2014) found that reduced spindles in older populations are associated with a reduction of the spindle-related overnight changes in activity in brain structures that are important for skill learning, e.g., the putamen and cerebellum for young, and only the cerebellum in older adults. This research suggested that spindle-related sleep-dependent increases in activity in structures such as the putamen appear to be needed for offline improvements in a motor skilled task, for which older adults do not derive the same benefit due to aged-related decline in sleep spindles. This study found that a daytime nap was detrimental to offline gains in performance in older adults. Importantly, this study utilized a simple motor sequence learning task, whereas the same analysis using a cognitively complex learning task is yet to be done (the focus of Study 2).

In addition, memory-related areas of the brain, such as the frontal cortex undergo substantial structural and functional alterations (Kalpouzos et al., 2009). Gray matter neurodegeneration is related to both age-related changes in sleep, and age-related changes in memory, including memory for problem-solving skills. Age-related changes in sleep might mediate cognitive decline due to neurodegenerative processes (Fogel, Vien et al. (2017). However, this study only investigated the impact of age-related changes in sleep on cognitively simple motor procedural skills. It remains to be investigated if sleep is similarly related to neurodegeneration of grey matter which underlies age-related changes in the consolidation of newly learned cognitive strategies required for problem-solving (the focus of Study 3).

To date, there have been no studies formally investigating sleep-related impairment in complex problem-solving skills with age, despite studies demonstrating that age-related changes in sleep have a negative impact on other types of memory (e.g., simple procedural and declarative memory). This obvious knowledge gap warrants formal scientific investigation. The main objective of this thesis is to investigate the functional, structural, and electrophysiological consequences and neurobiological mechanisms of age-related changes in sleep for cognitive procedural memory.

1.10 Focus of this thesis

Sleep plays a critical role in facilitating insight into the solution of a problem (Beijamini et al., 2014; Brand et al., 2010; Cai et al., 2009; Durrant et al., 2011; Fogel et al., 2015; Lewis et al., 2018; Monaghan et al., 2015; Perdomo et al., 2018; Sio et al., 2013; Stickgold & Walker, 2004; van den Berg, Al-Kuwatli, et al., 2019; van den Berg et al., 2021; Wagner et al., 2004). There is ample evidence providing support that memory for rule learning, and novel cognitive strategies are consolidated during sleep (Fogel, Smith, et al., 2007; Fogel et al., 2015; Mandai et al., 1989; Nielsen, O'Reilly, et al., 2015; Plihal & Born, 1997; Smith, 1995; Smith & Smith, 2003, 2001; Smith & Weeden, 1990; Smith & Wong, 1991; van den Berg, Al-Kuwatli et al., 2019, van den Berg et al., 2021). One such task that requires the acquisition of a novel strategy to solve the problem is the Tower of Hanoi (ToH). The ToH requires motor movements while following several rules which constrain the movements, necessitating a strategy (recursive logic) to be employed to reach the goal. It is a task commonly used to assess planning skills and related trait-like abilities. Neuroimaging studies have revealed that performance on this and related tasks engage the caudate nucleus (Dagher et al., 1999d; Doyon et al., 1996; Owen et al., 1996; Stocco

& Anderson, 2008; Unterrainer & Owen, 2006; van den Berg et al., 2021; Van Den Heuvel et al., 2003).

Optimal consolidation on these tasks is dependent on sleep. Evidence for this comes from several sources: 1) Sleep deprivation studies have shown that overnight improvement in performance on complex learning tasks is impaired following selective REM sleep deprivation (Plihal & Born, 1997), and following reduced REM density due to alcohol consumption on a post-training night of sleep (Smith & Smith, 2003); 2) TMR studies have shown that when a stimulus is presented during acquisition of a cognitive procedural task, and is presented again during post-learning REM sleep, next-day performance is enhanced (Guerrien et al., 1989; Smith & Weeden, 1990); 3) Sleep recording studies have shown that post-learning REM density is increased and correlated with improved performance (Smith, Nixon et al., 2004). Importantly, recent results show that both REM and NREM sleep play a role in the realization of the optimal strategy required to solve these challenging cognitive tasks (Fogel et al., 2015; Nielsen, Reilly, et al., 2015); and lastly, 4) By comparing consolidation intervals of sleep vs. wake.

Data from a recent study from our group shows that the series of movements which require knowledge of the underlying cognitive strategy (e.g., non-recursive moves) were preferentially enhanced following sleep vs. an equivalent period of wake, but not movements learned by simply repeating the series of movements (e.g., recursive moves) (van den Berg, Al-Kuwatli, et al., 2019). This provides compelling evidence that sleep is involved in the consolidation and enhancement of the cognitive strategy per se, over-and-above the consolidation of the series of motor movements needed to execute the ToH. After establishing that sleep preferentially benefits strategy and problem-solving skills over the accompanying motor execution movements, it remained unclear how acquiring new strategies benefits from sleep. In an even more recent study by our group (van den Berg et al., 2021), participants ages 20-35 performed the ToH task, while undergoing fMRI before and after an interval of either a full night sleep, a daytime nap, or wakefulness. The same participants also performed a motor control task, which precluded the opportunity to learn the strategy, with the objective being to subtract motor execution-related brain activations from activations specific to the strategy. Behaviorally, the sleep and nap groups experienced greater performance improvements compared to the wake group on the strategy-based task. Following sleep, enhanced activation of the caudate in addition to other regions in the hippocampal-striatal-cortical network were observed, compared to wakefulness. This study demonstrated for the first time that sleep is a privileged time to enhance newly acquired cognitive strategies needed to solve problems. However, evidence suggests that problem-solving skills are compromised as we age, impacting cognitive function and quality of life (Ronnlund et al., 2001; Rönnlund et al., 2007). As such, the overarching aim of this thesis is to investigate how the benefit that sleep affords to problem-solving skills is impacted by aging, and to identify the sleep-specific EEG markers of this deficit.

To date, we do not know the full extent, and how the process of age-related changes in sleep impact cognitively complex procedural memory. This thesis will, for the first time: 1) disentangle the role that sleep plays in novel problem-solving skills *vs*. motor skill acquisition in young vs. older adults, and 2) elucidate the neural, structural, and electrophysiological correlates of sleep-dependent memory consolidation for newly acquired cognitive strategies in young vs. older adults. This will advance our understanding of the physiological processes that support strategy-related skill learning and abilities, and how changes to sleep with age impact memory. Using an innovative combination of EEG, MRI, and behavioral testing, this series of studies will investigate how sleep supports memory consolidation for cognitively complex procedural memory, and how this benefit of sleep is reduced with age. Furthermore, this research will lead to the identification of novel physiological markers of the reduced benefit of sleep for memory consolidation with age.

1.11 General Hypotheses

1.11.1 Study 1

The main aim of Study 1 was to investigate the impact of age and the age-related reduction of SW-SP coupling on the consolidation of problem-solving skills. We hypothesized that: 1) SW-SP co-occurrence will be reduced in older *vs*. young adults, and will be less tightly coupled, especially during the upstate. In addition, 2) following the acquisition of a novel cognitive strategy decreased SW-SP coupling will be observed in older *vs*. young adults, and 3) the change in SW-SP coupling parameters from control to post-learning sleep will be differentially correlated with sleep-related behavioral gains in performance in young *vs*. adults.

1.11.2 Study 2

The main aim of Study 2 was to investigate the neuroanatomical functional consequences of age-related differences in sleep for the acquisition of problem-solving skills. We hypothesized that: 1) older adults will derive a reduced benefit of sleep for problem-solving skills relative to young adults. Furthermore, 2) following a period of sleep, older adults will have a reduced change in cerebral activation as compared to young adults in brain regions known to support problem-solving skills (e.g., the prefrontal cortex, hippocampus and caudate). Finally, 3) the sleep-related enhancements in memory trace consolidation will be correlated with sleep-related behavioral improvements in young, but not older adults.

1.11.3 Study 3

The main aim of Study 3 was to investigate how age-related changes in sleep and memory are related to neurodegeneration of grey matter in brain areas involved in the consolidation of problem-solving skills. We hypothesized that: 1) there will be grey matter differences in specific brain structures that support strategy learning in young compared to older adults (e.g., hippocampus, prefrontal regions, and the caudate), and, 2) grey matter density in brain structures that support problem-solving will be correlated to a different extent in young *vs*. older adults with both i) offline changes in performance for a newly acquired cognitive strategy, and, ii) spindle/slow wave characteristics.

1.12 Introduction References

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Chapter 2

Study 1: Spindle-slow wave coupling and problem-solving skills: Impact of age

2.1 Title Page

Spindle-slow wave coupling and problem-solving skills: Impact of age

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Keywords: sleep, aging, EEG, sleep, cognition slow waves, sleep spindles, NREM, procedural memory, coupling

2.2 Abstract

We investigated the electrophysiological consequences of age-related changes in sleep for acquiring novel cognitive strategies to solve problems. Twenty healthy young adults (20-35 years) and fifteen healthy older adults (60-85 years) were assigned to either nap or wake conditions. Participants were trained on the Tower of Hanoi in the AM, followed by either a 90-minute nap opportunity or period of wakefulness after which they were retested. The coupled interaction between slow-waves (SW) and sleep spindles (SP) during NREM sleep was examined as a function of age in relation to memory consolidation of problem-solving skills. We found that despite intact learning, older adults derived a reduced benefit of sleep for problem-solving skills relative to younger adults. As expected, the percentage of coupled spindles was lower in older compared to younger individuals from control to testing sessions both in general, and when limited to the upstate SW interval. Furthermore, coupled spindles in young adults were more tightly coupled to the slow-wave upstate compared to older individuals. In addition, older individuals had fewer coupled spindles, that were smaller compared to the young group. Lastly, there was a significant relationship between offline gains in accuracy and coupled spindle percent change during the upstate in older, but not younger adults. Multiple regression revealed that age accounted for differences in offline gains in accuracy, as did spindle coupling during the upstate. Thus, with age, coupling is reduced, but whatever coupling remains is a marker of the extent to which an individual will benefit from sleep in terms of offline consolidation for problem-solving skills.

2.3 Introduction

Good sleep has been linked to healthy cognitive aging (Hurd & Ralph, 1998; Scullin & Bliwise, 2015; Tufik et al., 2009). However, as we age, the quantity and quality of sleep are significantly reduced, impacting sleep-dependent memory processes. More specifically, recent studies suggest that the age-related changes in spindles and slow waves are associated with a reduced benefit of sleep for memory consolidation (Fogel et al., 2014; Mander et al., 2015; Mander et al., 2013; Pace-Schott & Spencer, 2011; Spencer et al., 2007; Wilson et al., 2012).

One of the most dramatic age-related changes to sleep is a the reduction in sleep spindles (Carrier et al., 2001; Crowley et al., 2002; Wei et al., 1999). With increasing age, spindle density, duration and amplitude are significantly reduced (Feinberg, 1974; Martin et al., 2012; Peters et al., 2014). There is growing consensus that non-rapid eye movement (NREM) sleep (Ackermann & Rasch, 2014), and spindles in particular, are necessary for the optimal consolidation of procedural memory (Barakat et al., 2012, 2013; Fogel, Smith, et al., 2007; Fogel & Smith, 2011, 2006; Milner et al., 2006; Morin et al., 2008; Nishida & Walker, 2007; Peters et al., 2007). The repeated and coherent firing pattern associated with spindles is thought to promote plastic changes underlying sleep-related memory consolidation (Dickey et al., 2021; Lindemann et al., 2016; Steriade & Timofeev, 2003).

In healthy young adults, sleep enhances the consolidation of newly acquired procedural skills (Born & Wagner, 2004; Fogel et al., 2007, 2015; Nielsen et al., 2015; Plihal & Born, 1997; Smith, 2003; Smith, 1995, 1996, 2001; Smith & Lapp, 1991; Smith & Weeden, 1990; Smith & Wong, 1991; van den Berg et al., 2019, 2021), which include problem-solving, rule-learning, procedures, habits, conditioned behaviours, and cognitive skills acquired through repeated practice (for a review see; (Rasch & Born, 2013). However, recent studies have found that older adults do not derive the same benefit from sleep for procedural memory consolidation as compared to young adults, despite a normal rate of initial learning (Brown et al., 2009; Fogel, Albouy, Vien, et al., 2014; Raz et al., 2000; Shea et al., 2006; Spencer et al., 2007; Toor et al., 2022; Wilson et al., 2012). Furthermore, learning-related increases in density, duration and amplitude of spindles are observed following intense periods of procedural motor skills learning, with the change in several of these spindle characteristics being correlated with offline gains in memory performance (Barakat et al., 2012, 2013; Fogel, Smith, et al., 2007; Fogel & Smith, 2006; Morin et al., 2008; Nishida & Walker, 2007; Peters et al., 2008). Two recent studies have shown that spindles may also be related to the consolidation of procedural skills that involve cognitively complex problem-solving (Fogel et al., 2015; Nielsen, Reilly, Carr, Dumel, Godin, Solomonova, Lara-Carrasco, O'Reilly, Carr, Dumel, Godin, Solomonova, Lara-Carrasco, Blanchette-Carrière, Paquette, O'Reilly, Carr, Dumel, Godin, Solomonova, Lara-Carrasco, Blanchette-Carrière, Paquette, et al., 2015), however, evidence is limited and it is not known how this relationship may be impacted by age. Taken together, these results suggest that the age-related reduction in spindles may underlie age-related deficits in procedural memory consolidation. However, much less is known about the role of spindles and slow waves for optimal consolidation of cognitively complex problem-solving skills, let alone the impact of age on this relationship.

In addition to age-related changes in spindles, slow waves are also dramatically reduced in older adults. This process begins as early as middle age (Bliwise, 1993; Blois et al., 1983; Cajochen et al., 2006; Carrier et al., 2001; Feinberg et al., 1967; Ohayon et al., 2004). Slow waves have two states: an "*up-state*" and a "*down-state*". Up-states consist of depolarization and increased neuronal firing, whereas down-states reflect hyperpolarization of the membrane potential and a reduction of neuronal firing (Landsness et al., 2009; Steriade, 2003). It is thought that during the up-states, reactivation strengthens newly formed memories (Diekelmann & Born, 2010; Göldi et al., 2019; Heib et al., 2013). As individuals age, the slope, amplitude, and density of slow waves are reduced (Bliwise, 1993; Carrier et al., 2011). In particular, older adults show decreased slow wave slope (Carrier et al., 2011; Feinberg & Campbell, 2003), and longer slow wave positive and negative phases compared to young adults (Carrier et al., 2011). These age-related differences suggest that cortical neurons take more time to synchronously enter SW depolarization and hyperpolarization phases, which is further impacted by microstructural degradation of specific cortical regions (Dubé et al., 2015); presumably impacting memory consolidation. Thus, age-related changes in spindles and slow waves may serve as electrophysiological markers of the earliest indicators of age-related cognitive decline, and the associated neurodegeneration.

More recently, the temporally coupled interaction between slow-waves and spindles during NREM sleep has been proposed to support memory consolidation (Helfrich et al., 2018; Muehlroth et al., 2019). Temporal interactions between slow waves, spindles, and hippocampal ripples are temporally coupled in a hierarchy that is hypothesized to facilitate information transformation between the hippocampus and neocortex (Clemens et al., 2007; Diekelmann & Born, 2010; Frankland & Bontempi, 2005; Helfrich et al., 2018; Latchoumane et al., 2017; Rasch & Born, 2013; Staresina et al., 2015; Steriade, 2006). Specifically, the depolarizing up-states of slow waves are proposed to group spindle and ripple events, with hippocampal ripples being temporally nested within spindle troughs (Rasch & Born, 2013; Staresina et al., 2015). Recently, Helfrich et al. (2018) revealed that slow wave - spindle (SW-SP) coupling was expressed in older adults similar to younger adults, but at an earlier phase. Thus, the mechanism that couples spindles and slow waves is impacted by age, whereby spindles systematically arrive prematurely in the SW cycle. In other words, the aging brain becomes increasingly "uncoupled" in terms of SP-SW complexes

(Helfrich et al., 2018; Muehlroth et al., 2019). Interestingly, Solano et al. (2020) found that motor learning modulated SW-SP coupling, and the extent of this modulation predicted long-term memory consolidation. However, most of the research to-date has focused on declarative memory and procedural motor skills. The current study examines these effects on procedural memory, particularly for cognitively complex problem-solving skills. The effect of age on the relationship between problem-solving skills and SW-SP coupling remains to be investigated.

Here, we investigated the impact of age on SW-SP coupling for the consolidation of novel cognitive strategies required to solve problems. We hypothesized that: 1) sleep-related behavioral improvements will be observed in younger, but not older adults, 2) SW-SP co-occurrence will be reduced in older *vs*. younger adults, and will be less tightly coupled, especially during the upstate, 3) following the acquisition of a novel cognitive strategy, increased SW-SP coupling will be observed in young *vs*. older adults, and, 4) the change in SW-SP coupling parameters from control to post-learning sleep will be differentially correlated with sleep-related behavioral gains in performance in young *vs*. adults.

2.4 Methods

2.4.1 Ethics Statement

This research was approved by the University of Ottawa's Research Ethics Board, as well as the Research Ethics Board at The Royal's Institute of Mental Health Research. All participants provided written informed consent prior to participation and were financially compensated for their participation.

2.4.2 Participants

All eligible participants described themselves as in good health with regular sleep schedules (normally between the hours of 10:00PM and 9:00AM). Eligible participants were right-handed, non-shift workers, did not take medications known to interfere with sleep, had normal or corrected-to-normal vision, a body mass index <30, were free from chronic pain, seizures, and had no previous head injury or any hand mobility problems. Participants were excluded if they had previous experience with the Tower of Hanoi (ToH), or similar puzzles/tasks. To be included in the study, all participants had to score <10 on the Beck Depression (Beck & Beamesderfer, 1974), and Beck Anxiety (Beck, Steer, et al., 1988) Inventories, in addition to having no signs of sleep disorders indicated by the Sleep Disorders Questionnaire (Douglass et al., 1994). To rule out signs of mild cognitive impairment or dementia, older participants were required to score ≥ 26 on the Montreal Cognitive Assessment (Nasreddine et al., 2005) and < 2 on the Everyday Cognition Scale (Tomaszewski et al., 2008).

To be included, all participants, who did not normally consume an excess of caffeinated or alcoholic beverages, were required to limit caffeine intake (no more than one beverage in the AM) and abstain from alcohol consumption during the experiment. To ensure compliance with the study protocol, participants were required to wear a Motionlogger actigraph (Ambulatory Monitoring Inc., Ardsley, NY, U.S.A) for the duration of the study, a wrist-worn accelerometer which measures sleep-wake-related limb movements. Participants were also asked to complete a log of their daily activities and sleep habits, keep a regular sleep-wake cycle (usual bedtime between: 22:00 h – 01:00 h, usual wake-time between: 06:00 h – 09:00 h), and abstain from daytime naps. Participants were excluded from the study if the actigraphy or sleep log indicated non-compliance with the study protocol.

In addition, all participants underwent an acclimatization and screening polysomnographic (PSG) recording to ensure they were able to sleep in the lab during a daytime nap opportunity. This PSG was also used to rule out signs of sleep disorders. The PSG recording followed AASM guidelines (Iber et al., 2007), and took place at least one week prior to the experimental session (see "*Polysomnographic Recording and Analysis*" section for details). To be included in the final sample, a sleep efficiency > 80%, a periodic limb movement (PLM) index < 10 events/hour, and an apnea-hypoapnea index < 5 events/hour was required.

Seven older participants and five young participants did not meet the above inclusion criteria for keeping a regular sleep schedule within the prescribed hours. An additional three older participants and one young participant did not meet the PSG pre-screening criteria. The final sample consisted of 40 healthy young adults aged 20-35 (23 females; M = 23.9, SD = 3.9 years old), and 30 healthy older adults aged 60-85 (20 females; M = 68.0, SD = 7.6 years old). N=20 young participants in the sleep (nap) condition (YN), N=20 young participants in the wake (no-nap) condition (YNN), N = 15 older participants in the sleep (nap) condition (ON), and, N = 15 older participants in the wake (no-nap) condition (ONN) were included in the analyses.

These data were part of a larger polysomnographic, behavioral, and MRI protocol employing various techniques intended to address a variety of research questions. The behavioral results have been partly reported previously (Toor et al., 2022; van den Berg, Al-Kuwatli, et al., 2019). These previous studies investigated functional brain activity and structural differences in relation to sleep and memory, whereas the current study is focused on the electrophysiological correlates of memory consolidation, which have not been reported elsewhere, and are unique to this study. See Toor et al. (2022) for additional details about the experimental protocol, specific to that study. All methods relevant to the current investigation are reported here.

2.4.3 Experimental Design

Following acclimatization/screening, participants were randomly divided into four groups: young nap (YN), young no-nap (YNN), older nap (ON), and older no-nap (ONN). All participants completed both a testing and control session (Figure 1), on which they were asked to arrive at the sleep laboratory at 09:00h. Beginning at 10:00h, participants completed either the training and testing sessions for the ToH task (on the testing day), or the control (CTRL) task (on the control day), in counterbalanced order across participants. Beginning at 13:00h, participants either had a 90-minute daytime nap opportunity, or remained awake. PSG recordings were taken during both nap and no-nap sessions. To ensure a minimum amount of data necessary for data analyses, participants were required to have at least 5 min of uninterrupted sleep during the nap opportunity. The retest session took place at 17:00h, more than 30 min following the nap to avoid sleep inertia effects.

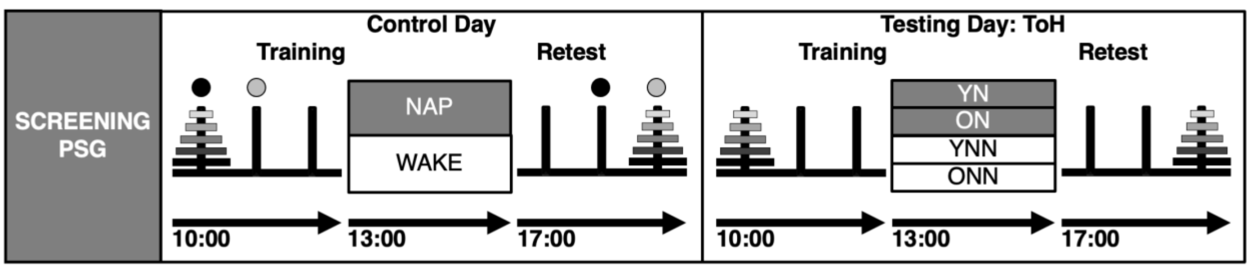

Figure 1. Study Design. Overview of experimental protocol. Acclimatization & screening: All participants underwent an initial acclimatization and screening polysomnographic (PSG) recording. Following this, each group (young nap (YN), young no-nap (YNN), older nap (ON), older no-nap (ONN)) underwent both a testing and a control day. Testing Day: Participants arrived at the lab at 09:00h. Beginning at 10:00h, participants completed the Tower of Hanoi (ToH) task. Those in the Nap condition then slept in the laboratory from 13:00h to 14:30h. Those in the Wake condition remained awake. Following this, all participants were retested on the ToH task at 17:00h. In addition, participants completed the Stanford Sleepiness Scale (SSS) and Psychomotor

Vigilance Test (PVT) before and after each session. Control Day: The same procedure was used, except there was no learning possible with the CTRL version of the ToH task.

2.5 Behavioral Measures and Analyses

Using the Psychophysics Toolbox extension v3.0.12 (Brainard, 1997; Kleiner et al., 2007) for Windows (Microsoft, Redmond, WA, USA) and coded in MATLAB R2016a (Mathworks Inc., Natick, MA, USA), two computerized versions of the ToH task were employed: (1) the "classic" Tower of Hanoi task, and (2) a control task version where learning the strategy was not possible.

2.5.1 Tower of Hanoi Task

The ToH consisted of 5 disks, with disks stacked in a starting position of increasing size. The disks could be moved to and from one of three pegs by pressing the corresponding keys on the keypad. The main objective of the task was to move all disks from the beginning position (far-left peg) to the final position (far-right peg) so that they were stacked in ascending order. Participants completed the task with the following constraints: 1) only one disk could be moved at a time, 2) only the upper-most disk on a peg could be moved, and, 3) only a smaller disk could be placed on top of a larger disk. The optimal number of moves to complete the ToH is 31 for the 5-disk solution, which is determined algebraically by $2^N - 1$, *where N is the number of disks*. A response button box (model HHSC-2x4-C; Current Designs Inc., Philadelphia PA, USA) comprised of three equally spaced buttons in a horizontal row was used to control the task. To move a disk from one peg to another, participants first pressed the key corresponding to the peg of the disk to be moved, and then, pressed the key corresponding to the peg of the goal location.

Participants performed eight training trials and four retest trials of the ToH, where each trial was followed by a 20-second rest period. A trial of the ToH task could end in two ways, either: 1) all five disks were stacked in ascending order on the far-right peg, or, 2) the maximum number of moves (two times the optimal number of moves = 62) was reached before successful completion of the task.

ToH performance was measured in terms of speed (time to complete each ToH trial) and accuracy (Mean Absolute Percentage Error; MAPE). The MAPE can be interpreted as the percentage of perfect performance (*e.g.*, 31 moves), whereby 100% represents perfect performance (*i.e.*, the optimal solution), and 0% theoretically represents an infinite number of moves. The MAPE for *n* observations is calculated as follows:

$$\text{MAPE} = \left(\frac{1}{\text{n}}\right) * \sum \left| \frac{\text{number of moves} - \text{ optimal number of moves}}{\text{number of moves}} \right| * 100$$

The % improvement for all measures, both speed and accuracy was calculated by taking the first retest trial minus the last training trial, divided by the last training trial multiplied by 100, to assess performance improvements from training to retest.

2.5.2 Control Task

The control (CTRL) task was visually identical to the Tower of Hanoi task, including sensorimotor, spatial, and visual aspects of the task, *except* participants were guided through a series of cued, random moves, thus making learning the underlying strategy impossible. Green and red dots would appear above the disk to be moved and the goal peg, respectively, indicating to the participant which buttons on the keypad to press and in which sequence. A trial was considered complete after 31 guided moves, corresponding to the minimum number of moves it takes to complete the 5-disk ToH task. Participants performed four trials of the CTRL task, where each trial was followed by a 20-second rest period.

2.5.3 Behavioural Analysis

The behavioral analyses were completed using SPSS Statistics software version 27 (IBM, Armonk, New York, U.S.). To ensure learning did take place on the ToH task in both young and older groups of participants, age (Young, Older) x training/testing block (blocks 1 to 8) 2x8 ANOVAs were conducted for speed and accuracy. Simple effects repeated measures ANOVAs were used to follow-up any significant effects.

Age (Young, Older) x sleep/wake condition (Nap, Wake) 2x2 ANOVAs were conducted for % change in speed and accuracy to explore whether sleep facilitated performance on the ToH task in young and older groups. Independent samples t-tests were then used to follow-up any significant group effects.

2.6 Polysomnographic Recording Parameters

In-laboratory PSG was recorded using Embla N7000 amplifer systems (Natus, Pleasonton, CA, USA), sampled at 500 Hz. EEG (Fp1, Fpz, Fp2, F3, Fz, F4, C3, Cz, C4, P3, Pz, P4, Oz, A1, A2) and EOG (placed on the left and right outer canthus of the eyes) was referenced online to Fpz. EEG and EOG were placed according to the international 10-20 system (Jasper, 1958). In addition, submental EMG channels were recorded as a bipolar derivation. During the initial screening PSG recording, a nasal/oral thermistor, respiratory effort belts, and leg EMG electrodes were also used to screen for signs of sleep apnea, restless leg syndrome, and other parasomnias.

2.6.1 Polysomnographic Data Analysis

Manual sleep stage scoring, according to standard criteria (Iber et al., 2007) was completed by a single expert registered polysomnographic technologist, using the "Counting Sheep PSG" toolbox (https://github.com/stuartfogel/CountingSheepPSG) for EEGlab (Delorme & Makeig, 2004). EEG and EOG were re-referenced offline to average mastoid derivations (A1 and A2). EEG was filtered from 0.3 to 35 Hz, EOG was filtered from 0.3 to 10 Hz and EMG was filtered from 10 to 100 Hz.

2.6.2 Sleep Spindle Detection

Sleep spindles were automatically detected from Fz, Cz, and Pz during movement artifact-free NREM Stage 2 (NREM2) and slow wave (SWS) using an established (Albouy et al., 2015; Fogel, Albouy, Vien, et al., 2014) and validated (Ray et al., 2015) method employing EEGlab-compatible (Delorme & Makeig, 2004) software (https://github.com/stuartfogel/detect_spindles) written for MATLAB R2019b (The MathWorks Inc.). Detailed processing steps, procedures, and validation are reported elsewhere (Ray et al., 2015). Briefly, the spindle data were extracted from movement artifact-free, NREM epochs. The detection method (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 (*i.e.*, 11–16 Hz). The method employs an adaptive amplitude threshold at the 99th percentile on the transformed signal. Following automatic detection, detected spindles were visually verified by a single expert scorer. The variables of interest extracted from this method include spindle number, size (area under the curve), and density (number of spindles/minute of NREM sleep), for each participant (Supplemental Table S1). From the spindle data, the onset of and latency of the peak for each spindle event was extracted.

2.6.3 Slow Wave Detection

Slow waves were automatically detected from Fz, Cz and Pz during movement artifact-free NREM sleep (NREM2 and SWS) via a period amplitude analysis detection algorithm (https://github.com/stuartfogel/Period-Amplitude-Analysis) similar to that previously described (Bersagliere & Achermann, 2010), adapted for EEGlab (Delorme & Makeig, 2004) and written for MATLAB R2019b (The MathWorks Inc.). The detection method employs band-pass filtering to detect waves between 0.5-2.0 Hz. Derivations were band-pass filtered 0.46 Hz (64th-order Chebyshev type II high-pass filter, -80 dB stopband attenuation) and 2.15 Hz (32nd-order Chebyshev type II low-pass filter, -80 dB stopband attenuation) to achieve minimal attenuation in the band of interest (0.5–2.0 Hz) and good attenuation at neighboring frequencies. The filters were applied in the forward and reverse directions to achieve zero-phase distortion. Next, half-waves were determined as negative or positive deflections between two consecutive zero crossings in the band-pass filtered signal for frequencies between 0.5 and 2 Hz. Only consecutive half-waves with a peak-to-peak amplitude higher than 75 μV and longer than 0.25 seconds were considered for the analysis. The latency of the negative peak of each slow wave was extracted. Refer to (Supplemental Table 2) for details on SW characteristics.

2.6.4 Slow Wave-Spindle Coupling Analysis

Using the slow wave negative peak latencies and the spindle peak latencies from Fz, Cz, and Pz, we performed coupling detection procedures using the approach developed by (Mölle et al., 2011) employing EEGlab-compatible (Delorme & Makeig, 2004) software written for MATLAB R2019b (The MathWorks Inc.). Spindles were marked as coupled SW-SP complexes when the spindle onset occurred within a 4-second time window of the slow wave peak (i.e., to capture spindles within a full cycle of a 0.5 Hz SW, about either side of the peak). Alternately, spindles were marked as "uncoupled" when the spindle onset occurred outside the 4-second time window. Lag was measured as the distance between the slow wave negative peak and the spindle onset. The lag variance was then calculated as a measure of coupling strength. Paired sampled t-tests were used for the comparison of the SW-SP complexes occurrence, measured in time bins of 200ms along the 4 s window.

Additionally, the phase of the bandpass-filtered slow-wave signal in radians at the spindle onset location was computed. The mean direction of the phase angles for all coupled spindle events was determined using the CircStat toolbox (Berens, 2009). We computed the preferred phase of SW-SP coupling for each participant by averaging all individual events preferred phases. Then, we perform uniformity tests (Rayleigh test) and uniformity with a predefined mean direction (V-test). From the SW-SP coupling data, and in addition to a list of SW-SP and uncoupled spindle events for each recording, the spindle peak oscillatory frequency and lag for the SW-SP events were extracted.

2.7 Results

2.7.1 Behavioural data

2.7.1.1Training session

Mixed-design, age group (Young, Older) by training block (blocks 1-8) 2 x 8 ANOVAs for speed and accuracy were used to ensure that learning did take place during the training session in both young and older participants. A significant increase in speed over the course of the training session (F (7,476) = 36.71, $p < 0.0001$, $\eta^2 = 0.35$) was observed in both the young (F (7,273) = 35.17, $p < 0.0001$, $\eta^2 = 0.47$) and older (F (7,203) = 12.22, $p < 0.0001$, $\eta^2 = 0.30$) groups. There was no significant interaction with age (F (7,476) = 1.17, $p = 0.32$, $\eta^2 = 0.02$), suggesting that both young and older adults improved on the task and to the same extent (Figure 2). Similarly, a significant increase in accuracy over the course of the training session (F (7,476) = 5.70, $p < 0.0001$, $\eta^2 = 0.08$) was observed in the young (F (7,273) = 7.30, $p < 0.0001$, $\eta^2 = 0.16$), but not the older adults (F (7,203) = 1.41, $p = 0.202$, $\eta^2 = 0.05$), as their change in performance was flatter overall. However, there was no significant difference in accuracy between the young and older adults by the end of the training session (t (68) = 0.06, $p = 0.960$, $d = 0.01$), suggesting that, importantly, the young and older participants did learn the task to the same extent by the end of the training session (Figure 2).

2.7.1.2 Offline gains

Between groups, age group (Young, Older) by sleep condition (Nap, Wake) 2 x 2 ANOVAs were used to investigate the age and sleep-related changes in performance improvements across the consolidation period. This analysis revealed a significant interaction for % increase in speed (F (1,66) = 64.39, $p < 0.0001$, $\eta^2 = 0.49$) and accuracy (F (1,66) = 15.73, $p < 0.0001$, $\eta^2 = 0.19$). Follow-up tests revealed that the YN condition had significantly greater performance improvements than the YNN (speed: t (38) = 8.86, $p < 0.0001$, $d = 2.80$; accuracy: t (38) = 2.36, $p = 0.024$, $d = 0.75$) and ON groups (speed: t (33) = 12.13, $p < 0.0001$, $d = 4.14$; accuracy: t (33) = 4.54, $p < 0.0001$, $d = 1.55$). No difference was found between the YNN and ONN groups (speed: t (33) = -1.16, $p = 0.256$, $d = -0.40$; accuracy: t (33) = -0.57, $p = 0.573$, $d = -0.19$). However, the ONN group performed significantly better than the ON group (speed: t (28) = -2.87, $p = 0.008$, $d = -1.05$; accuracy: t (28) = -4.04, $p < 0.0001$, $d = -1.47$).

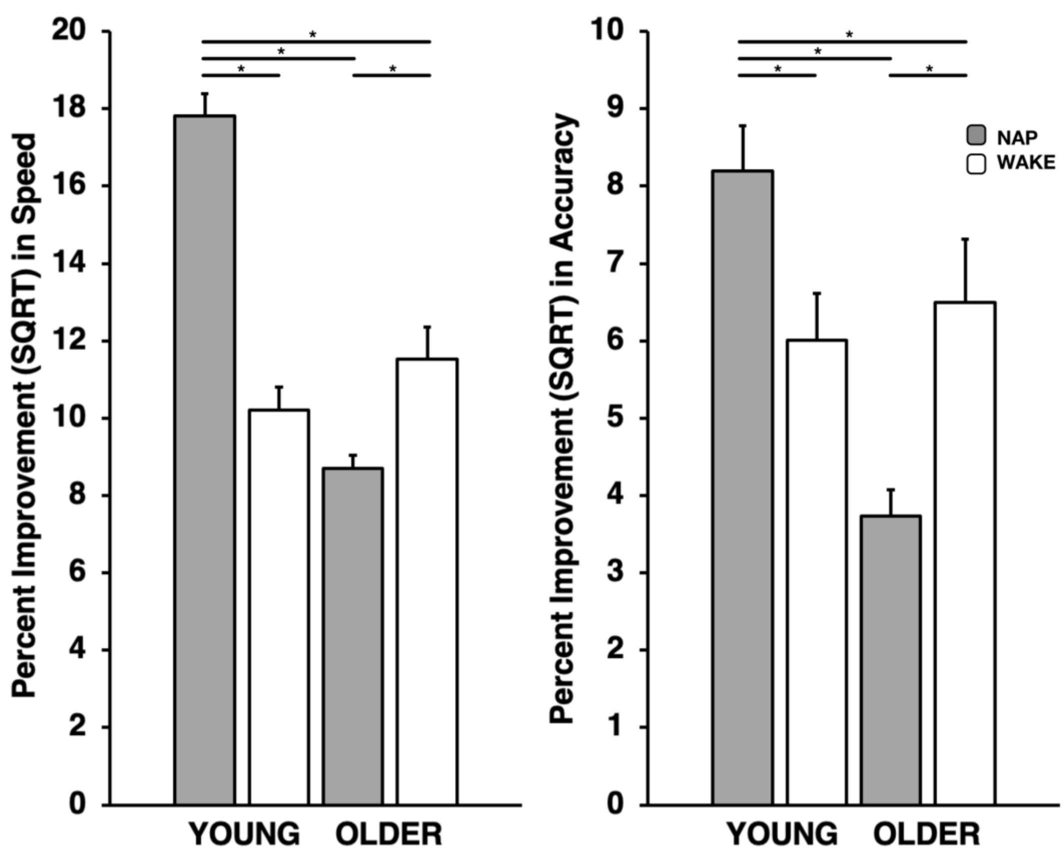

Figure 2. ToH performance. Mean percent improvement for speed and accuracy on the ToH from Training to Retest in young and older participants. Young adults benefited from a daytime nap as compared to wake, whereas older adults did not. Error bars represent standard error of the mean. Figure adapted from Toor, B.A., et al, (2022), *Neurobiology of Aging*, 116, p. 60.

2.7.2 Sleep Data

2.7.2.1 Sleep architecture

As expected, young and older participants differed in terms of sleep architecture characteristics (Table 1). Mixed-design, age group (Young, Older) by task condition (Control, ToH) 2 x 2 ANOVAs were used to investigate the age-related changes in sleep architecture from the control to the testing sessions in young *vs.* older adults. A significant group effect was observed for TST (F (1,66) = 8.30, $p < 0.007$, $\eta^2 = 0.20$). Young adults spent significantly more time asleep both at the control nap (t [33] = -2.65, p = 0.012, d = -0.91) and at the testing nap (t [33] = -2.53. p = 0.017, d = -0.86), relative to older adults. In addition, young participants spent significantly more time in SWS (t [30] = -2.29, p = 0.029, d = -0.82) at the testing nap compared to older adults. There were no significant condition by age group interactions observed.

Table 1. Sleep architecture for the control and testing sessions. Means (M) and standard deviations (SD) in minutes, for WASO, NREM1, NREM2, SWS, REM, and TST in young and older participants.

	Young		**Older**		**Young *vs*. Older**	
	M	***SD***	**M**	***SD***	***t***	***P***
Control						
WASO	15.02	14.58	17.57	10.28	0.58	0.569
NREM1	7.76	5.33	7.67	4.55	-0.05	0.958
NREM2	41.23	14.88	31.40	16.25	-1.86	0.072
SWS	12.15	17.15	13.15	13.85	-1.01	0.322
REM	10.57	6.59	15.25	10.96	0.86	0.409
TST	66.95	15.78	49.87	22.35	-2.65	*0.012
Testing						
WASO	13.21	12.85	12.17	13.27	0.13	0.898
NREM1	5.63	4.52	6.54	4.29	0.93	0.361
NREM2	36.92	12.76	38.50	18.78	-0.41	0.686
SWS	21.09	15.45	7.21	7.98	-2.29	*0.029
REM	8.23	4.79	6.75	3.89	-0.32	0.750
TST	68.79	13.62	53.38	24.79	-2.58	*0.017

Abbreviations: Wake after sleep onset (WASO), total sleep time (TST). * Indicates $p < 0.05$, corrected for heterogeneity of variance where appropriate.

2.7.2.2 Percentage Coupled SW-SP

Mixed-design, age group (Young, Older) by task condition (Control, ToH) 2 x 2 ANOVAs were used to investigate the change in the percentage of coupled spindles from control to testing sessions in young *vs.* older adults (Figure 3). There was no significant age group by task condition interaction ($F(1,63) = 0.245$, $p = 0.622$, $\eta^2 = 0.004$). There was a significant main effect of age for coupled spindles percentage ($F(1,63) = 35.26$, $p = > 0.001$, $\eta^2 = 0.370$) suggesting that older individuals had a lower percentage of coupled spindles compared to young. The same approach was used to investigate the change in the percentage of coupled spindles during the up-state interval (from 0 to 1 sec relative to SW negative peak). There was no significant age group by task condition interaction ($F(1,63) = 0.281$, $p = > 0.598$, $\eta^2 = 0.005$). There was a main effect of age ($F(1,63) = 30.95$, $p = > 0.001$, $\eta^2 = 0.340$) suggesting that older individuals had a lower percentage of coupled spindles during the SW up-state compared to young.

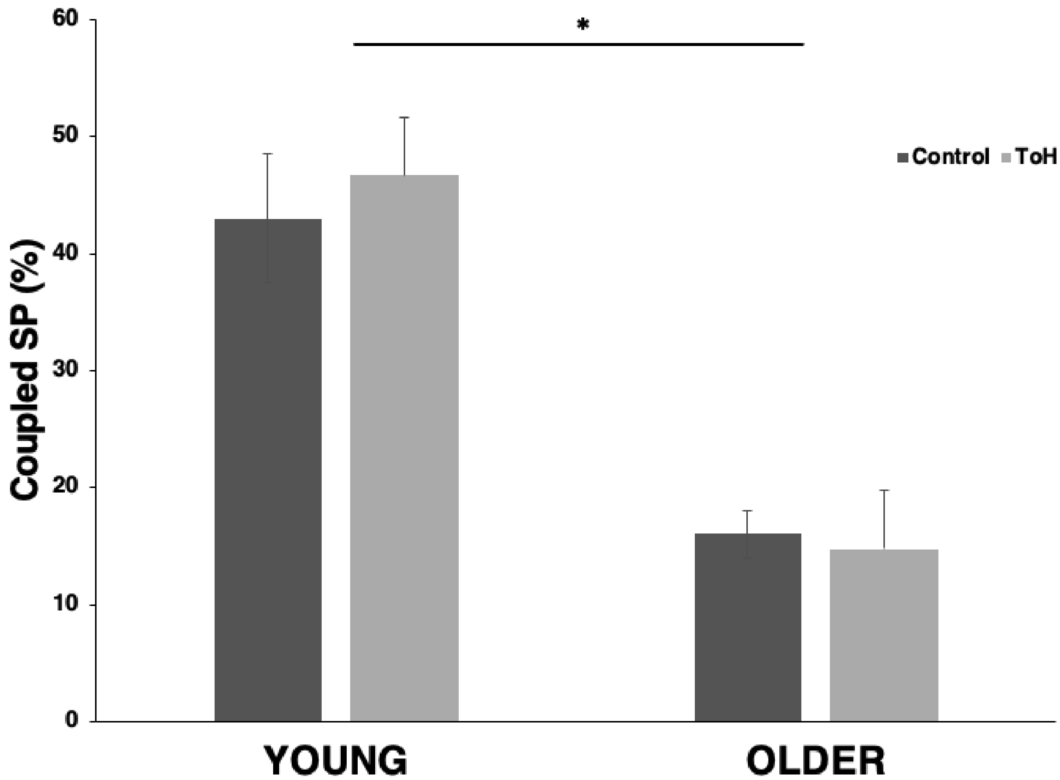

Figure 3. Percentage of coupled spindles for older and young participants during control and testing sessions. Each bar represents the number of coupled spindles divided by the total number of spindles. Coupling percentage was lower in older compared to young individuals both at control and testing sessions.

Next, to investigate the phase relationship between spindles and slow waves, the slow wave phase at the spindle maximum for each SW-SP event was extracted, and the mean phase angle was computed for each individual event. Mixed-design, age group (Young, Older) by task condition (Control, ToH) 2 x 2 ANOVAs were used to investigate the change in coupling strength measured as the mean vector length (MVL) from control to testing sessions in young *vs.* older adults. There was no significant age group by condition interaction ($F(1,63) = 0.002$, $p = 0.963$, $\eta^2 = 0.000$), no significant main effect of age ($F(1,63) = 0.004$, $p = 0.947$, $\eta^2 = 0.000$) or condition ($F(1,63) = 0.057$, $p = 0.813$, $\eta^2 = 0.001$). The same approach was used to investigate the change in coupling phase measured as the mean circular direction. There was no significant age group by task condition interaction ($F(1,63) = 1.561$, $p = 0.216$, $\eta^2 = 0.025$) or a main effect of condition for coupling phase ($F(1,63) = 0.940$, $p = 0.336$, $\eta^2 = 0.015$). Consistent with previous literature, there was however, a significant main effect of age for coupling phase ($F(1,63) = 4.166$, $p = 0.046$, $\eta^2 = 0.065$) suggesting that coupled spindles in younger individuals are more tightly locked to the slow wave upstate compared to older individuals.

2.7.2.3 Coupled SW-SP and uncoupled spindle characteristics

Mixed-design, age group (Young, Older) by task condition (Control, ToH) 2 x 2 ANOVAs were used to investigate coupled spindle characteristic changes from control to testing sessions in young *vs.* older adults. There were no significant age group by task condition interactions for any of the coupled sleep spindle variables. However, there was a main effect of age for both density ($F(1,63) = 31.10$, $p = < 0.001$) and size ($F(1,63) = 19.715$, $p < 0.001$, $\eta^2 = 0.247$) whereby older individuals had fewer coupled spindles, that were smaller compared to the young group.

The same analysis strategy was used to investigate uncoupled spindle characteristics changes from control to testing sessions in young *vs.* older adults. There were no significant age group by task condition interactions for any of the uncoupled sleep spindle variables. Unlike coupled events, there was no main effect of density, thus suggesting that spindle production is greater for young *vs*. older adults for coupled events only, whereas uncoupled spindle production is comparable in young and older adults. Similar to coupled events, there was a main effect of age for size ($F(1,63) = 29.633$, $p < 0.001$, $\eta^2 = 0.331$), whereby older individuals had smaller uncoupled spindles compared to the young group.

Table 2. Sleep spindle parameters for coupled SW-SP and uncoupled spindles during NREM sleep from EEG recording sessions for older and young individuals on the control and testing sessions.

	Older		**Young**	
	Mean	**SD**	**Mean**	**SD**

Control					
Coupled	Density	1.13	0.68	5.15	3.72
	Size	4.80	1.47	6.93	2.19
Uncoupled	Density	5.90	1.96	5.87	2.55
	Size	5.12	1.54	8.02	2.19
Testing					
Coupled	Density	1.30	0.82	5.36	3.24
	Size	4.44	1.29	6.90	2.33
Uncoupled	Density	7.42	2.56	5.55	2.28
	Size	4.73	1.11	7.88	2.79

2.7.3 Relationship between spindle coupling and ToH performance

First, bivariate correlation analyses were used to assess if offline gains in performance were related SW-SP coupling. There was a significant relationship between offline gains in accuracy and coupled spindle percent change during the upstate in older adults (r = 0.742, p = 0.006) but not in young adults (r = 0.362, p = 0.117). However, inspection of the scatterplots does reveal a similar pattern between age groups (Figure 4). There was no significant relationship between offline gains in terms of speed with any coupling metrics.

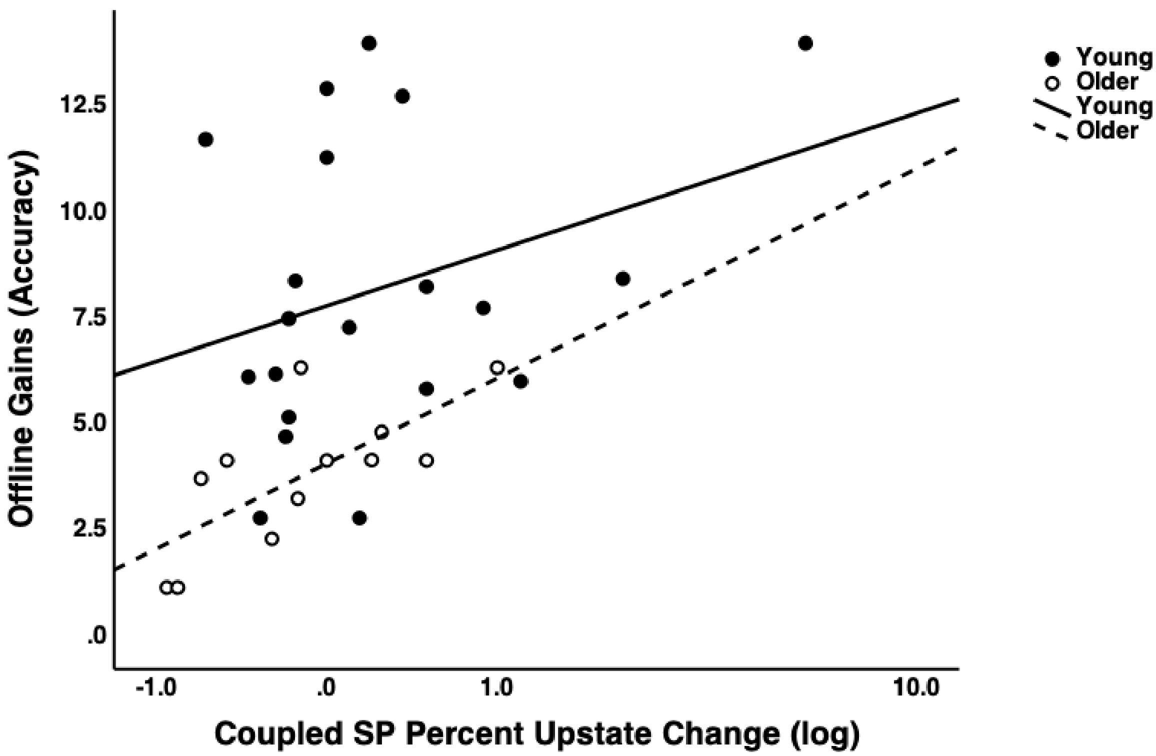

Figure 4. Percentage of coupled spindles during the upstate for older and young participants corelated to offline gains in performance (accuracy scores). There was a significant relationship between offline gains in accuracy and coupled spindle percent change during the upstate in older, but not younger adults.

To follow-up and further explore the nature of this relationship, standard multiple linear regression analyses were used to assess if the magnitude of the offline gains in accuracy were related to coupled events during the upstate to a different extent in young *vs*. older adults. Offline gains in accuracy were entered as the dependent variable. Age group and coupled SP percentage change, and the interaction term were entered as independent variables. Results revealed that percent change from control to testing session for coupled spindles during the upstate accounted for variability in offline gains in accuracy (F (2,31) = 12.18, R^2= 0.46, p < 0.001). Age (t = 3.67, p = 0.003, sr = -0.57) and coupled spindle percent (t = 1.99, p = 0.031, sr = 0.46) were significant predictors, but not the age by spindle interaction term (t = 0.87, p = 0.088, sr = 0.21). Suggesting that age accounts for differences in gains in accuracy, as does spindle coupling during the upstate. The above bivariate correlations suggest the latter relationship is more robust in older adults, but the regression interaction term indicates that the relationship between gains and coupling does not differ significantly between age conditions.

2.8 Discussion

In the present study, we investigated the electrophysiological consequences of age-related changes in sleep for acquiring novel cognitive problem-solving skills. Memory consolidation during sleep relies on the precisely timed interaction of spindles and slow waves (Baena et al., 2020; Bergmann & Born, 2018; Helfrich et al., 2018; Latchoumane et al., 2017; Muehlroth et al., 2019). However, no study to date has specifically examined the consequences of age-related changes in sleep microstructure (e.g., spindles and slow waves) for the consolidation of problem-solving skills. The results of our study revealed: 1) despite intact learning, older adults derived a reduced benefit of sleep for problem-solving skills relative to younger adults, 2) as expected, the percentage of coupled spindles was lower in older compared to younger individuals from control to testing sessions both in general, and when limited to the upstate SW interval, 3) coupled spindles in younger adults were more tightly locked to the slow-wave upstate compared to older individuals, 4) older individuals had fewer coupled spindles, that were smaller compared to the young group, and finally, 5) there was a significant relationship between offline gains in accuracy and coupled spindle percent change during the upstate in older, but not younger adults.

Consistent with previous literature focused on cognitively simple procedural motor skills (Brown et al., 2009; Fogel, Albouy, Vien, et al., 2014; Pace-Schott & Spencer, 2011; Spencer et al., 2007), despite slower performance in older participants compared to younger participants, older participants learned the ToH to the same extent as the young participants. However, older adults seem to benefit less from retention intervals that include sleep compared to young adults, suggesting age-related changes in offline learning processes (Fogel et al., 2014, 2017; Mander et al., 2015; Mander et al., 2013; Pace-Schott & Spencer, 2011; Raz et al., 2000; Spencer et al., 2007; Wilson et al., 2012; Wright & Payne, 1985). A recent fMRI study by our group (Toor et al., 2022), found that sleep facilitated the realization of a novel cognitive strategy in young, but not older adults through consolidation-based hippocampal-neocortical transfer of information. By contrast, a period of daytime sleep may be detrimental to consolidation in older adults. This may reflect incomplete consolidation, or as a result of an undesirable destabilizing effect of sleep in the hippocampus and related brain areas. The current study suggests that reduced spindle-slow wave coupling in older adults may be a possible explanation of why sleep did not provide the same benefit to consolidation as compared to young adults. However, this is not consistent across all older individuals, as older individuals with more young-like SW-SP coupling is associated with offline gains in performance, whereas those with less coupling tend to lower gains (see Figure 4).

Our results are consistent with the extant literature suggesting a loss of coupling integrity due to normal aging (Carrier et al., 2011; Helfrich et al., 2018; Mander et al., 2017; Muehlroth et al., 2019; Ulrich, 2016). Moreover, the impact of the age-related loss of coupling has also been known to impact memory consolidation (Backhaus et al., 2007; Cherdieu et al., 2018). Here, we report significantly fewer coupled spindles, that were smaller compared to the young group However, we did not find that the change in SW-SP coupling parameters differed from Control to ToH post-training sleep as a function of age group. This may suggest that SW-SP coupling is not a vital requirement in the earliest stages of the consolidation process of complex problem-solving skills, regardless of age. Interestingly, using a different protocol whereby training was distributed over a longer period of time, and to allow for expertise on the ToH to be attained, previous work from our group (Fogel et al., 2015) suggests that spindles are involved in the consolidation of cognitively complex procedural skills, but, this may not be observed until expertise on the task is very well-developed.

It would appear, spindle-SW coupling is unrelated to consolidation of the ToH in young adults. It is possible that in younger subjects, rapid eye movement (REM) sleep may be more valuable to consolation of the ToH. For example, a recent study in our lab (Van Den Berg et al., 2023), utilized the same task as our study, reported that both theta and central-parietal-occipital sensorimotor rhythm (SMR) activity are associated with the consolidation of novel cognitive strategies (the ToH), and that eye movements during REM sleep are electrophysiological markers of this underlying process. Importantly, REM sleep was not measured in our current study as we followed a napping protocol that did that allow for enough REM sleep. In stark contrast, in older adults while there was no significant learning-dependent change in coupling from CTL to ToH, the extent of the change in spindle-SW coupling acted as a marker of consolidation. As such, in healthy older adults, the extent of coupling may be important. That suggests that older adults may be using a different means of consolidating the ToH strategy, or they may be learning it differently or consolidating different aspects of the task than the young.

Due to the limited and variable sleep available during a daytime nap, it was not possible to subdivide spindles into slow spindles (11-13 Hz) and fast spindles (13-16 Hz), nor was NREM2 or SWS considered separately. A daytime nap is advantageous when comparing young *vs*. older adults to better control for age-related time-of-day effects. Nonetheless, future studies employing overnight sleep during the consolidation interval would allow for more fine-grained analysis of the sleep microstructure.

2.9 Conclusion

Overall, this paper provides evidence for the electrophysiological consequences of age-related changes in sleep for acquiring novel cognitive problem-solving skills. In terms of behavior, we show that learning is intact in older adults, however, older adults derived a reduced benefit of sleep for problem-solving skills relative to young adults. In terms of sleep architecture and microstructure, SW-SP coupling was compromised as a function of age. This was observed during the upstate and there was a reduction in coupled spindle size and density in older adults. Lastly, there was a significant relationship between offline gains in accuracy and coupled spindle percent change during the upstate in older, but not younger adults. Thus, with age, SW-SP coupling is reduced, but whatever coupling is occurring is a marker of the extent to which older individuals will benefit from sleep in terms of offline consolidation for novel problem-solving skills.

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Chapter 3

Study 2: Age-related differences in problem-solving skills: Reduced benefit of sleep for memory trace consolidation

3.1 Title Page

Age-related differences in problem-solving skills: Reduced benefit of sleep for memory trace consolidation

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3.2 Abstract

We investigated the behavioural and neuronal functional consequences of age-related differences in sleep for gaining insight into novel cognitive strategies. Forty healthy young adults (20–35 years), and twenty- nine healthy older adults (60–85 years) were assigned to either nap or wake conditions. Participants were trained on the Tower of Hanoi in the AM, followed by either a 90-minute nap opportunity or period of wakefulness, and were retested afterward. Functional magnetic resonance imaging scans examined differences in brain activation from training to retest in young versus older adults as a function of sleep. Sleep enhanced performance and transformed the memory trace in young adults via hippocampal-neocortical transfer, but not older adults. This is consistent with the notion that as the consolidation of a newly formed memory trace progresses, the hippocampus becomes less involved; especially so when sleep occurs during that time. These results demonstrate a critical role for sleep in supporting problem-solving skills and suggest that the benefit of sleep for consolidation of these skills is reduced with age.

Keywords: sleep, aging, memory consolidation, problem-solving

3.3 Introduction

When faced with a new problem to solve, the old adage to "sleep on it", is good advice (Spiers & Bendor, 2014; Wagner et al., 2004). Sleep acts as a cognitive catalyst; facilitating novel solutions to problems (Lewis et al., 2018; Perdomo et al., 2018; Wagner et al., 2004). However, evidence suggests that problem-solving skills are compromised as we age, impacting cognitive function and quality of life (Rönnlund et al., 2001, 2007). This reduced capacity for problem-solving skills may be due to age-related changes in sleep. However, this possibility remains to be explored, and is the focus of the current study.

In healthy young adults, sleep enhances the consolidation of newly acquired procedural skills (Born & Wagner, 2004; den Berg van et al., 2021; Fogel, Smith, et al., 2007; Fogel et al., 2015; Nielsen, Reilly, Carr, Dumel, Godin, Solomonova, Lara-Carrasco, O'Reilly, Carr, Dumel, Godin, Solomonova, Lara-Carrasco, Blanchette-Carrière, Paquette, O'Reilly, Carr, Dumel, Godin, Solomonova, Lara-Carrasco, Blanchette-Carrière, & Paquette, 2015; Plihal & Born, 1997; Smith, 1995, 1996, 2001, 2003; Smith & Lapp, 1991; Smith & Weeden, 1990), which include problem-solving, procedures, habits, conditioned behaviours, and cognitive skills acquired through repeated practice (for a review, see; (Rasch & Born, 2013). The benefit of sleep is reflected by sleep-related gains in performance that are not observed after an equivalent period of wakefulness (Fogel, Smith, et al., 2007; Fogel et al., 2015; Nielsen, O'Reilly, et al., 2015; Plihal & Born, 1997; Smith, 1995, 1996, 2001, 2003; Smith & Lapp, 1991; Smith & Weeden, 1990; van den Berg, Al-Kuwatli, et al., 2019; Wagner et al., 2004). An intriguing dissociation between sleep states and subtypes of procedural skills has been proposed (for a review, see; (Smith, Aubrey, et al., 2004). Early human studies revealed that rapid eye movement (REM) sleep is involved in consolidating memory for newly acquired procedural skills that involve problem-solving (Diekelmann et al., 2009; Peigneux et al., 2001; Rasch & Born, 2013; Smith, Nixon, et al., 2004; Stickgold et al., 2001; Walker, Liston, et al., 2002), and eye movements during REM may be an important marker of this process (Fogel, Smith, et al., 2007; Mandai et al., 1989; Smith & Smith, 2003; Smith, Nixon, et al., 2004; Smith & Lapp, 1991; Smith & Weeden, 1990). By contrast, it is well-established that non-rapid eye movement (NREM) sleep is important for the consolidation of cognitively simple motor skills (Ackermann & Rasch, 2014; Born & Wilhelm, 2012; Doyon, Bellec, et al., 2009; Fogel, Smith, et al., 2007; Fogel et al., 2015; King et al., 2017; Laventure et al., 2016; Mantua et al., 2016; Meier-Koll et al., 1999; Nader & Smith, 2003; Peigneux et al., 2015; Smith, 2001; Smith & MacNeill, 1994; Smith & Rose, 1997; Stickgold, 2005; Stickgold & Walker, 2013; Tweed et al., 1999; Walker, Brakefield, et al., 2002). Sleep spindles (brief <3sec bursts of oscillatory activity ~11-16Hz) define NREM stage 2 sleep (NREM2), and are an important marker of the related behavioral and neural enhancements that support the memory consolidation process (Astori et al., 2013; Fogel, Smith, et al., 2007; Fogel & Smith, 2011; Fogel & Smith, 2006; Gais et al., 2002; Lüthi, 2013; Ulrich, 2016). More recently, sleep spindles have also been shown to be involved in the consolidation of problem-solving skills both in adults (Fogel et al., 2015), and school aged children (Vermeulen et al., 2019). Thus, suggesting a possibly synergistic contribution of REM and NREM sleep to the acquisition of problem-solving skills (Ackermann & Rasch, 2014; Fogel, Smith, et al., 2007; Fogel et al., 2009, 2015; Smith, Aubrey, et al., 2004; Tweed et al., 1999). However, the role of sleep in the realization of the solution to a novel problem, the changes in brain activity that accompany this process, and how these sleep-memory relationships evolve with age, remain to be investigated. Further investigation may elucidate the neural substrates that support memory consolidation of newly acquired cognitive strategies and the related neural mechanisms.

Importantly, functional neuroimaging studies in young adults have identified the neuroanatomical substrates that support the mental components of problem-solving skills (for a review, see; (Unterrainer & Owen, 2006). These studies show that the dorsolateral and medial prefrontal cortex, posterior hippocampus (Dagher et al., 2001), supplemental motor cortex, posterior parietal, cerebellum, and striatum; and in particular, the caudate nucleus (Baker et al., 1996; Dagher et al., 1999, 2001; Goldfine et al., 2013; Owen et al., 1996; Rowe et al., 2001; Unterrainer & Owen, 2006; Vahdat, Albouy, et al., 2017) are recruited during the acquisition of a novel cognitive strategy. Our recent work has demonstrated that either a night of sleep, or a daytime nap enhances performance on problem-solving skills compared to wake (den Berg van et al., 2021). In addition, we observed enhanced activation of the caudate and the hippocampal-striatal-cortical network as compared to wakefulness. As such, sleep tends to act as a privileged time to enhance newly acquired cognitive strategies that are required to solve novel problems.

Procedural skill learning is intact in older adults (Brown et al., 2009; Fogel, Albouy, King, et al., 2014; Spencer et al., 2007). Despite intact learning, older adults seem to benefit less from retention intervals that contain sleep, as compared to young adults, suggesting age-related deficits in latent/offline learning processes (Raz et al., 2000; Wright & Payne, 1985). With increasing age, there are increased reports of early awakenings, easily disturbed sleep, decreased total time asleep, excessive daytime sleepiness (Bliwise et al., 1992; Foley et al., 1995; Vitiello et al., 2004) and increased daytime napping (Foley et al., 2007). Age-related changes in sleep may compromise the benefit that sleep affords to problem-solving (Debarnot et al., 2017). However, very little is known about the reason for this putative deficit, *e.g.*, specific sleep disruptions, changes in neurobiological substrates, or neural mechanisms impacted by age. Remarkably, when age-related changes in REM sleep are normalized pharmacologically, overnight enhancement of problem-solving skills in older adults is improved (Hornung et al., 2007). This suggests that age-related sleep disturbances may prevent the sleep-dependent processing required for problem-solving (Debarnot et al., 2017).

However, much less is known about the impact of age on sleep-dependent memory consolidation of newly acquired problem-solving skills. To address this gap, the present study investigated the putative sleep-related impairment in the realization of solutions to cognitive problems with increasing age, and their functional neuroanatomical correlates. We investigated the functional consequences of age-related changes in sleep for acquiring novel cognitive strategies to solve problems. Groups of young and older adults underwent functional magnetic resonance imaging (fMRI) while practicing a classic and commonly used cognitively complex procedural task (*e.g.*, the Tower of Hanoi; ToH). The ToH is considered a task that requires executive function, involves planning. The acquisition of a novel cognitive strategy is necessary to execute the solution to the puzzle (Ashworth et al., 2014; Humes et al., 1997; Welsh & Huizinga, 2005). Specifically, the solution to the ToH involves the use of recursive logic, learned implicitly through trial-and-error. To investigate the consequences of sleep and aging on the neural and behavioural correlates of the consolidation of novel problem-solving skills, functional magnetic resonance imaging (fMRI) was conducted during training and retesting on the ToH before and after a retention interval filled with either daytime sleep or wakefulness in groups of young and older participants. We hypothesized that: (1) older adults will derive a reduced benefit of sleep for problem-solving skills relative to young adults, (2) following a period of sleep, older adults that slept will have a reduced change in cerebral activation as compared to young adults that slept in brain regions known to support problem-solving skills, such as the prefrontal cortex, hippocampus and caudate, and, 3) sleep-related enhancements in memory trace consolidation will be correlated with sleep-related behavioural improvements in young, but not older adults.

3.4 Methods

3.4.1 Ethics Statement

All participants gave written informed consent prior to participation. This research was approved by the University of Ottawa's Research Ethics Board, as well at the Research Ethics Board at The Royal's Institute of Mental Health Research. All participants were compensated financially for their participation.

3.4.2 Participants

A-priori power analyses based on studies employing the closest experimental designs, techniques and methodology suggested that N = 15 is sufficient for the study to be adequately powered to test our main hypotheses. Previous studies (Fogel, Albouy, Vien, et al., 2014) (α=0.05), indicate that we would need a bare-minimum of N=15/group to obtain 80% power (Mumford, 2012) to detect age effects for the behavioural and fMRI data. This is based on observed effect sizes from follow-up t-tests of the difference between young nap (age 20-35) *vs*. older snap (age >65) groups (f = 0.7). All young (age 20-35 years) and older (age 60-85 years) participants were right-handed, non-shift workers, who did not take medications known to interfere with sleep, described themselves as good sleepers, were in good health, and maintained regular sleep schedules (usual bed-time between: 22:00 h – 01:00 h, usual wake-time between: 06:00 h – 09:00 h). Included participants had normal or corrected-to-normal vision, had a body mass index <30, were free from chronic pain, seizures, and had no previous head injury or any mobility problems with their hands or fingers. To be included in the study, young and older participants had to score <10 on the Beck Depression (Beck & Beamesderfer, 1974), and Beck Anxiety (Beck, Epstein, et al., 1988) Inventories, as well as no signs of sleep disorders, indicated by the Sleep Disorders Questionnaire (Douglass et al., 1994). Participants were excluded if they had previous experience with the ToH task, or familiarity with a similar task. In addition, older participants underwent additional screening measures to rule out signs of mild cognitive impairment or dementia, *e.g.*, scored ≥ 26 on the Montreal Cognitive Assessment (Nasreddine et al., 2005) and >2 on the Everyday Cognition Scale (Tomaszewski et al., 2008).

Furthermore, all participants included were non-smokers, were not considered heavy drinkers and did not consume more than 2-3 caffeinated beverages/day on a regular basis. For the duration of the study, participants were required to abstain from excessive caffeine (no more than one beverage in the AM), any alcohol, and to abstain from nicotine consumption. They were also required to keep a regular sleep-wake cycle (bedtime between: 22:00 h–01:00 h, wake-time between: 06:00 h–09:00 h) and abstain from daytime naps, which was verified via both actigraphy and daily sleep diaries. Furthermore, there were no differences in habitual napping behaviors between young and older adults assessed by the Napping Behavior Survey (Milner et al., 2006). In addition, to verify that participants maintained a regular sleep schedule for the duration of their participation in the study, and to verify compliance with the study protocol, they were asked to wear a 'Motionlogger' (Ambulatory Monitoring, Inc., Ardsley, NY, U.S.A.) actigraph; a wrist-worn accelerometer which measures sleep-wake-related limb movements for a minimum of two weeks, and to complete a log of their daily activities and sleep habits. Participants were excluded if the results of their actigraphy or sleep diary identified variability in their sleep schedule outside of the aforementioned criteria, or non-compliance with the study protocol. For the participants that met the initial eligibility criteria via telephone screening, seven older participants and five young participants did not meet the follow-up inclusion criteria for keeping a regular sleep schedule within the prescribed hours.

In addition, all participants underwent an acclimatization and screening polysomnography (PSG) recording to acclimatize to sleeping in the laboratory setting, ensure they were able to sleep adequately, and to rule out signs of sleep disorders. The PSG recording followed AASM guidelines (Ancoli-Isreal & Cheeson, 2007), and took place one week prior to the experimental session (see "*Polysomnographic Recording and Analysis*" section for details). Based on the results of the screening PSG, participants who slept poorly (*i.e.*, sleep efficiency (SE) < 80%), had an apnea-hypoapnea index (AHI) > 5, or a periodic limb movement (PLM) index > 10) were excluded from further participation in the study. In total, five participants were excluded from the young group (four participants for non-compliance with the study protocol based on irregular sleep schedules, and one participant who voluntarily dropped out of the study following the screening PSG). A total of two older participants were excluded for signs of cognitive impairment.

Following telephone pre-screening, participants were randomly assigned to either the Nap or Wake condition yielding four groups: Young Nap (YN), Young No Nap (YNN), Older Nap (ON), and Older No Nap (ONN). Randomized sex-stratified blocked of N = 4 were used to minimize imbalances in the number of males and females across experimental conditions (females: young nap N = 12, young no-nap N = 11, older nap N = 9, older no-nap N = 11). The proportion of males and females did not significantly differ across age group (X^2 (1) = 0.941, p = 0.332), or condition (X^2 (1) = 0.163, p = 0.687). A nap protocol was selected in order to mitigate time-of-day effects in learning and memory performance in young *vs*. older adults. The final sample consisted of 40 healthy young adults, 20 randomly assigned to the nap condition (YN) and 20 assigned to the wake condition (YNN) (23 females; *M* = 23.85, *SD* = 3.86). In addition, 29 healthy older adults, 15 randomly assigned to the nap condition (ON) and 14 to the wake condition (ONN) were included in the final sample (20 females; *M* = 67.06, *SD* = 7.62). All fMRI, EEG and behavioural data were analyzed blind. Participant data were de-identified, and there were no indicators of group or experimental condition. Analyses were carried out employing automated pipelines coded in Matlab. Participant condition was revealed to the researcher at the last step of the statistical analysis procedures, necessary to interpret the outcomes of the analyses.

3.4.3 Experimental Design

Following the screening process, all participants were asked to arrive in the laboratory at 09:00 h (Figure 1). Upon arrival at 9:00 h, they were administered the Stanford Sleepiness Scale (SSS) (Maclean et al., 1992) and the Psychomotor Vigilance Task (PVT) (Dinges & Powell, 1985) to collect both subjective and objective measures of sleepiness immediately prior to and following the MRI scanning sessions. The ToH and control (CTL) tasks (starting at 10:00 h) were performed while obtaining functional blood oxygen level dependent (BOLD) images using a block design (see "*Brain Imaging Data Acquisition and Analysis*" section for details). Beginning at 13:00 h, participants had either a 90-minute daytime nap with PSG recording (nap condition) or remained awake (wake condition). Participants in the Wake condition were required to remain awake during wake interval and were allowed to read quietly while supine in bed under dim ambient light. EEG recordings were continuously monitored during the 90-minute interval to ensure participants remained awake and was subsequently verified. The retest session took place at 17:00 h, more than 30 minutes after the end of the nap to avoid sleep inertia effects.

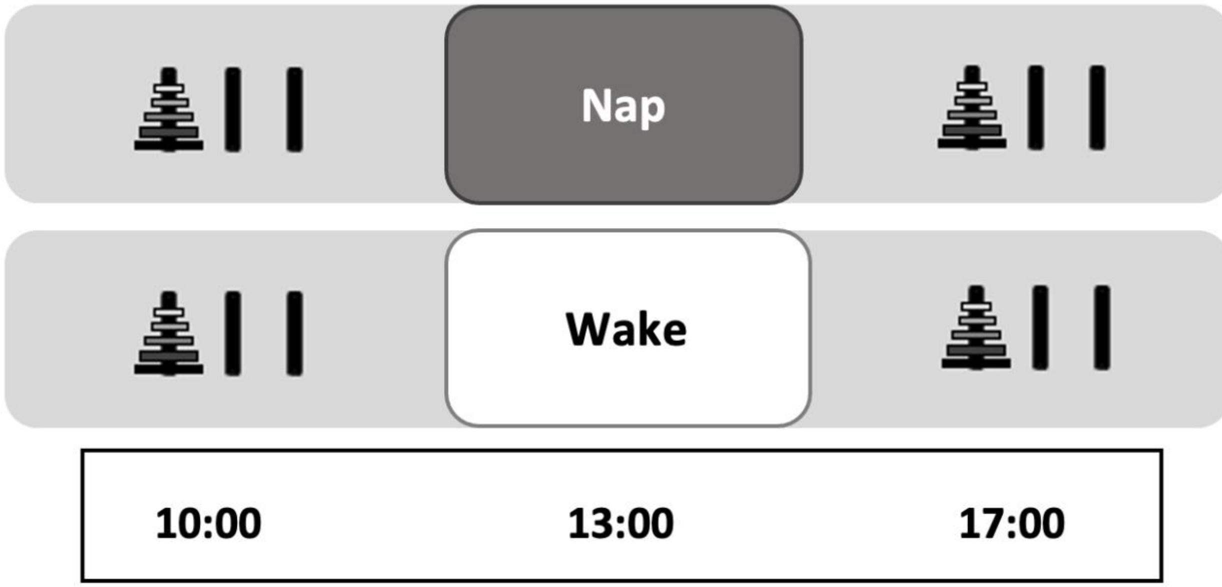

Figure 1. Study design. Overview of experimental protocol in the Nap and Wake conditions. Nap Condition: Participants arrived in the laboratory at 9:00 h. At 10:00 h, they were trained on the ToH and performed the CTL task in the MRI, and then slept in the laboratory from 13:00 h to 14:30 h while their sleep was recorded via PSG. Upon awakening, but after sleep inertia dissipation, participants were retested on the ToH and performed the CTL task in the MRI. In addition, participants completed the SSS and PVT before and after the MRI session. Wake Condition: The same procedure was used in the Wake conditions, except that instead of a nap, individuals remained awake. All sessions of the ToH and CTL tasks were completed while obtaining functional blood oxygen level dependent (BOLD) images using a block design (see "*MRI Imaging Acquisition and Analysis*" for details). During the ToH testing and retesting sessions, participants performed a 5-disk version of the classic ToH task in addition to the CTL task, to control for brain activations associated with motor execution of a random sequence of moves (see "*Behavioural Tasks and Analysis*" for details). The order of ToH and CTL tasks was counterbalanced across conditions and age groups. Abbreviations: CTL, control; MRI, magnetic resonance imaging; PSG, polysomnography; PVT, Psychomotor Vigilance Task; SSS, Stanford Sleepiness Scale; ToH, Tower of Hanoi.

3.5 Behavioural Tasks and Analysis

Two computerized versions of the classic Tower of Hanoi (ToH) task were employed, coded in MATLAB R2016a (Mathworks Inc., Natick, MA, USA) using the Psychophysics Toolbox extension v3.0.12 (Brainard, 1997b; Kleiner et al., 2007) for Windows (Microsoft, Redmond, WA, USA).

3.5.1 Tower of Hanoi Task

The computerized version of the ToH used in the present study consisted of 5 disks of different sizes that could be moved to and from one of three pegs by pressing the corresponding keys on the keypad. Participants were instructed that the objective of the task was to transfer all disks from the beginning position on the far-left peg, to the goal configuration on the far-right peg in the same ascending order. The ToH has the following constraints: 1) disks can only be moved one at a time, 2) each move could consist of taking an upper-most disk from one of the stacks and placing it on another peg, and, 3) only a smaller disk could be placed on top of a larger disk. These constraints thus require the problem to be solved according to a prescribed strategy, employing recursive logic (by breaking down the overall optimal solution into smaller components and recursively performing this sequence of moves several times), which is learned through trial-and-error. Participants were informed of these constraints prior to training. The optimal number of moves to complete the ToH is determined algebraically by $2^N - 1$, *where N is the number of disks*, or 31 moves for the 5-disk task. All ToH testing occurred while acquiring fMRI BOLD images in a block design (alternating blocks of practice and rest). An MR-compatible fibre optic response button box (model HHSC-2x4-C; Current Designs Inc., Philadelphia PA, USA) that comprised of four buttons in a horizontal row, with equal distance between one another was utilized. Using their right hand only, and with their index, middle and ring fingers, participants pressed the buttons controlling the movement of the disks to and from the different locations.

Participants performed eight training trials (to ensure adequate practice) and four retest trials of the ToH, where each trial was followed by a 20-second rest period. During the rest periods, participants were shown the three pegs with no disks and were instructed not to press any buttons. A trial of the ToH task ended when all five disks were in ascending order on the far-right peg, or if the maximum number of moves was reached before successful completion of the task, which was set at two times the optimal number of moves ($2^N - 1$*, where N is the number of disks, i.e.,* $2^5 - 1 = 31$), or in this case, 62 moves. ToH performance was measured in terms of speed (time to complete each ToH trial) (Supplemental Table S1), errors (invalid moves), and accuracy (Mean Absolute Percentage Error of valid moves; MAPE). The MAPE for *n* trials was calculated as follows:

$$\text{MAPE} = 100 - \left(\frac{1}{\text{n}}\right) * \sum \left(\frac{|\text{number of moves} - \text{optimal number of moves}|}{\text{number of moves}}\right) * 100$$

The MAPE can be interpreted as the percentage of perfect performance (e.g., 31 moves), whereby 100% represents perfect performance (*i.e.*, the optimal solution), whereas 50% reflects making twice as many moves as perfect performance and 0% theoretically represents an infinite number of moves. For all measures, to assess performance improvements from training to retest, the % improvement for both speed and accuracy was calculated by taking the first retest trial minus the last training trial, divided by the last training trial multiplied by 100. A measure of speed-accuracy trade-off was not used, as we have previously shown that sleep does not preferentially enhance this aspect of performance (den Berg van et al., 2021).

$$\%\ \text{improvement} = \left(\frac{\text{Retest} - \text{Training}}{\text{Training}}\right) * 100$$

Skewness in the distributions of % improvement measures was normalized by taking the square root of the raw scores.

3.5.2 Control Task

An adapted version of the ToH task was used to control for (i.e., subtract out) brain activations associated with motor execution of movements and the visual characteristics of the ToH. The CTL task was identical to the ToH task in every way, except that each move was prompted from one pseudo-random location to another without violating the constraints of the task. Importantly, the CTL task required the same type of motor execution as the ToH (*e.g.*, speed and number of movements per trial), but the movements did not follow the movements required to learn the underlying strategy needed to complete the ToH (*i.e.*, recursive logic). Thus, learning the strategy and reaching the optimal solution was not possible. All sensorimotor, spatial, and visual aspects of the task were the same as the ToH. Each move was prompted by the appearance of a green dot above a peg at a possible random location to identify the disk to be moved, followed by a red dot above the destination peg to complete the move. Each trial of the CTL task ended when a total of 31 randomly guided moves, corresponding to the minimum number of moves it takes to complete the 5-disk ToH task were completed. Participants performed four trials of the CTL task, where each trial was followed by a 20-second rest period.

3.5.3 Behavioural Analysis

SPSS Statistics version 27 (IBM, Armonk, New York, U.S.) was used to carry out the behavioral statistical analysis. To ensure that learning did take place on the ToH task in both the young and older groups of participants, Age (Young, Older) x Trial (trails 1 to 8) 2x8 ANOVAs were conducted for speed, errors, and accuracy. Simple effects repeated measures ANOVAs in each group were used to follow up any significant effects. To explore whether sleep facilitated performance on the ToH task in young and older groups, Age (Young, Older) x sleep/wake condition (Nap, Wake) 2x2 ANOVAs were conducted for % change in speed, errors, and accuracy. Independent samples t-tests were used to follow-up any significant group effects.

PVT scores from before and after the MRI scanning sessions were also analyzed using a PVT session (PVT1, PVT2, PVT3, PVT4) x by Age (Young, Older) x sleep/wake condition (Nap, Wake) 4x2x2 ANOVAs on mean speed (i.e., 1/RT), in order to ensure that time-of-day did not differentially impact vigilance in young and older adults, and also, that the nap did not impose sleep inertia effects that might impact ToH performance.

3.6 Polysomnographic Recording and Analysis

In-laboratory PSG was recorded with the Embla N7000 amplifier system (Natus, Pleasonton, CA, USA) sampled at 500 Hz. EEG (Fp1, Fpz, Fp2, F3, Fz, F4, C3, Cz, C4, P3, Pz, P4, Oz, A1, A2) and EOG (placed on the outer canthus of the eyes) was referenced online to Fpz with Afz ground. EEG and EOG were re-referenced offline to average mastoid derivations (A1 and A2), placed according to the international 10-20 system (Jasper, 1958). Submental EMG channels were recorded as a bipolar derivation. Manual sleep stage scoring, according to standard criteria (Allan Hobson, 1969; Iber et al., 2007), was completed by a single scorer using Hume analysis software for Matlab (https://www.jaredsaletin.org/hume), in 30-s epochs (Supplemental Table S2). During the preliminary acclimatization and screening PSG, recordings from a nasal/oral thermistor, and respiratory effort belts were additionally used to screen for signs of sleep apnea. As well, recordings from EMG leg electrodes were used to screen for signs of parasomnias.

3.7 MRI Imaging Acquisition and Analysis

3.7.1 Recording Parameters

Functional magnetic resonance imaging (fMRI) data was collected on a Siemens Biograph mMR 3.0 Tesla MRI whole body scanner (Siemens, Erlangen, Germany) using a 12-channel head coil. The entire brain (including the entire cerebral cortex and the cerebellum) was covered by the FoV, with the orientation aligned along the anterior commissure – posterior commissure line. Anatomical images were acquired using a standard 3D Multislice MPRAGE sequence (TR = 2300 ms, TE = 2.98 ms, TI = 900 ms, FA = 9°, 176 slices, FoV = 256 × 256 mm^2, matrix size = 256 ×

256 × 176, voxel size = 1 × 1 × 1 mm^3). In addition, Multislice T2-weighted functional MRI images were acquired during the ToH and CTL tasks (TR = 2.16 sec; TE = 30 ms, FA = 9º, 40 transverse slice, 3 mm slice thickness, 10% inter-slice gap, FoV = 220 x 220 mm^2, matrix size = 64 x 64 x 40, voxel size = 3.44 x 3.44 x 3 mm^3).

3.7.2 Preprocessing

Using MATLAB R2018a for OS X (Apple, Cupertino, CA), functional volumes were preprocessed and analyzed using SPM12 (https://www.fil.ion.ucl.ac.uk; The Welcome Centre for Human Neuroimaging, London, UK). Anatomical images were first roughly auto-oriented. Then, functional images obtained for each participant were realigned to the first functional volume of the session, and co-registered to the T1-weighted anatomical image. The co-registered anatomical images were then segmented into grey matter, white matter, and cerebrospinal fluid. Movement correction of both translations and rotations around *x*, *y* and *z* was performed. If movement exceeded 6 mm, participants were excluded from further analysis. Next, an average subject-based template was created using DARTEL in SPM12, used to normalize all anatomical and functional images. Lastly, spatial smoothing was applied on all functional images (Gaussian kernel, 8 mm full-width at half-maximum (FWHM)).

3.7.3 First-Level Fixed Effects Analysis

At the individual level, using the General Linear Model (GLM) in a block design (i.e., task vs. rest), canonical hemodynamic response function (HRF), and its temporal and dispersion basis functions were estimated. The onsets for each block of task and rest were entered into the GLM to build the block design. Slow drifts were removed from the time series using a high pass filter with a cut-off period of 128 seconds. Serial correlations in the fMRI signal were estimated using an autoregressive (order 1) plus white noise model and a restricted maximum likelihood algorithm.

Linear contrasts tested for the main effect of: (1) the training session (ToH–CTL training) in order to assess what brain regions were initially recruited during learning, and (2) the difference between the training and retest sessions [(ToH–CTL retest) – (ToH–CTL training)]. In this way, we could investigate the increase in brain activations specifically associated with problem-solving minus the motor movements (i.e., ToH-CTL) required to execute the strategy from training to retest (i.e., retest-training) in young and older adults. Each of these subject-level contrasts included a set of 3 contrasts: the HRF, the temporal and dispersion basis functions. This informed basis set was passed onto group-level analyses, to examine the impact of the experimental condition of a retention interval of either a nap or wake, in young and older adults, for consolidation of the newly acquired memory trace.

3.7.4 Second-Level Random-Effects Analysis

The resulting subject-level sets of contrast images were passed onto the group-level analysis. ANOVAs were used to consider the HRF, temporal and dispersion basis functions together. This approach is advantageous as it takes into account not only the amplitude of the canonical HRF, but also, incorporation of the time derivative allows variations in the peak response to be accounted for, and incorporation of the dispersion derivative allows for variations in the width of the response to be accounted for (Friston et al., 1998). We examined: 1) the brain activations recruited for all participants in the training session, the difference in brain activations between young and older participants recruited during the training session, and, 2) to test our main hypotheses, the difference (i.e., interaction effect) in activation between the Nap and Wake groups in Young and Older adults [(YN-YNN) – (ON-ONN)] for the first-level contrasts of interest, and their main effects. All hypotheses were tested at a threshold of $p < 0.05$, controlling for multiple comparisons using the False Discovery Rate (FDR), whole brain correction. To interpret the direction of the effects from the second level-analyses, plots of the magnitude of the HRF and 95% confidence intervals were generated.

3.8 Brain-Behaviour Relationships

Finally, we then followed-up whether pre *vs*. post retention interval (Retest - Training) changes in brain activation were differentially related to changes in behavioural performance in young and older adults. To do so, we included gains in performance (speed and accuracy) scores for each participant as covariates into the group-level GLM analysis. This analysis was carried out for significant activations from the interaction effect for the coordinates presented in Table 1, using small volume correction (p < 0.05, FWE) with a 10mm sphere at each peak coordinate.

3.9 Results

3.9.1 Behavioural data

First, to ensure that learning did take place in both young and older participants, an Age (Young, Older) x Trial (trails 1 to 8) 2x8 ANOVA revealed a significant increase in speed over the course of the training session overall (F (7,476) = 36.71, $p < 0.0001$, $\eta^2 = 0.35$), which was observed in both the Young (F (7,273) = 35.17, $p < 0.0001$, $\eta^2 = 0.47$) and Older groups (F (7,203) = 12.22, $p < 0.0001$, $\eta^2 = 0.30$). There was no significant interaction with Age (F (7,476) = 1.17, $p = 0.32$, $\eta^2 = 0.02$), suggesting that both young and older adults improved on the task with practice and did so, to the same extent. Again, a generally similar pattern was observed for accuracy in terms of overall improvement with practice at training (F (7,476) = 5.70, $p < 0.0001$, $\eta^2 = 0.08$). Young participants significantly improved in terms of accuracy with practice (F (7,273) = 7.30, $p < 0.0001$, $\eta^2 = 0.16$), however, older adults did not (F (7,203) = 1.41, $p = 0.202$, $\eta^2 = 0.05$). However, it should be noted that there was no significant difference in accuracy between young and older participants by the end of the training session (t (68) = 0.06, p = 0.960, d = 0.01), suggesting that, importantly, by the end of the training session, young and older participants did learn the task to the same extent.

To investigate the age and sleep-related changes in performance improvements, a Sleep (Nap, Wake) x Age (Young, Older) condition 2x2 ANOVA revealed a significant interaction for % increase in speed (F (1,66) = 64.39, p < 0.0001, η^2 = 0.49) and accuracy (F (1,66) = 15.73, p < 0.0001, η^2 = 0.19), but not errors (Figure 2). Follow-up tests showed that the Young Nap (YN) condition had significantly greater improvement than the Young No Nap (YNN; speed: t (38) = 8.86, p < 0.0001, d = 2.80; accuracy: t (38) = 2.36, p = 0.024, d = 0.75) and Older Nap (ON) conditions (speed: t (33) = 12.13, p < 0.0001, d = 4.14; accuracy: t (33) = 4.54, p < 0.0001, d = 1.55). There was no difference between the YNN and Older No Nap (ONN) conditions (speed: t (33) = -1.16, p = 0.256, d = -0.40; accuracy: t (33) = -0.57, p = 0.573, d = -0.19). However, individuals in the ON condition performed significantly worse than the ONN condition (speed: t (28) = -2.87, p = 0.008, d = -1.05; accuracy: t (28) = -4.04, p < 0.0001, d = -1.47).

It is important to note that mean speed (i.e., 1/RT) in PVT performance did not change over the course of the testing sessions, as a function of age or sleep/wake condition (F(3,192) = 2.13, p = 0.120). No other main effects or interaction effects were significant. Thus, suggesting that a daytime nap did not differentially impact vigilance in young and older adults over the course of the experimental protocol.

Taken together, these results suggest that older adults did not exhibit deficits in acquiring the task initially, during training relative to young adults. However, while young adults benefitted from a consolidation interval filled with sleep as compared to wakefulness, interestingly, in older adults, sleep appears to have been significantly less beneficial to the consolidation of the newly acquired strategy as compared to a period of wakefulness.

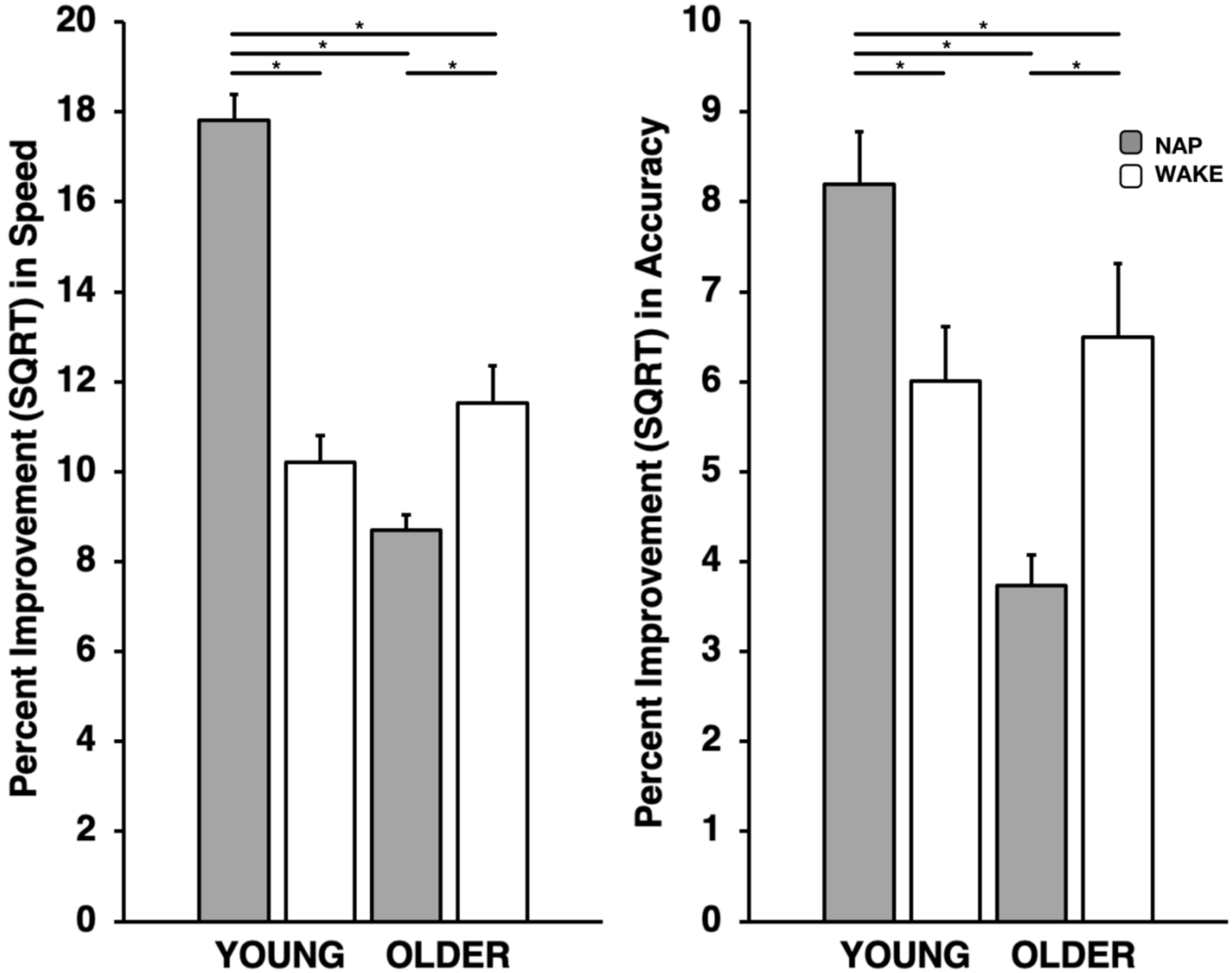

Figure 2. ToH performance. Mean percent improvement for speed and accuracy on the ToH from Training to Retest in young and old participants. Young adults benefited from a daytime nap as compared to wake, whereas older adults did not. Error bars represent standard error of the mean.

3.10 MRI Data

3.10.1 Group x Session Interaction [(YN-YNN)- (ON-ONN)]

We tested for the possible changes in brain activation over the retention interval (Retest – Training) between young and older participants in those that either napped or remained awake

(Figure 3). As hypothesized, a bilateral difference in activation of the hippocampus was observed from training to retest (Table 1) between young and older participants (also see main effects of YN vs. ON, Supplemental Table S3). Consistent with previous studies investigating procedural motor skills (Fogel, Albouy, Vien, et al., 2014) inspection of the direction of the effects (*i.e.*, contrast estimates, with 95% confidence intervals) revealed that that YN displayed a decrease in activation in the hippocampus, whereas YNN showed increased activation. Meanwhile, the older groups showed the opposite pattern whereby ON displayed an increase in activation in the hippocampus, while ONN displayed no difference in activation. Thus, suggesting that sleep differentially contributed to the consolidation of the memory trace in young *vs*. older individuals, consistent with the notion that as consolidation progresses, the hippocampus becomes less involved over time – but especially so when sleep occurs during that time. Our results suggest that sleep preferentially contributes to this process in the young, but not in older individuals. Interestingly, the pattern of MRI results are strikingly similar/analogous to the overall pattern of behavioural results (Figure 2).

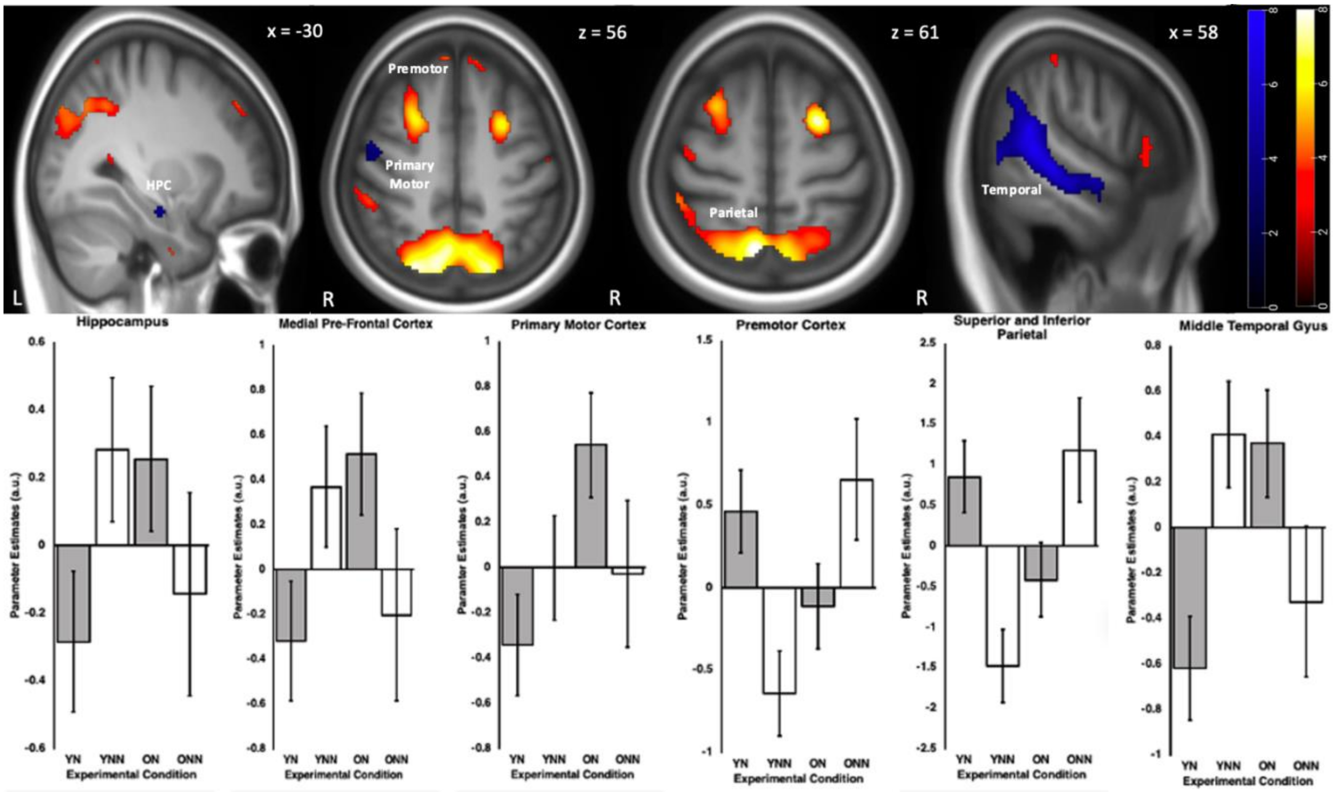

Figure 3. Brain regions with significant activations from Group (Young, Old) x Session (Nap, Wake) interaction. Error bars indicate 95% confidence intervals. Values on activation maps are *F* statistic values. Warm values represent increase and cool color scales represent decreases in activation. Note: Brain images shown using neurological convention. Abbreviations: Hippocampus (HPC); Arbitrary Units (A.U.); Right (R); Left (L).

In addition, this group x session interaction (Figure 3) also revealed changes in activation in several of the same set of neocortical areas that were recruited during training (Supplemental Table S4: training session), that support procedural skill learning including the premotor cortex, superior and inferior parietal cortex, and middle temporal gyrus. Specifically, from training to retest, the YN showed an increase in activation and the YNN showed a decrease in activation in the premotor area, superior and inferior parietal cortex, whereas there was no change for ON and an increase in activation for ONN. Other cortical regions involved in planning and executive function, such as the middle temporal gyrus and medial prefrontal cortex (mPFC) (not shown in Figure 3), showed a similar pattern as the hippocampus, whereby there was a decrease in activation from training to retest in YN, and an increase in activation in YNN, whereas there was an increase in activation in ON, but no difference in ONN. In the inferior frontal gyrus, the same, but less robust, pattern was also observed. A somewhat different pattern emerged in the primary motor cortex, whereby only the ON group showed an increase in activation. Lastly, the medial frontal gyrus (not shown in Figure 3), also revealed an unusual pattern with ON and ONN both displaying increases in activation, while YN and YNN revealed a decrease in activation from training to retest.

Table 1. Group by session interaction. Changes in activation for ToH-CTRL from training to retest between young nap (YN), young no-nap (YNN), older nap (ON) and older no-nap (ONN) groups.

L/R	Level	Region	X	Y	Z	Size	Z	p
		(YNN-YN) – (ONN-ON)						
Bilateral	Cerebral Cortex	Superior and inferior parietal	8	-66	58	10638	7.46	0.000
Bilateral	Cerebral Cortex	Middle temporal gyrus	64	-46	18	3651	7.06	0.000
Bilateral	Cerebral Cortex	Premotor	24	8	52	1462	5.71	0.000
Bilateral	Cerebral Cortex	Medial prefrontal cortex	6	46	52	3020	4.48	0.032
Bilateral	Cerebral Cortex	Primary motor cortex*	44	-8	56	246	4.42	0.036
Bilateral	Cerebral Cortex	Inferior frontal gyrus*	52	32	-10	389	4.48	0.032
Bilateral	Cerebral Cortex	Medial frontal gyrus	-36	44	36	1432	4.78	0.010
Bilateral	Limbic	Hippocampus*	-30	-14	-18	81	4.44	0.050
Bilateral	Hindbrain	Cerebellum*	22	-78	-32	382	4.93	0.006

Results shown for significant activations at p < 0.05, corrected for multiple comparisons using False Discovery Rate (FDR) whole brain correction. * Indicates bilateral activation significant on the contralateral side at p<0.001 (uncorrected).

3.10.2 Brain-behaviour relationships

To follow-up the relationship between significant changes in brain activation (from training to retest) with significant performance improvements (percent change in speed and accuracy), we included gains in performance as covariates into the GLM at the group level. Interestingly, offline gains in performance for accuracy were significantly and exclusively associated with differences in cerebral activation in the hippocampus (F = 3.56, p = 0.015, *SVC*). Thus, suggesting that the nature of the relationship between brain activations in the hippocampus and offline gains in performance significantly differed between groups (Figure 4). There were no other brain-behaviour relationships for any other regions reported in Table 1 for speed or accuracy.

These results suggest that sleep-dependent changes in brain activation that support the acquisition of novel cognitive strategies required for problem-solving are associated with sleep-related changes in performance. The pattern of these relationships is consistent with the notion that in young adults, the greater the decrease in recruitment in the hippocampus, the greater the performance improvements. On the other hand, in older adults, the opposite pattern is observed, whereby greater increases in the hippocampus are related to a worsening of performance. Thus, suggesting that sleep facilitates the realization of a novel cognitive strategy in young, perhaps through consolidation-based hippocampal-neocortical transfer of information. On the other hand, sleep may be detrimental in older adults, perhaps reflecting incomplete consolidation, or as a result of an undesirable destabilizing effect of sleep in the hippocampus and related brain areas.

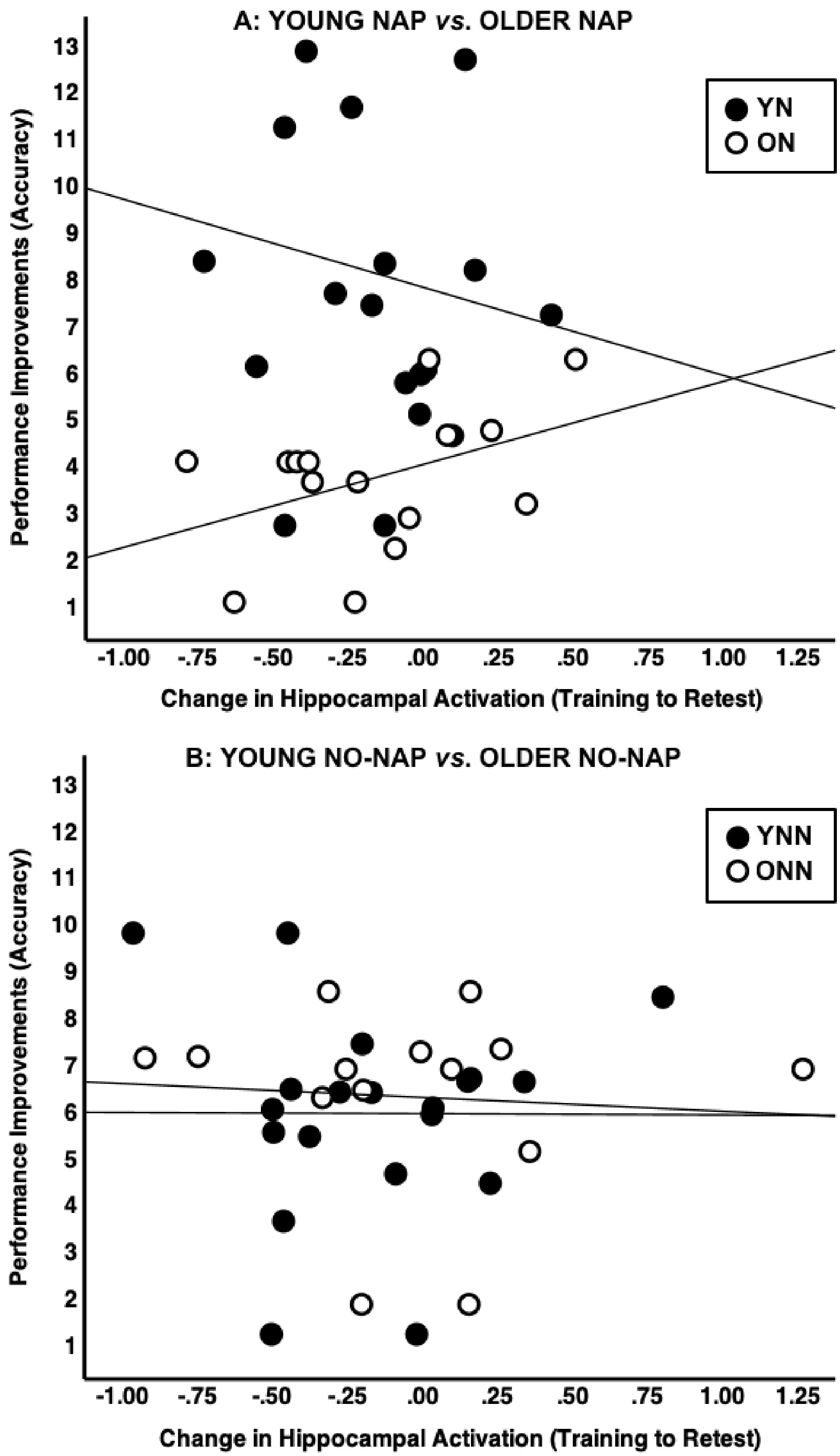
A: YOUNG NAP vs. OLDER NAP
YN
ON
Performance Improvements (Accuracy)
Change in Hippocampal Activation (Training to Retest)
B: YOUNG NO-NAP vs. OLDER NO-NAP
YNN
ONN
Performance Improvements (Accuracy)
Change in Hippocampal Activation (Training to Retest)

Figure 4. The relationship between the changes in performance and changes in brain activation from training to retest differed across the four experimental conditions (YN, YNN, ON, ONN).

3.11 Discussion

We investigated how age impacts the benefit of sleep for the consolidation of problem-solving skills in terms of both brain function and behaviour. This was accomplished by disentangling the brain activations that occur during motor movements (on a control task) from the rule-learning components of a procedural problem-solving skills task (*i.e.*, the ToH) in young and older adults, before and after a period of either daytime sleep or wakefulness. Consistent with our hypotheses, we showed that from training to retest: (1) by the end of training, older adults reached the same level of performance as young adults, however, they derived a reduced benefit of sleep for problem-solving skills in terms of speed and accuracy relative to young adults and older adults that were awake, (2) following a period of sleep, young but not older adults displayed a reduced change in BOLD activation from training to retest in both the hippocampus and dorsolateral prefrontal cortex (structures thought to be involved in the consolidation process of problem-solving), as well as decreased activation of the middle temporal gyrus, and increased activation of the premotor and parietal cortex (structures involved in planning and mental and visuospatial imagery), and, 3) in young participants who slept, the greater the reduction in hippocampal activation (presumably reflecting consolidation via hippocampal-neocortical transfer), the better their improvements in terms of speed and accuracy. On the other hand, in older individuals that slept, increased activation in these regions was detrimental to performance improvements. The same pattern was observed in the medial prefrontal cortex. This may be the case because consolidation is not completed during sleep, and instead, sleep is putting the hippocampal aspect of the memory trace (and highly interconnected regions such as the medial prefrontal cortex) into a labile state, making it more susceptible to things like forgetting or interference. The opposite pattern was observed for brain regions such as the premotor cortex and prefrontal cortex, again suggesting successful hippocampal-neocortical consolidation via transfer in young but not older adults that slept. This suggests that sleep differentially contributes to the consolidation of the memory trace in young *vs*. older individuals, whereby sleep contributes to the consolidation process in the young, but not in older individuals for a set of brain areas which support problem-solving skills.

As predicted, and in alignment with previous studies investigating procedural motor skill learning (Brown et al., 2009; Fogel, Albouy, Vien, et al., 2014; Siengsukon & Boyd, 2008, 2009; Spencer et al., 2007), older participants' ability to learn the skill was intact, *i.e.*, they improved in terms of speed at the same rate as younger participants, and reached the same level of performance by the end of training. In terms of consolidation of the newly learned skill; although older participants did retain what was learned during training, they did not derive the same benefit from a daytime nap during the subsequent retention interval, as compared to the young adults. Interestingly, and consistent with the current study, both Fogel et al. (Fogel, Albouy, Vien, et al., 2014) and Spencer et al. (Spencer et al., 2007) revealed that older individuals who napped performed worse on a motor skills task, relative to older non-nappers, suggesting that in some cases, a nap can actually be detrimental to procedural memory performance. This suggests that a nap is insufficient for older adults to consolidate the newly formed memory but is enough to place the memory trace into a labile state, thereby resulting in reduced performance improvements as compared to young adults, or older adults who remain awake during that time. In summary, our behavioral findings for problem-solving skills are consistent with previous studies investigating more cognitively simple motor skills and suggest that sleep enhances memory consolidation for a newly acquired cognitive strategy in young but not older adults. Furthermore, the present study suggests that there is a differentiation between young and older adults in terms of sleep-related transformation of memory trace consolidation for procedural problem-solving skills, and that a brief daytime nap may beneficial to young adults, but may be contraindicated for older adults.

3.11.1 The role of the hippocampus and related cortical areas in problem-solving skills

Sleep had a differential effect on the hippocampus between young and older adults. Specifically, and as predicted, decreased activation was observed from training to retest in the hippocampus for young participants that slept, whereas young participants that were awake, or older participants that slept experienced increased activation. By contrast, older participants that were awake displayed no apparent change in activation. Thus, sleep differentially contributed to the consolidation of the memory trace, consistent with the notion that as consolidation progresses, the hippocampus becomes less involved over time (Alvarez et al., 1994; Buzaki et al., 1996; Takashima et al., 2009). Sleep facilitates this process in younger adults, but with age, this benefit is lost.

The hippocampus is responsible for encoding newly acquired information, and later transferring it to the cortex for long-term storage (Dudai, 1996; Dudai et al., 2015; Squire & Zola, 1996). As consolidation progresses, information is integrated into neocortical circuits and reorganized so that it can ultimately be retrieved independently of the hippocampus (Takashima et al., 2009). Our results suggest that older adults do not derive the same benefit from sleep which normally facilitates this process. Alternatively, it is possible that the consolidation process is the same in young and older adults, and that for older adults, more time in sleep is required (*e.g.*, a night of sleep, or several nights) to achieve the same result as young adults. Importantly, at the training session (Supplemental Table S4: training session), there were no differences in activation between young and older groups for the hippocampus or frontal cortex, thus suggesting that young and older groups initially had comparable hippocampal involvement. In line with previous studies investigating consolidation of motor skills (Bendor & Wilson, 2012; Fogel, Albouy, Vien, et al., 2014; Spencer et al., 2007), our results suggest that age-related differences in sleep result in reduced hippocampal-dependent memory consolidation processes. Finally, it is unlikely that sleep inertia could explain the reduced performance improvements in older adults, as there were no differences in psychomotor vigilance between young and older adults.

The same pattern of activation changes from training to retest was observed in related brain areas that are associated with the hippocampal-dependent consolidation process (Albouy, Fogel, et al., 2013; Albouy et al., 2015; Fogel, Albouy, Vien, et al., 2014), including the mPFC. Compared to other cortical areas, projections from the hippocampus to the mPFC are particularly strong (Cenquizca & Swanson, 2007; Jay & Witter, 1991). Specifically, and consistent with our results, visual-motor mappings formed within the premotor cortex become stronger and independent of the hippocampus over time (Wise & Murray, 2000), whereas a decrease in prefrontal activity is usually observed as motor performance becomes more automatic (for a review, see; (Albouy, King, et al., 2013). It has been hypothesized (Albouy, Vandewalle, et al., 2013; King et al., 2017) that, together with the hippocampus, the prefrontal cortex participates in spatial mapping of motor sequences during early learning. This map is then consolidated during subsequent sleep through hippocampo-frontal networks, which would reactivate during retrieval, ultimately manifesting itself through faster and more accurate behavioural performance. Our observation of a reduction of activation in the hippocampus and mPFC for problem-solving skills is consistent with this notion (Albouy, King, et al., 2013; Carr et al., 2011; Chen et al., 2017; King et al., 2013; Rothschild et al., 2016; Wilson & McNaughton, 1994), and suggests that sleep in young but not older adults confers an additional benefit to this memory transformation process. Moreover, there was little change in activation in older adults in the wake condition, suggesting that while the benefit of sleep is lost, a period of wakefulness during the consolidation interval does not lead to forgetting, but rather, a maintenance of the newly acquired strategy.

3.11.2 The role of cortical areas in problem-solving skills

The hippocampus is the first stop in a systematic transfer of information to cortical areas, encompassing both the ventral and dorsal visual stream. The ventral (*i.e., "what"*) visual stream extends through the temporal lobe, playing an important role in the perceptual identification of objects, while the dorsal (*i.e*., *"where"*) visual stream projects to the parietal regions mediating sensorimotor transformations for visually guided actions (Goodale & Milner, 1992). Both sets of skills would be necessary to perform the ToH. Our results revealed an extensive cluster that encompassed brain regions forming much of the ventral (*i.e*., "*what* ") visual stream, which extended through the temporal lobe.

These widespread activations are in line with PET and fMRI studies employing the ToH and similar tasks that require object identification and recognition (Baker et al., 1996; Lazeron et al., 2000; Owen et al., 1996). This is not surprising given the nature of the task, which requires objects of different colours and sizes to be moved from one spatial location to another as determined by higher-order processing and planning. In addition, differences in widespread activations within the dorsal (*i.e*., *"where"*) visual stream were observed in an extensive and strong bilateral activation, which was maximal in the superior parietal cortex, extending ventrally into the inferior parietal and superior occipital cortex. This processing pathway is responsible for long-term representation of spatial working memory and action-oriented behaviors, specifically specializing in capturing spatiotemporal relationships between multiple items, the guidance of actions and recognizing where objects are in space (Kravitz et al., 2012), all of which are functions necessary to perform the ToH task. Our results are consistent with studies of motor sequence memory consolidation (Albouy et al., 2015; Albouy, Fogel, et al., 2013; Cohen et al., 2005; King et al., 2013), which suggest that sleep is involved in the integration of spatial representations. In addition, the parietal cortex is thought to support schema formation (*i.e.*, reorganising new memories into existing, related memories) (Brod et al., 2015; Landmann et al., 2014; Moscovitch et al., 2006). These differences in activation might therefore reflect integration of the newly acquired cognitive strategy into existing schema.

Finally, we observed increased activation in young nappers and old non-nappers (but not in young no-nap or older nap conditions) in the premotor area, which supports abilities needed to carry out the solution for the ToH, such as the planning of movements. More specifically, during early learning, the premotor cortex ensures the transformation between different coordinate frames (*i.e.*, spatial *vs*. motor) (Hikosaka et al., 2002). Interestingly, greater activation of the premotor area is correlated with reduction in errors during motor sequence learning (Lehéricy et al., 2005; Owen et al., 1996; Vyas et al., 2020).

One important limitation to point out is the relatively small sample size and small effect sizes. It is worthwhile noting however, that the sample size meets or exceeds most similar previous studies in the topic area, that the behavioral results have been reliably replicated here, and that the primary MRI results presented here did survive strict control for multiple comparisons (i.e., False Discovery Rate (FDR) whole brain correction). Nonetheless, the results should be interpreted with caution, and future studies employing similar techniques should aim to include larger samples.

3.11.3 Implications and Future Directions

While the current study suggests that sleep supports the optimization and transformation of memory for a newly acquired cognitive strategy, and that this benefit of sleep is reduced with age, it is not clear precisely what age-related changes in sleep (*e.g.*, sleep quality, spindles, slow waves, etc.) might explain the age-related changes in memory consolidation. One of the most dramatic age-related changes in sleep is the reduction of slow waves and sleep spindles (Bliwise, 1993; Blois et al., 1983; Cajochen et al., 2006; Carrier et al., 2001; Feinberg et al., 1967; Ohayon et al., 2004; Reynolds et al., 1991; Scullin, 2014; Webb, 1982), both of which have been shown to be important for procedural memory consolidation in young adults (Clemens et al., 2005; Fogel, Smith, et al., 2007; Fogel & Smith, 2011; Lau et al., 2010; Poe et al., 2010; Ruch et al., 2012). It is thus possible that age-related changes in sleep, such as a reduction in sleep spindles and slow waves contribute to a reduced capacity for the consolidation of procedural memory during sleep (Fogel, Albouy, Vien, et al., 2014; King et al., 2013). Considering our recent work suggesting an involvement of sleep spindles for consolidating problem-solving skills (Fogel, Albouy, Vien, et al., 2014; Fogel et al., 2015), the possibility remains to be explored whether age-related changes in spindles might explain the lost benefit of sleep for behavioural improvements and memory trace transformation for problem-solving skills.

In addition, simultaneous EEG-fMRI sleep studies would enable the investigation of whether an analogous reactivation process occurs for problem-solving skills. Recent reactivation studies have shown that the neuroanatomical regions that are active when acquiring new memories are subsequently reactivated during post-learning sleep (Bergmann et al., 2012; Boutin et al., 2018; Dang-Vu, Schabus, Desseilles, Albouy, Boly, Darsaud, Gais, Rauchs, Sterpenich, & Vandewalle, 2008; Fogel, Albouy, King, Lungu, Vien, Boré, et al., 2017; Maquet, Laureys, Peigneux, Fuchs, Petiau, Phillips, Aerts, Del Fiore, Degueldre, & Meulemans, 2000). For procedural motor skills, the strength of brain reactivation in the putamen time-locked to sleep spindles, was associated with offline gains in performance (Fogel, Albouy, King, Lungu, Vien, Bore, et al., 2017). A similar process has been observed for declarative memory (Clemens et al., 2005; Fogel, Nader, et al., 2007; Gais et al., 2002; Ruch et al., 2012; Schabus et al., 2004; Wolansky et al., 2006). It remains to be investigated if a similar process occurs for problem-solving skills.

3.12 Conclusion

Taken together, our behavioural and functional imaging results suggest that with age, there is a reduction in the benefit that sleep affords to acquiring the solution to a novel problem. This was reflected by age-related differences in the recruitment of brain structures that are enhanced by sleep and are involved in reward learning, planning and problem-solving. Young, but not older adults displayed a reduced change in activation after sleep in structures thought to be involved in the consolidation process of problem-solving (*e.g.,* hippocampus, medial prefrontal cortex); whereas an increase in activation was observed in young adults in structures involved in planning and mental visuospatial imagery (*e.g.,* premotor, parietal cortex). As consolidation progresses, information is integrated into neocortical circuits and reorganized so that it can ultimately be retrieved independently of the hippocampus (Takashima et al., 2009). Our results in young adults suggest that this is also the case for problem-solving skills and that sleep is involved in facilitating this process. By contrast, older adults showed increased activation in the hippocampus post sleep, suggesting that the memory trace remained in a labile state. It is even possible that sleep may have been responsible for inducing this labile state, as this was not observed when older participants remained awake during the retention interval. Thus, sleep may be an opportune time, and perhaps, actively involved in facilitating the strengthening and transfer of information to other brain areas for more permanent storage, a process that is compromised with age.

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3.14 CRediT author statement

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Chapter 4

Study 3: Sleep spindles and slow waves are physiological markers for age-related changes in grey matter in brain regions supporting problem-solving skills

4.1 Title Page

Sleep spindles and slow waves are physiological markers for age-related changes in grey matter in brain regions supporting problem-solving skills

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4.2 Abstract

As we age, the added benefit of sleep for memory consolidation is lost. One of the hallmark age-related changes in sleep is the reduction of sleep spindles and slow waves. Grey matter neurodegeneration is related to both age-related changes in sleep, and age-related changes in memory; including memory for problem-solving skills. Here, we investigated whether spindles, and slow waves might serve as biological markers for neurodegeneration of grey matter, and for the related memory consolidation deficits in older adults. Forty healthy young adults (20-35 years) and thirty healthy older adults (60-85 years) were assigned to either nap or wake conditions. Participants were trained on the Tower of Hanoi in the AM, followed by either a 90-minute nap opportunity, or period of wakefulness, and were retested afterward. We found that age-related changes in sleep spindles and slow waves were differentially related to grey matter intensity in young and older adults in brain regions that support sleep-dependent memory consolidation for problem-solving skills. Specifically, we found that spindles were related to grey matter in neocortical areas (e.g., somatosensory, and parietal cortex), and slow waves were related to grey matter in the anterior cingulate, hippocampus and caudate; all areas known to support problem-solving skills. These results suggest that both sleep spindles and slow waves may serve as biological markers of age-related neurodegeneration of grey matter, and the associated reduced benefit of sleep for memory consolidation in older adults.

4.3 Introduction

Sleep is important for good physical and mental health, as well as memory (for a review, see: Rasch and Born 2013), including declarative memory (Gais et al. 2000; Plihal and Born 1997), procedural motor skills (Fogel et al. 2007, 2015; Nader and Smith 2003; Smith and MacNeill 1994), and for cognitively complex procedural skills, necessary for problem-solving (van den Berg et al. 2019). However, the benefit of sleep for offline memory consolidation is impacted by reductions in both quantity and quality of sleep with increasing age (Fogel et al. 2012; Mander et al. 2017; Sergeeva et al. 2020). For example, as we age, the total amount of slow wave sleep (SWS) is dramatically reduced (Bliwise 1993; Blois et al. 1983; Cajochen et al. 2006; Carrier et al. 2001; Feinberg et al. 1967; Ohayon et al. 2004). Aging also impacts the electrophysiological signatures of non-rapid eye movement (NREM) stage 2 sleep (NREM2); most notably, sleep spindles (Carrier et al. 2011; Lafortune et al. 2012; Martin et al. 2012). Spindles are brief (<3sec) bursts of oscillatory activity (~11-16Hz) generated from rhythmic depolarization of thalamocortical neurons (Steriade 2006). In addition, age impacts the production of other oscillations in NREM sleep including slow waves (Bliwise, 1993; Blois et al. 1983; Cajochen et al. 2006; Carrier et al. 2001; Feinberg et al. 1967; Ohayon et al. 2004). Slow waves occur within the broader delta band (*e.g.*, <4Hz), and are typically characterized by high-amplitude, low frequency (*e.g.*, ~0.5-2.0 Hz), synchronized, discrete phasic oscillations (Bersagliere & Achermann, 2010; Helfrich et al., 2018; McCarley, 2007). These marked decreases in spindles and slow waves begin as early as middle age and become progressively reduced with increasing age (Bliwise 1993; Blois et al. 1983; Cajochen et al. 2006; Carrier et al. 2001; Feinberg et al. 1967; Ohayon et al. 2004).

Significant progress has been made in terms of understanding the structural correlates of sleep-related declarative memory consolidation (Helfrich et al., 2018; Mander et al., 2013;

Muehlroth et al., 2019) and procedural motor skills (Fogel, Vien, Karni, Benali, Carrier, Doyon, et al., 2017; Muehlroth et al., 2019). Moreover, important dissociations have been identified in terms of the unique contributions that sleep makes to different forms of memory (e.g., declarative *vs*. procedural (Born & Wilhelm, 2012; Diekelmann & Born, 2010; Peigneux et al., 2015; Rasch & Born, 2013; Stickgold, 2013; Walker, 2005; Walker & Stickgold, 2004, 2009). Indeed, even within the category of procedural memory, sleep contributes in different ways to motor procedural skills as compared to problem-solving skills that require the acquisition of novel cognitive strategies. It remains to be determined whether distinct neurobiological substrates and their electrophysiological correlates support sleep-related consolidation of newly acquired problem-solving skills. This is the main aim of the current study.

Both sleep and memory issues are the most common complaints reported in aging populations. Age-related changes in sleep have a negative impact on sleep-dependent memory consolidation (for review, see: Mander et al. 2017; Sergeeva et al. 2020). Simultaneous EEG-fMRI brain imaging studies in healthy, young adults have revealed that spindles are associated with increased hemodynamic responses in the thalamic nuclei, paralimbic areas, the frontal cortex, cortical areas involved in sensorimotor processing, as well as the hippocampus (Schabus et al. 2007). Moreover, brain areas that are recruited during both declarative (Bergmann et al. 2012; Jegou et al. 2019), and procedural learning (Fogel et al. 2017; Vahdat et al., 2017) are subsequently reactivated during sleep, time-locked to spindles. The extent of the memory trace reactivation was associated with offline gains in performance, whereby greater post-learning spindle activity is accosiated with stronger memory reactivation and the related offline gains in performance.

Spindles and slow waves form a temporally related complex of events that also include hippocampal ripples (Latchoumane et al. 2017; Mölle et al. 2006; Mölle and Born 2009). These events are believed to work in concert to support memory reactivation and replay during sleep, providing a benefit to the consolidation. Recent studies have shown that spindles and slow waves become decoupled with incresing age (Helfrich et al. 2018), and that this may be related to a reduced benefit of sleep for memory consolidation. Thus, age-related changes in spindles and slow waves may serve as electrophysiological markers of the earliest indicators of age-related cognitive decline, and the associated neurodegeneration.

Age-related changes in sleep are associated with a reduced enhancement of overnight memory consolidation for procedural skills (Brown et al. 2009; Pace-Schott and Spencer 2011; Spencer et al. 2007). Importantly, functional neuroimaging studies in young adults have identified the functional neuroanatomical substrates that support problem-solving skills (for a review, see; (Unterrainer & Owen, 2006). These studies show that the dorsolateral, medial prefrontal cortex, posterior hippocampus (Dagher et al., 2001), supplemental motor cortex, posterior parietal, cerebellum, and striatum; and in particular, the caudate nucleus (Baker et al., 1996; Dagher et al., 1999, 2001; Goldfine et al., 2013; Owen et al., 1996; Rowe et al., 2001; Unterrainer & Owen, 2006) support the acquisition of a novel cognitive strategy (one that involves problem-solving and planning). However, fMRI studies on the role of sleep for supporting motor procedural skills (Fogel, Albouy, Vien, et al., 2014) and complex problem-solving skills (Toor et al., 2022) have shown that older adults do not derive the same benefit from sleep for distinct types of procedural memory consolidation.

Recently, Toor et al. (2022) investigated differences in brain activation from training to retest in young *vs*. older adults as a function of sleep *vs*. wake. Following a period of sleep, young but not older adults displayed a reduced change in activation from training to retest in both the hippocampus and dorsolateral prefrontal cortex (structures thought to be involved in the consolidation process of problem-solving skills), and increased activation of the premotor and parietal cortex (structures involved in planning and mental and visuospatial imagery). Furthermore, sleep enhanced performance and transformed the memory trace in young adults in a pattern consistent with hippocampal-neocortical transfer. However, this pattern was not observed in older adults. This suggests that sleep contributes to the consolidation process in young, but not to the same extent in older individuals for a set of brain areas which support problem-solving skills including the hippocampus, prefrontal regions, and the caudate.

Spindles are an electrophysiological marker of the extent of the age-related reduction in memory consolidation (Fogel et al. 2012, 2014; Fogel et al. 2017). The structural changes in the brain that underlie these functional consequences are beginning to be identified and understood. For example, age-related structural changes in brain regions such as the striatum, hippocampus, frontal cortices, and motor cortical regions are associated with altered sleep physiology in older age (Dubé et al. 2015; Fogel et al. 2017). Furthermore, age-related grey matter loss has been linked to reductions in spindle and slow oscillation generation (Fogel et al. 2017; Mander et al. 2013; Muehlroth et al. 2019). In young adults, measures of slow wave characteristics including amplitude, density, and spectral power of slow waves are strongly associated with structural grey matter density and volume in the prefrontal cortex (Saletin et al. 2013). In older adults, grey matter atrophy is associated with reduced slow wave activity (Mander et al. 2013). In addition, Saletin et al. (2013) reported differences in grey matter density within the insula and auditory cortex that were related to slow spindles (~11-13.5Hz), while grey matter density in the hippocampus was associated with fast spindles (~13.5-16Hz). The extent of the SWA reduction in older adults was associated with reduced grey matter and mediated overnight declarative memory consolidation.

Recently, we identified sleep spindles to be biological markers of age-related neurodegeneration of grey matter in the hippocampus, and memory consolidation deficits for motor procedural skills (Fogel et al. 2017). Thus, suggesting that age-related changes in sleep might mediate cognitive decline due to neurodegenerative processes. However, this study only investigated the impact of age-related changes in sleep for cognitively simple motor procedural skills. It remains to be investigated if sleep is similarly related to neurodegeneration of grey matter which underlies age-related changes in the consolidation of newly learned cognitive strategies required for problem-solving.

We hypothesize that: 1) there will be grey matter differences in specific brain structures that support strategy learning in young compared to older adults (*e.g.*, hippocampus, prefrontal regions, and the caudate), 2) grey matter density in brain structures that support strategy learning will be correlated to a different extent in young *vs*. older adults with both i) offline changes in performance for a newly acquired cognitive strategy, and, ii) spindle/slow wave characteristics. We aim to investigate whether spindles, and slow waves might serve as biological markers for neurodegeneration of grey matter, and the related reduced benefit of sleep for memory consolidation in older adults.

4.4 Methods

4.4.1 Ethics Statement

All participants provided informed consent and were financially compensated for their participation. This research was approved by the University of Ottawa's Research Ethics Board, as well as the Research Ethics Board at The Royal's Institute of Mental Health Research.

4.4.2 Participants

A-priori power analyses, based on studies employing the closest experimental designs, techniques and methodology suggested that N = 15 is sufficient for the study to be adequately powered to test our main hypotheses. Previous studies (Fogel, Albouy, Vien, et al., 2014; Fogel, Vien, Karni, Benali, Carrier, Doyon, et al., 2017), indicate that we would need a bare-minimum of N=15/group to obtain 80% power (Mumford, 2012) to detect age effects for the behavioral and MRI data, and N=12/group for spindle effects at 95% power. This is based on an observed effect size f = ~0.7 in young (age 20-35) *vs*. older participants (age >65). A recent meta-analysis (Leong et al., 2022) has shown that the effect of a nap on procedural tasks is Cohen's *D* = 0.5 (CI_{95} = 0.3–0.7; or, medium to large effect sizes).

Participants were asked to complete a preliminary screening questionnaire to determine their eligibility, which confirmed that they were in good health, right-handed, non-shift workers, free from chronic pain and seizures, did not take medications known to interfere with sleep, had normal or corrected-to-normal vision, a body mass index <30, had no previous history of head injury, or any hand mobility problems and considered themselves to be non-smokers, and normally consumed <2–3 caffeinated beverages/day. In addition, all participants were required to have no previous experience with the Tower of Hanoi (ToH), or similar tasks. Eligible participants were then asked to complete additional screening questionnaires to rule out depression, anxiety, and any sleep disorders. To be included in the study, participants were required to score <10 on the Beck depression (Beck and Beamesderfer 1974) and Beck anxiety (Beck et al. 1988) inventories, in addition to having no signs of sleep disorders, indicated by the Sleep Disorders Questionnaire (Douglass et al. 1994). To rule out signs of mild cognitive impairment or dementia, older participants were also required to score ≥ 26 on the Montreal Cognitive Assessment (Nasreddine et al. 2005) and >2 on the Everyday Cognition Scale (Tomaszewski et al. 2008).

For the duration of the study, all participants were required to limit caffeine intake (no more than one beverage in the AM) and abstain from alcohol and nicotine consumption during the experiment. To ensure compliance with the study protocol, participants were required to wear a Motionlogger (Ambulatory Monitoring Inc., Ardsley, NY, U.S.A) actigraph; a wrist-worn accelerometer which measures sleep-wake-related limb movements. In addition to actigraphy, participants were also asked to complete a log of their daily activities and sleep habits, keep a regular sleep-wake cycle (bedtime: 10:00PM – 1:00AM, wake time: 6:00AM – 9:00AM), and abstain from daytime naps. Participants were excluded from the study if the results of the actigraphy or sleep log indicated non-compliance with the study protocol.

Participants who met the initial eligibility criteria, were then asked to complete a polysomnographic (PSG) recording which served to acclimate them to sleeping in the laboratory, to confirm that they were able to sleep in these conditions, as well as to screen for signs of sleep disorders. During the screening PSG, electroencephalography (EEG) was recorded from six scalp electrodes (*i.e.*, Fz, Cz, Pz, Oz, M1 and M2), placed according to the 10-20 system (Jasper 1958). In addition to the EEG, eye movements were recorded via electrooculography (EOG) from electrodes placed on the outer canthus of the eyes. Bipolar chin muscle activity and heart rhythm were recorded via submental electromyography (EMG) and electrocardiography (ECG), respectively. All electrodes were referenced to Fpz online with Afz ground and impedances kept below 5 KΩ. In addition, an electrode was placed on the anterior tibialis muscle of each leg, to screen for restless leg syndrome and periodic limb movement disorder. To screen for sleep apnea, blood oxygen saturation was recorded via pulse oximetry, nasal airflow was recorded via a thermistor, and both thoracic and abdominal respiratory effort was recorded via respiratory belts. Based on the results of the PSG screening, participants were included in the final sample if they had a sleep efficiency >80%, a periodic limb movement (PLM) index <10 events/hour, and an apnea-hypopnea index <5 events/hour.

Following PSG screening, all participants were randomly assigned to either the Nap or Wake (*i.e.*, “No-Nap”) condition, yielding four groups: Young Nap (YN), Young No Nap (YNN), Older Nap (ON), and Older No-Nap (ONN). To minimize time of day effects for learning and memory performance in young *vs.* older adults, a nap protocol was utilized. For the participants that met the initial eligibility criteria, seven older participants and five young participants did not meet the inclusion criteria for keeping a regular sleep schedule within the prescribed hours. Furthermore, three older participants did not meet the PSG pre-screening criteria, due to not achieving any sleep during the nap opportunity. Finally, one younger participant did not meet the PSG pre-screening criteria for bruxism, and another for periodic leg movements. The final sample consisted of 40 healthy young adults aged 20-35 (23 females; mean age = 23.85, SD = 3.86) and 30 healthy older adults aged 60-85 (20 females; mean age = 68.00, SD = 7.62) years old. The final groups included N=20 (12 females; mean age = 23.05, SD = 3.0) young participants in the nap condition (YN), N=20 (11 females; mean age = 24.65, SD = 4.50) young participants in the wake condition (YNN), N=15 (9 females; mean age = 66.13, SD = 6.97) older participants in the nap condition (ON), and finally, N=15 (11 females; mean age = 68.07, SD = 8.41) older participants in the wake condition (ONN).

The data analyzed in this study were part of a larger polysomnographic, behavioural, and MRI protocol employing various techniques intended to address a variety of research questions. The behavioural results have been partly reported previously (Toor et al., 2022; van den Berg et al., 2021). These previous studies investigated functional brain activity in relation to sleep and memory, whereas the current study is focussed on structural grey matter in relation to sleep and memory. The structural MRI data and VBM analyses have not been reported elsewhere and are unique to this study. See Toor et al., 2022 for additional methodological details about the experimental protocol specific to that study. All methods relevant to the current investigation are reported here and methods employed in related studies are reported in the Supplemental Methods.

4.4.3 Experimental Design

One-week following the screening process, all eligible participants returned to the sleep laboratory for ToH testing with MRI structural scans in addition to PSG (Figure 1). Participants completed the training session of the Tower of Hanoi (ToH) at 10:00AM (see: Toor et al. (2022) for corresponding behavioral and functional neuroimaging results in these participants). At 1:00PM, the Nap participants engaged in a 90-minute daytime nap opportunity, whereas participants in the Wake condition remained awake while reading and lying in a supine position under dim ambient lighting. Both Nap and Wake conditions were monitored via PSG recording (*n.b.*, in part to ensure the participants in the Wake conditions did not fall asleep). At 5:00PM, more than 30 minutes after the end of the nap opportunity (to avoid sleep inertia effects), participants completed the retest session of the ToH. The Stanford Sleepiness Scale (Maclean et al. 1992) and the Psychomotor Vigilance Test (PVT) (Dinges and Powell 1985) were administered prior to and following the training and retest sessions to obtain subjective and objective measures of sleepiness across the testing protocol.

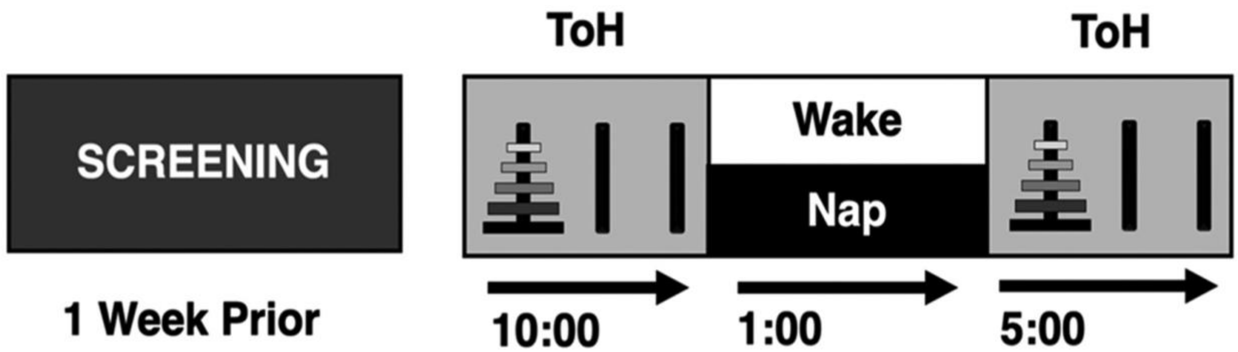

Figure 1. Study design. Overview of experimental protocol in the nap and wake conditions. After an initial screening and acclimatization polysomnography (PSG), participants were divided into young nap (YN), young no nap (YNN), older nap (ON), and older no nap (ONN) conditions. Nap condition: Participants arrived at the sleep laboratory at 9:00 a.m. and were trained and tested on the ToH at 10:00 a.m. They then had a nap opportunity from 1:00 p.m. to 2:30 p.m. while their sleep was recorded via PSG. Upon awakening, but after sleep inertia dissipation participants were retested at 5:00 p.m. Wake condition: The same procedure was used in the eake condition, except that instead of a daytime nap opportunity, individuals remained awake and read in a supine position with polysomnographic recording.

4.5 Behavioral Tasks & Analysis

A computerized version of the ToH task was employed, coded in MATLAB R2016a (Mathworks Inc., Natick, MA, USA) using the Psychophysics Toolbox extension v3.0.12 (Brainard, 1997a; Kleiner et al., 2007) for Windows (Microsoft, Redmond, WA, USA). The ToH task included 5-disks of increasing size stacked in ascending order which could be moved to and from one of three pegs by pressing the corresponding key on the button pad. The main goal of the task was to move all disks from the start (far-left hand peg) position to the goal (far right-hand peg) position in the same ascending order while abiding by the following constraints: 1) disks could only be moved one at a time, 2) each move required taking an upper-most disk from one of the stacks and placing it on another peg, and, 3) only a smaller disk could be placed on top of a larger disk. The task can be solved through trial-and-error in order to learn to employ recursive logic; breaking down the overall optimal solution into smaller components and recursively performing this sequence of smaller solutions several times. The optimal number of moves to complete the ToH is determined algebraically by $2^N - 1$, *where N is the number of disks*, or 31 moves for the 5-disk task.

In total, participants performed eight training trials (to ensure adequate practice), and four retest trials of the ToH, where each trial was followed by a 20-second rest period. During the rest, participants were shown the three pegs with no disks and were instructed not to press any buttons. A trial of the ToH ended when either the participant solved the task (*i.e.*, all five disks were in ascending order on the far-right peg), or if the maximum number of moves was reached prior to solving the task. The maximum number of moves was set to two times the optimal number of moves ($2^N - 1$, *where N is the number of disks, i.e.,* $2^5 - 1 = 31$), or in this case, 62 moves. ToH performance was measured in terms of speed (time to complete each ToH trial) and accuracy (Mean Absolute Percentage Error; MAPE). The MAPE for *n* trials was calculated as follows:

$$\text{MAPE} = 100 - \left(\frac{1}{\text{n}}\right) * \sum \left(\frac{|\text{number of moves} - \text{ optimal number of moves}|}{\text{number of moves}}\right) * 100$$

The MAPE can be interpreted as the percentage of perfect performance (*e.g.*, 31 moves), whereby 100% represents perfect performance (*i.e.*, the optimal solution), whereas 50% reflects making twice as many moves as perfect performance, and 0% theoretically represents an infinite number of moves. For all measures, the % improvement for both speed and accuracy was calculated as follows:

$$\% \text{ improvement} = \left(\frac{\text{Retest} - \text{Training}}{\text{Training}}\right) * 100$$

4.5.1 Behavioural Analysis

SPSS Statistics version 27 (IBM, Armonk, New York, U.S.) was used to carry out the behavioural statistical analyses. To ensure that learning did take place on the ToH task in both the young and older groups, 2x8 Age (Young, Older) x Trial (trails 1 to 8) ANOVAs were conducted for speed and accuracy. Simple effects repeated measures ANOVAs in each group were used to follow up any significant effects.

To explore whether sleep facilitated performance on the ToH task in young and older groups, 2x2 Age (Young, Older) x Condition (Nap, Wake) ANOVAs were conducted for % change in speed and accuracy. Independent samples t-tests were used to follow-up any significant group effects.

4.6 Polysomnographic Recording & Analysis

4.6.1 Recording Parameters

Embla N7000 amplifier systems (Natus, Pleasonton, CA, USA) were used for in-laboratory PSG recordings. All signals were sampled at 500 Hz. EEG (F3, Fz, F4, C3, Cz, C4, P3, Pz, P4, Oz, M1, M2) and EOG (placed on the outer canthus of each eye) were referenced online to Fpz with a ground electrode placed at Afz. EEG and EOG were re-referenced offline to average mastoid derivations (M1 and M2), placed according to the international 10-20 system (Jasper 1958). Submental EMG channels were recorded as bipolar derivations. EEG was filtered offline from 0.3 to 35 Hz, EOG was filtered from 0.3 to 10 Hz and EMG was filtered from 10 to 50 Hz.

Manual sleep stage scoring was conducted by an expert PSG technologist, according to the American Academy of Sleep Medicine criteria (Iber et al., 2007b) in 30 second epochs using Hume analysis software (https://www.jaredsaletin.org/hume) for EEGlab (Delorme & Makeig, 2004). Movement artifacts were automatically detected using custom MATLAB (The Mathworks Inc., Natick, MA, United States) scripts. This method employs a variance-based (*i.e.*, first-derivative) transformation of the EMG channels, then, movements event markings are visually inspected by an expert to validate the automatic detection algorithm before being used to exclude EEG from further analyses.

4.6.2 Sleep Spindle Detection

A well-established (Albouy et al. 2015; Fang et al., 2017, 2019; Fogel et al. 2017; Fogel et al. 2014; Fogel et al. 2017) and validated method (Ray et al. 2015) implemented in EEGlab using the "*Detect_Spindles*" plugin (https://github.com/stuartfogel/detect_spindles) was used to detect spindles from Fz and Pz in movement artifact-free NREM sleep. For more details see: (Ray et al. 2015). Spindles were identified in the 11-16 Hz range (Ferrarelli et al. 2010; Fogel et al. 2007, 2014; Landolt et al. 1996; Zeitlhofer et al. 1997), and identified as either slow (11-13.5 Hz) or fast (13.5-16Hz) at the sites where they are maximal (Anderer et al. 2001; De Gennaro and Ferrara 2003; Terrier and Gottesmann 1978); *i.e.*, at Fz and Pz, respectively. The number of spindles during NREM sleep, density (#/min) and size (sum of absolute amplitude) were extracted from these analyses.

4.6.3 Slow Wave Detection

Slow waves were detected using period amplitude analysis (PAA), adapted from previously published methods (Bersagliere & Achermann 2010; Feinberg et al. 1978; Geering et al. 1993), using the EEGlab (Delorme & Makeig 2004) "*PAA*" plugin (https://github.com/stuartfogel/Period-Amplitude-Analysis) written for MATLAB (The MathWorks Inc., Natick, MA, United States). The slow wave data was extracted from movement artifact-free NREM sleep epochs. In line with previous research (Bersagliere & Achermann, 2010), the detection method employs band-pass filtering to detect waves between 0.5-2.0 Hz. Derivations Cz, Fz, Oz, and Pz were band-pass filtered 0.46 Hz (64^{th}-order Chebyshev type II high-pass filter, -80 dB stopband attenuation) and 2.15 Hz (32^{nd}-order Chebyshev type II low-pass filter, -80 dB stopband attenuation) to achieve minimal attenuation in the band of interest (0.5–2.0 Hz) and good attenuation at neighbouring frequencies. The filters were applied in the forward and reverse directions, to achieve zero-phase distortion resulting in doubling of the filter order. Half-waves were determined as deflections (negative or positive) between two consecutive zero crossings in the band-pass filtered signal. In line with scoring rules for slow waves, the peak-to-peak amplitude threshold of 75µV (Iber et al. 2007) was applied to neighbouring half waves. Slow wave detection was visually verified following automated detection. As described in (Bersagliere and Achermann 2010), half wave number, density (#/min) area (μV^2), were extracted for each participant where slow waves are typically maximal (Fz). Exploratory bivariate correlations between behavioral performance improvements on the ToH (accuracy and speed) and sleep oscillations (fast spindles, slow spindles, and slow waves) during NREM sleep in young and older adults are presented in Supplemental Table S1.

4.7 MRI Imaging Acquisition & Analysis

4.7.1 Recording Parameters

Functional magnetic resonance imaging (fMRI) data was collected on a Siemens Biograph mMR 3.0 Tesla MRI whole body scanner (Siemens, Erlangen, Germany) using a 12-channel head coil. Anatomical images were acquired using a standard 3D Multislice MPRAGE sequence (TR = 2300 ms, TE = 2.98 ms, TI = 900 ms, FA = 9◦, 176 slices, FoV = 256 × 256 mm^2, matrix size = 256 × 256 × 176, voxel size = 1 × 1 × 1 mm^3) was used to obtain high-resolution T1-weighted images for all participants used for subsequent VBM analyses.

4.7.2 Preprocessing

Structural data were analyzed with FSL (Douaud et al. 2007) using an optimized VBM protocol (Good et al. 2001; Smith et al. 2004). Similar to a previously published study employing this method (Fogel et al. 2017), the following steps were employed: (1) structural images were brain extracted and grey matter segmented before being registered to MNI 152 standard space using nonlinear registration (Andersson et al. 2007); (2) a study specific grey matter template was created using FSL-VBM protocol; (3) all brain-extracted images were segmented into grey matter, white matter, and cerebrospinal fluid (CSF); (4) grey matter images were then affine-registered to the MNI grey matter ICBM-152 template, concatenated, and averaged; (5) the grey matter images were then re-reregistered to this first-pass "affine" grey matter template using non-linear registration, concatenated into a 4D image, averaged and flipped along the x-axis; (6) both mirror images were then averaged to create the final symmetrical, study-specific non-linear grey matter template at 2 x 2 x 2 mm^3 resolution in standard space; (7) all native grey matter images were non-linearly registered to the study-specific template generated in the previous step, and modulated to correct for local expansion due to the nonlinear component of the spatial transformation (Good et al. 2001); and lastly, (8) all images were then smoothed with an isotropic Gaussian kernel with a sigma of 3 mm.

4.7.3 Statistical Analysis

To investigate age-related differences in grey matter, voxel-wise General Linear Modelling (GLM) using FSL VBM was applied to investigate grey matter for the linear contrasts for: (1) young; (2) older; and (3) young-older participants using threshold-free cluster enhancement (TFCE) permutation-based non-parametric testing using 10,000 permutations (Nichols and Holmes 2002; Winkler et al. 2014). This procedure generated maps of t-statistics, the corresponding uncorrected *p*-value maps, and family-wise error (FWE) corrected *p*-value maps for young *vs*. older groups of participants. Total intracranial volume, age, sex and depression scores were mean-centered and included in the GLM as variables of non-interest in the model. To follow-up age-related differences in grey matter in young *vs*. older adults, the offline changes in: 1) ToH performance, 2) spindles, 3) slow waves, and, 4) total sleep time were entered as covariates of interest into the GLM. Contrast images were generated to identify brain regions where grey matter correlated with the covariates of interest to a different extent in young *vs*. older individuals.

Finally, to co-localize differences in grey matter in young *vs*. older participants which correlated with both offline changes in performance and sleep characteristics, the conjunction of performance-related grey matter t-maps and spindle, or, slow wave-related grey matter t-maps was taken as the minimum t-statistic using the global null hypothesis (Friston et al. 2005). These conjunction maps were able to identify brain regions where grey matter was correlated to a different extent in young and older (and young *vs*. older) participants with offline changes in performance, spindles, or, slow waves over: (1) the performance-correlated statistical parametric maps in young and older participants with (2) each spindle-correlated map (*e.g*., density, area) in young and older participants (*e.g*., young, older, and young vs. older), and (3) each slow wave-correlated map (*e.g*., density, area) in young and older participants (*e.g*., young, older, and young vs. older). The conjunction maps were thresholded so that results were significant at a combined *p*-level of $p < 0.001$. Note that a significant conjunction does not necessarily mean all the contrasts were individually significant (*i.e*., a conjunction of significance). Instead, it indicates that the effects were consistently high across all conditions included in the conjunction, such that they were jointly statistically significant (Friston et al. 2005). Note that the minimum t-values do not have the usual Student *t*-distribution and small minimum t-values can be highly significant.

4.8 Results

4.8.1 Behavioural Data

First, to ensure that learning did take place in both young and older participants, an Age (Young, Older) x Trial (trails 1 to 8) ANOVA revealed a significant increase in speed over the course of the training session overall (F (7,476) = 36.71, $p < 0.0001$, $\eta^2 = 0.35$), which was observed in both the Young (F (7,273) = 35.17, $p < 0.0001$, $\eta^2 = 0.47$) and Older groups (F (7,203) = 12.22, $p < 0.0001$, $\eta^2 = 0.30$). There was no significant interaction with Age (F (7,476) = 1.17, $p = 0.32$, $\eta^2 = 0.02$), suggesting that both young and older adults improved on the task with practice and did so, to the same extent. Again, a generally similar pattern was observed for accuracy in terms of overall improvement with practice at training (F (7,476) = 5.70, $p < 0.0001$, $\eta^2 = 0.08$). Young participants significantly improved in terms of accuracy with practice (F (7,273) = 7.30, $p < 0.0001$, $\eta^2 = 0.16$), whereas older adults did not (F (7,203) = 1.41, $p = 0.202$, $\eta^2 = 0.05$). However, it should be noted that there was no significant difference in accuracy between young and older participants by the end of the training session (t (68) = 0.06, $p = 0.960$, $d = 0.01$), suggesting that, importantly, by the end of the training session, young and older participants did learn the task to the same extent.

To investigate the age and sleep-related changes in performance improvements, a sleep/wake condition (Nap, Wake) x Age (Young, Older) group ANOVA revealed a significant interaction for % increase in speed (F (1,66) = 64.39, $p < 0.0001$, $\eta^2 = 0.49$) and accuracy (F (1,66) = 15.73, $p < 0.0001$, $\eta^2 = 0.19$) (Figure 2). Follow-up tests showed that the Young Nap (YN) condition had significantly greater improvement than the Young No Nap (YNN; speed: t (38) = 8.86, $p < 0.0001$, $d = 2.80$; accuracy: t (38) = 2.36, $p = 0.024$, $d = 0.75$) and Older Nap (ON) conditions (speed: t (33) = 12.13, $p < 0.0001$, $d = 4.14$; accuracy: t (33) = 4.54, $p < 0.0001$, $d = 1.55$). There was no difference between the YNN and Older No Nap (ONN) conditions (speed: t (33) = -1.16, $p = 0.256$, $d = -0.40$; accuracy: t (33) = -0.57, $p = 0.573$, $d = -0.19$). However, individuals in the ON condition performed significantly worse than the ONN condition (speed: *t* (28) = -2.87, *p* = 0.008, *d* = -1.05; accuracy: *t* (28) = -4.04, *p* < 0.0001, *d* = -1.47).

It is important to note that mean speed (i.e., 1/RT) in PVT performance did not change over the course of the testing sessions, as a function of age or sleep/wake condition (F (3,192) = 2.13, p = 0.120). No other main effects or interaction effects were significant. Thus, suggesting that a daytime nap did not differentially impact vigilance in young and older adults over the course of the experimental protocol.

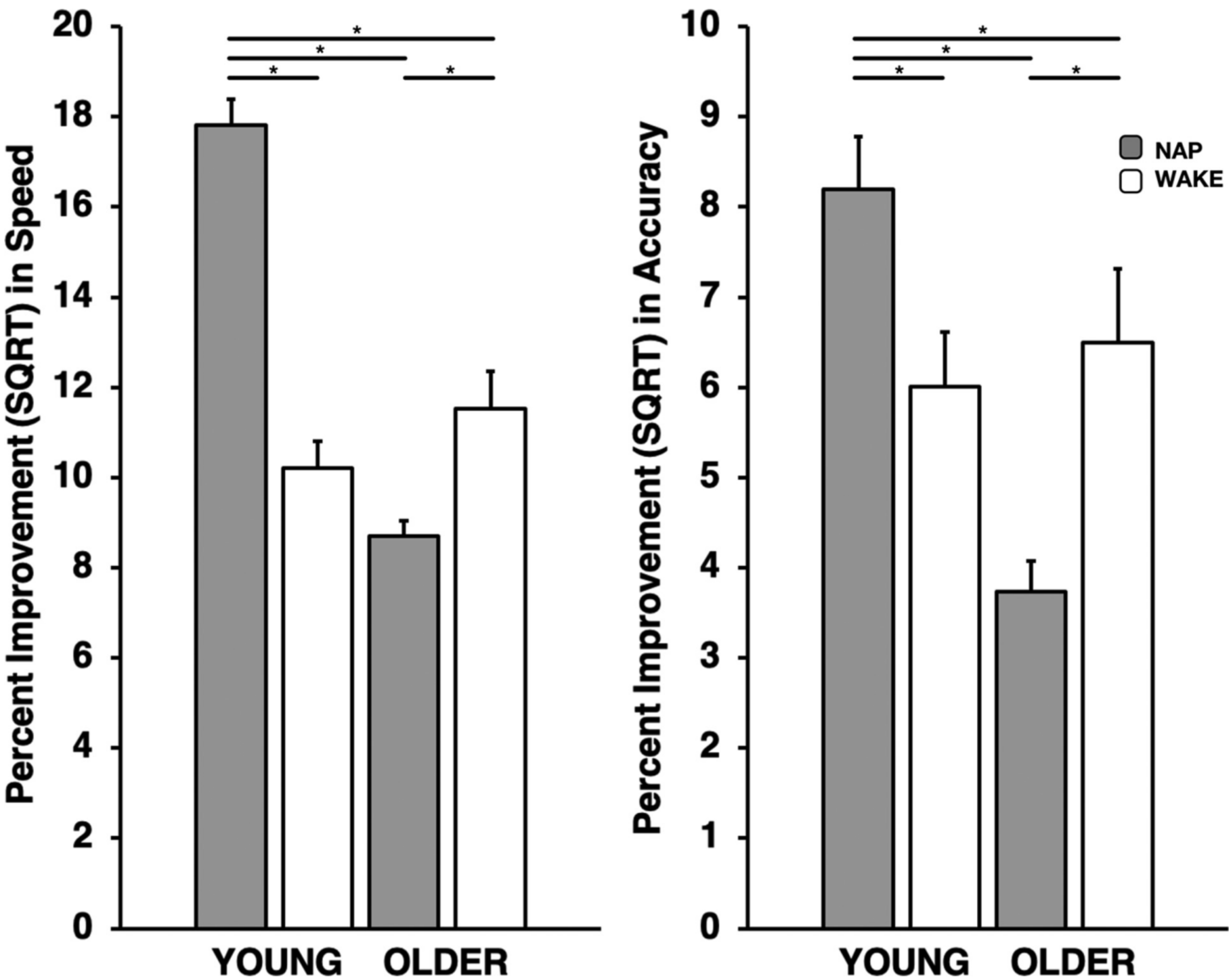

Figure 2. ToH performance. Mean percent improvement for speed and accuracy on the ToH from training to retest in young and old participants. Young adults benefited from a daytime nap

as compared with wake, whereas older adults did not. Error bars represent standard error of the mean. (Figure adapted with permission from Toor et al. [2022]).

4.8.2 Sleep Architecture

As expected, young and older participants differed in terms of sleep characteristics (Table 1). Older participants spent significantly more time awake (minutes: t (33) = 4.00, p = <0.001; %TST: t (33) = 4.00, p = <0.001). Furthermore, it took older adults significantly longer to initially fall asleep at lights out (t (33) = 4.75, p = <0.001), and they displayed reduced total sleep time (t (33) = -2.52, p = 0.017) relative to younger adults. Older participants exhibited significantly less time spent in SWS (minutes: t (33) = -2.46, p = 0.019; %TST: t (33) = -2.48, p = 0.018) and had significantly more time in lighter, NREM2 sleep (%TST: t (33) = 2.16, p = 0.038) relative to younger adults. Lastly, there was significantly more REM sleep (minutes: t (33) = -2.96, p = 0.006; % TST: t [33] = -4.18, p = <0.001) in young compared to older adults. However, it should be noted that this was largely due to a floor effect, whereby 87% of older participants had no REM sleep at all, compared to only 25% of young participants. Due to the variable duration of NREM2 sleep and an insufficient quantity of SWS across participants during a daytime napping protocol, NREM2 and SWS were combined into a total measure of NREM sleep for spindle and slow wave detection and subsequent analyses.

It has been previously shown that as little as 5 minutes of sleep is sufficient to afford a measurable benefit on the ToH and related procedural tasks (Fang et al., 2021; Fogel, Albouy, Vien, et al., 2014; King et al., 2013; Milner et al., 2006; Toor et al., 2022; van den Berg et al., 2021). In the current study, young participants had on average 68.79 +/-3.19 minutes of sleep and older adults had 51.53 +/-6.83 minutes of sleep; which is in line with, or greater than previous studies, and would be sufficient to lead to the hypothesized effect of sleep (Leong et al., 2022). In addition, sleep duration did not correlate with offline gains in performance in either young (r(20)

= -0.300, p = 0.199), or older participants (r(15) = 0.371, p = 0.173). Thus, it is unlikely that sleep duration on its own could explain differences in memory consolidation.

Table 1. Mean (and standard error; [SE]) sleep parameters recorded during the 90-min daytime nap retention interval in both young and older participants.

	Young		**Older**		***t***	***P***
Sleep Feature	**M**	**SE**	**M**	**SE**		
Wake (min)	19.52	3.11	47.37	7.03	4.00	<0.001
Stage 1 (min)	5.63	1.06	7.07	1.19	0.93	0.361
Stage 2 (min)	36.92	2.99	34.70	5.03	-0.44	0.663
SWS (min)	20.04	3.69	8.30	2.88	-2.46	0.019
REM (min)	6.21	1.29	1.47	0.84	-2.96	0.006
TST (min)	68.79	3.19	51.53	6.83	-2.52	0.017
Wake (%)	21.69	3.29	52.63	7.80	4.00	<0.001
Stage 1 % TST	8.86	1.84	17.62	4.75	1.92	0.064
Stage 2 % TST	54.53	3.83	67.00	4.53	2.16	0.038
SWS % TST	27.86	4.40	13.64	3.51	-2.48	0.018
REM % TST	8.75	1.89	2.00	1.00	-4.18	<0.001
SOL (min)	6.31	0.80	15.23	1.93	4.75	<0.001
WASO (min)	13.21	3.01	13.80	3.56	0.13	0.898

Standard error (SE); minutes of sleep (min); rapid eye movement (REM); slow wave sleep (SWS); total sleep time (TST), sleep onset latency (SOL); wake after sleep onset (WASO).

4.8.3 Sleep Spindles & Slow Waves

Younger participants had significantly more spindles per minute (slow: t (33) = -2.74, *p* = 0.010), fast: t (33) = -2.77, *p* = 0.009) and significantly larger spindles (slow: t (33) = -3.67, *p* = <0.001) relative to older adults (Table 2). Younger adults had significantly more slow waves per minute (t (31) = -3.57, *p* = 0.001), and significantly larger slow waves (t (31) = -3.60, *p* = 0.001) relative to older adults (Table 2).

Table 2. Density and size of slow (11-13.5 Hz) and fast (13.5-16 Hz) spindles and slow waves during the 90-min daytime testing nap intervals in young and older participants.

		Young		Older		*t*	*P*
		M	SE	M	SE		
Spindle Density							
	Slow	2.73	0.23	1.79	0.26	-2.74	0.010
	Fast	3.59	0.32	2.38	0.28	-2.77	0.009
Spindle Size							
	Slow	34.89	2.56	22.25	2.01	-3.67	<0.001
	Fast	36.36	2.42	41.24	17.82	1.00	0.321
Slow wave Density		23.83	4.70	3.63	0.91	-3.57	0.001
Slow wave Size		38.44	1.64	29.94	1.47	-3.60	0.001

4.9 Structural MRI results

4.9.1 Grey Matter Differences in Young vs. Older Adults

As expected, greater grey matter density was observed in young *vs*. older adults in a widespread set of brain regions including cortico-striatal-hippocampal and cortico-cerebellar regions. There was greater grey matter density in the cerebellum, cingulate cortex, and the precentral gyrus bilaterally. Other regions such as mid temporal, medial frontal gyrus, visual associative, temporal lobe, superior frontal, anterior prefrontal cortex, and the primary motor cortex also displayed greater grey matter density in young relative to older adults (Table 3, Figure 3). Importantly, greater grey matter density was observed in young adults in areas important for acquisition of novel cognitive strategies such as the striatum, including the putamen and the caudate, as well as bilaterally in the hippocampus. Finally, the widespread grey matter differences observed frontally included the prefrontal and dorsolateral prefrontal cortex in young *vs*. older adults.

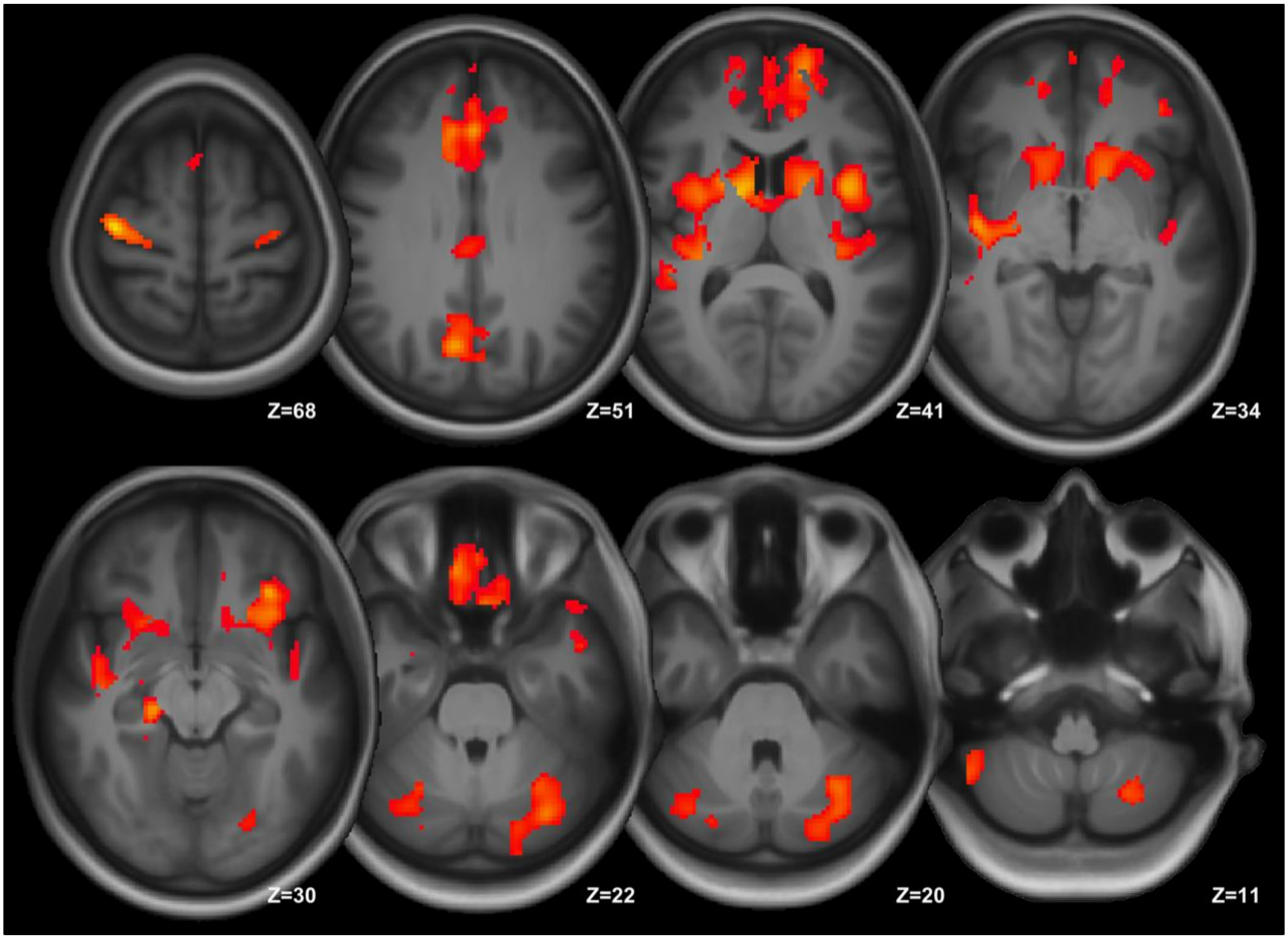

Figure 3. Gray matter differences in young versus older adults. Several areas that support procedural problem-solving skills differed between young and older adults, including motor cortical sensorimotor areas, the mPFC, the precuneus, the cingulate cortex, the caudate nucleus, the putamen, the hippocampus, and the cerebellum. Clusters thresholded at $P < 0.005$, FWE. X, Y, and Z coordinates are given in MNI coordinates, displayed in radiological orientation.

Table 3. Brain regions with significantly greater GM in young versus older participants

L/R	Covariates of interest	Brain region	Voxels	t	*p*	X	Y	Z
		Young vs. Older						
L	None	Middle temporal	8062	7.73	<0.001	-46	4	-28
L	None	Medial frontal gyrus	5629	6.16	<0.001	-12	50	6
L&R	None	Cerebellum VIIb	921	5.64	<0.001	-24	-68	-50
L&R	None	Posterior cingulate cortex	537	5.61	0.000	6	-26	26
L&R	None	Sensorimotor	363	7.52	0.000	40	-18	60
R	None	Visual associative	44	4.49	0.000	30	-90	-18
R	None	Temporal lobe	17	3.13	0.001	26	-38	-14
R	None	Superior frontal	15	5.64	0.000	24	38	46
L	None	Prefrontal cortex	13	3.24	0.001	-30	48	0
R	None	Cerebellum crus II	12	4.20	0.001	26	-78	-34
L	None	Primary motor cortex	11	5.21	0.000	-6	-28	78

Aligned anatomical coordinates for side where effects were maximal are reported when bilateral. $p < 0.005$, FWE using TFCE.

4.9.2 Grey Matter Correlates Differently with ToH Performance, Spindles, & SW in Young vs. Older Adults

To follow-up the age-related differences in grey matter between young and older adults, a series of regressions were conducted by including ToH performance, spindle, and slow wave parameters (*e.g.*, density and size) into the GLMs as covariates of interest. Here, we controlled for age, sex, and depression scores. Grey matter in young and older individuals correlated to a different extent in young (*i.e.*, more positive) *vs*. older adults (*i.e.*, more negative) with improvements in ToH speed in the brainstem (the pons, in particular), putamen, hippocampus, cerebellum, the temporal lobe, parietal lobe, and the prefrontal cortex (Table 4A). In addition, grey matter correlated to a different extent in young (*i.e.*, more positive) *vs*. older adults (*i.e.*, more negative) with spindles in the parieto-occipital sulcus (*n.b.*, a region important for planning), the premotor, supplementary motor area, the pons, and bilaterally in the primary motor cortex (Table 4B). Finally, grey matter in young and older individuals correlated to a different extent in young (*i.e.*, more positive) *vs*. older individuals (*i.e.*, more negative) with slow waves in the pons, cerebellum and in both the anterior and posterior hippocampus (Table 4C). In addition, to determine if total sleep duration was significantly related to grey matter in young *vs*. older adults, we also entered total sleep time into the model. However, there was no significant difference in the relationship between grey matter and sleep duration in young *vs*. older adults. Thus, suggesting that the duration of the nap itself is unlikely to explain the above findings.

Table 4. Brain regions where relationship between gray matter and the covariates of interest (e.g., performance improvements, slow waves, and spindles) differed significantly between young (i.e., more positive correlation) and older (i.e., more negative correlation) adults

L/R	Covariates of interest	Brain region	Voxels	t	*p*	X	Y	Z
(A) Young vs. older: GM correlated with ToH speed								
L&R	Speed	Brainstem/pons	987	4.93	<0.001	-6	-42	-44
L	Speed	Cerebellum	138	4.53	<0.001	-40	-44	-40
R	Speed	Putamen	129	6.47	<0.001	22	-12	20
L&R	Speed	Temporal	81	3.66	0.001	62	-46	-12
L	Speed	Prefrontal	37	4.39	<0.001	-48	52	2
R	Speed	Parietal	12	3.96	0.001	14	41	51
L	Speed	Hippocampus (posterior)	12	3.56	0.001	-38	-34	-10
(B) Young vs. older: GM correlated with spindles								
R	Slow spindle size	Premotor & SMA	338	5.33	<0.001	2	-10	56
R	Slow spindle size	Pons	48	5.19	<0.001	2	-14	25
L&R	Fast spindle size	Premotor & SMA	487	4.79	<0.001	-2	2	48
L&R	Fast spindle size	Primary Motor Cortex	45	3.44	0.001	18	-16	62
L	Fast spindle size	Parieto-Occipital Sulcus	33	3.68	0.001	-14	-82	44
C: Young vs. older: GM correlated with slow waves								
R	Slow wave size	Pons	59	3.53	<0.001	2	-14	-22
R	Slow wave size	Cerebellum	40	4.19	0.001	2	-64	-4
R	Slow wave size	Hippocampus (posterior)	21	4.16	0.001	30	-36	4
L&R	Slow wave size	Hippocampus (anterior)	17	2.47	0.001	20	-20	-24

Significant differences in gray matter–covariate correlations for offline changes in ToH performance (A), spindles (B), and slow waves (C). X, Y, and Z coordinates are given in MNI coordinates. (SMA) Supplementary motor area. Aligned anatomical coordinates for the side where effects were maximal are reported when bilateral. $P < 0.001$, uncorrected using TFCE.

4.9.3 Conjunction Between ToH Performance Gains & Sleep in Young & Older Adults

The next step was to perform conjunction analyses, which allowed us to co-localize differences in grey matter in which correlated to a different extent in young and older participants with both offline changes in performance and sleep oscillation characteristics (*e.g.*, spindles, slow waves). Conjunction analyses (Figure 4) revealed regions where grey matter was correlated to a different extent in young versus older adults with both ToH performance gains and sleep parameters. Grey matter correlated with both ToH gains and slow waves to a different extent in young versus older adults in the anterior cingulate cortex, hippocampus (Figure 4F-G & inset), cerebellum, caudate (Figure 4C-D), putamen and the thalamus (Table 5B). Again, the same overall pattern was observed whereby grey matter was positively correlated in young individuals, and negatively in older individuals.

In addition, grey matter correlated with both ToH gains and spindles to a different extent in young versus older adults in the superior temporal, cerebellum, brainstem (in particular, the pons), somatosensory, prefrontal, orbitofrontal, anterior cingulate, and the parietal cortex. Similar to previous work (Fogel et al. 2017), for all regions, the same overall pattern was observed, whereby positive correlations were observed in young adults, while negative correlations were observed in older adults (Table 5A), which significantly differed from one another.

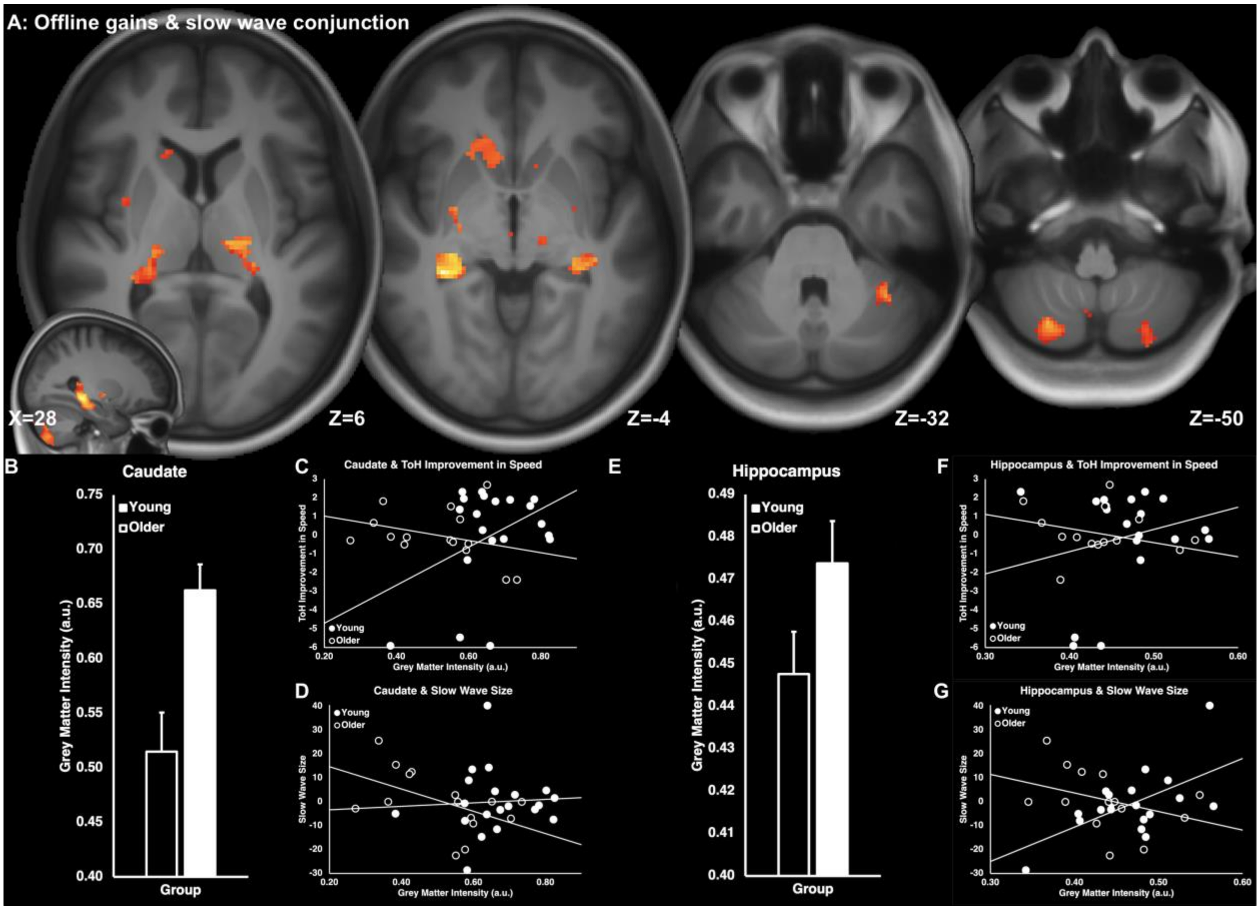

Figure 4. (A) Significant clusters of gray matter positively correlated with offline changes in performance in conjunction with slow wave size in the hippocampus, caudate, putamen, and cerebellum in young versus older adults (Table 5). The relationship between gray matter and the conjunction of the covariates of interest (e.g., performance improvements and slow waves) differed significantly between young (i.e., more positive correlation) and older (i.e., more negative correlation) adults. **(B,C)** Mean gray matter density in the caudate was higher ($P < 0.005$, FWE) on average in young versus older adults **(B)** and was more negatively correlated with offline changes in performance in older individuals than in young participants, who showed a positive relationship between changes in performance and gray matter **(C)**. **(D)** A similar pattern of differences between correlations in young versus older adults was observed between gray matter and slow wave size. **(E–G)** The same overall pattern was observed for the hippocampus. (Inset) Sagittal view at X = 28. X, Y, and Z coordinates are given in MNI coordinates, displayed in radiological orientation.

Table 5. Brain regions where relationship between gray matter and the conjunction of the covariates of interest (e.g., performance improvements, slow waves, spindles) differed significantly between young (i.e., more positive correlation) and older adults (i.e., more negative correlation).

L/R	Covariates of interest	Brain region	Voxels	t	*p*	X	Y	Z
(A) Young vs. older: ToH gains & spindle conjunction								
L	ToH & slow spindle density	Superior Temporal	103	2.57	0.010	-50	-28	18
L&R	ToH & slow spindle density	Brainstem/pons	41	2.85	0.015	2	-34	-32
L	ToH & slow spindle density	Cerebellum	40	2.97	0.018	-42	-48	-34
L	ToH & slow spindle density	Somatosensory	37	2.13	0.013	-64	-8	24
R	ToH & fast spindle size	Orbitofrontal	50	2.26	0.013	28	56	-14
L&R	ToH & fast spindle size	Somatosensory	49	1.83	0.013	-42	-16	40
R	ToH & fast spindle size	Parietal	45	2.06	0.011	56	-30	48
R	ToH & fast spindle size	Anterior Cingulate	38	1.80	0.015	14	38	14
L&R	ToH & fast spindle size	Prefrontal	14	1.70	0.021	-18	66	10
(B) Young vs. older: ToH gains & slow wave conjunction								
R	ToH & slow wave density	ACC	25	2.09	0.014	18	30	2
L&R	ToH & slow wave size	Hippocampus	478	2.77	0.004	30	-32	-6
L&R	ToH & slow wave size	Thalamus	478	2.37	0.015	22	-24	4
L&R	ToH & slow wave size	Cerebellum	274	2.15	0.016	26	-74	-52
L&R	ToH & slow wave size	Caudate	185	1.87	0.019	14	20	0
L	ToH & slow wave size	Cerebellum	96	2.17	0.024	-38	-52	-22
R	ToH & slow wave size	Insula	51	1.91	0.026	38	0	10
R	ToH & slow wave size	Putamen	14	1.94	0.021	28	-10	-4

Significant differences in gray matter-covariate correlations for ToH performance gains and spindles (A) and ToH performance gains and slow waves (B). X, Y, and Z coordinates are given in MNI coordinates. (PFC) Prefrontal cortex, (ACC) anterior cingulate cortex. Aligned anatomical coordinates for the side where effects were maximal are reported when bilateral. $P < 0.001$ conjunction P-level using TFCE.

4.10 Discussion

Here, we investigated whether age-related changes in grey matter intensity relate to key features of NREM sleep (spindles and slow waves) that are known to be important for memory consolidation and are reduced with age. Consistent with the extant literature, we observed reduced grey matter density in a widespread network of brain areas within cortico-striatal-hippocampal and cortico-cerebellar regions in older compared to younger adults (Figure 3, Table 3). We followed up these analyses employing a conjunction analysis approach, which revealed grey matter density correlated with both offline improvements in ToH performance and sleep spindles to a different extent in young *vs*. older adults in primarily cortical areas. These included superior temporal lobe, parietal cortex, somatosensory cortex, orbitofrontal and prefrontal cortex. In contrast, ToH performance gains and slow wave characteristics correlated with grey matter density to a different extent in young *vs*. older adults almost exclusively in subcortical areas that support learning and offline improvement for newly learned cognitive strategies needed for problem-solving. These areas included the anterior cingulate cortex, hippocampus, thalamus, cerebellum, putamen and the caudate nucleus. The overall pattern of the relationships between grey matter and improvements in ToH performance and sleep characteristics was consistent, whereby grey matter density was generally more positively correlated (with both offline gains and sleep EEG) in the young, and by comparison, generally more negatively correlated in older individuals. These results suggest that sleep spindles, and slow waves serve as markers for age-related changes in grey matter in regions which support sleep-related memory consolidation of newly learned cognitive strategies; whereby spindles may be primarily related to the cortical aspects, and slow waves primarily to subcortical regions. These brain areas are critical for the consolidation of novel problem-solving skills.

In terms of behavioural improvements, despite slower performance consistently reported in older participants compared to younger participants (Brown et al. 2009; Pace-Schott and Spencer 2011; Spencer et al. 2007), older participants displayed the same pattern of increasing performance over the course of the training session as the young participants did on the ToH. Thus, suggesting that initial learning of the strategy was not significantly impacted by age. Despite intact learning, older adults benefited less from retention intervals that contain sleep, as compared to young adults. It is worth noting that psychomotor vigilance did not differ in young and older adults over the course of the experimental protocol. Thus, changes in ToH performance are unlikely to be due to the impact of a nap on psychomotor vigilance. Together, these results suggest age-related deficits in latent/offline learning processes (Fogel et al. 2014; Fogel et al. 2017; Mander et al. 2013; Pace-Schott and Spencer 2011; Spencer et al. 2007).

Consistent with well-known age-related reductions in grey matter as a part of the normal aging process (Fjell and Walhovd 2010; Gunning-Dixon et al. 1998; Raz et al. 2015), we observed the most pronounced changes in grey matter in the thalamus, hippocampus, striatum, frontal cortex, motor cortical regions and the cingulate cortex. These regions support procedural memory, and are critical for planning, learning new strategies and problem-solving skills (Baker et al. 1996; Dagher et al. 1999; Lazeron et al. 2000; Owen et al. 1996; Rowe et al. 2001; Unterrainer and Owen 2006). Our results revealed that grey matter correlated with both performance gains and slow waves to a different extent in young (*i.e.*, more positive) *vs*. older adults (*i.e.*, more negative) in primarily subcortical regions (*e.g.*, anterior cingulate cortex, hippocampus, cerebellum, caudate, putamen, thalamus), and by contrast, largely in cortical regions (*e.g.*, superior temporal, somatosensory, parietal, prefrontal, orbitofrontal cortex) for spindles. The differential association between grey matter and both spindles and offline gains in performance in the parietal, temporal lobe, and the somatosensory cortices are in line with PET and fMRI studies in healthy young adults employing similar tasks requiring planning and strategy (Baker et al. 1996; Dagher et al. 1999; Lazeron et al. 2000; Owen et al. 1996; Rowe et al. 2001; Unterrainer and Owen 2006). Our results suggest that spindles are a marker of age-related neurodegeneration of grey matter which relate to the extent of the lost benefit of sleep for the consolidation of newly acquired cognitive strategies.

The differential association between grey matter and both slow waves and offline gains in performance in the hippocampus and the caudate in particular, are in line with studies showing that slow waves are associated with the degree of increasing hippocampal independence during post-sleep memory retrieval (Takashima et al. 2006). The hippocampus is responsible for encoding newly acquired information, and later transferring it to the cortex for long-term storage (Dudai 1996; Dudai et al. 2015; Squire and Zola-Morgan 1996). As consolidation progresses, information is integrated into neocortical circuits and reorganized so that it can ultimately be retrieved independently of the hippocampus (Takashima et al. 2009). Previous behavioural (Brown et al. 2009; Pace-Schott and Spencer 2011; Spencer et al. 2007), EEG (Debarnot et al. 2017; Fogel et al. 2014), and fMRI studies (Fogel et al. 2014; Toor et al. 2022) have shown that older adults do not derive the same benefit from sleep for procedural memory consolidation.

The present study indicates that slow waves are a marker of the age-related neurodegeneration in the hippocampus which impacts memory consolidation for newly acquired cognitive strategies. Moreover, a similar pattern was observed in the caudate nucleus. The caudate supports higher order reasoning, goal-directed behavior, novel learning (*e.g.*, strategies) and problem-solving skills (Dagher et al. 1999; Owen et al. 1996), all of which are required to perform the ToH. Activation of the caudate nucleus is observed during active planning of a novel action versus continuous rule following (Monchi et al. 2006), suggesting a role for novel and potentially higher order learning. Our results suggest that slow waves are an electrophysiological marker of neurodegeneration of the caudate, which relates to reduced sleep-dependent memory consolidation in older adults.

4.11 Limitations

The current study was limited in terms the use of a daytime nap protocol. A nap protocol is preferable to control for time-of-day effects when comparing young *vs*. older adults, but is limited in terms of sleep duration and architecture. Recent studies have shown that the coupling between slow-waves and sleep spindles is reduced with age and impacts memory consolidation

(Helfrich et al. 2018; Muehlroth et al. 2019). However, due to the relatively short duration of the nap recordings, these data are insufficient for this type of analysis. There was also limited REM sleep, which precluded further analysis of REM-related covariates. This type of procedural memory consolidation has been found to be related to the features of REM sleep (Conway and Smith 1994; Fogel et al. 2015; Smith and Smith 2003). Future studies employing overnight sleep recordings could address these important issues.

The ToH is widely considered to be an archetypal implicitly learned strategy task, however, it is possible that participants could have memorized the strategy. This possibility is unlikely given the limited number of trials used at training, and the use of the relatively complex 5-disk version of the ToH, which requires a minimum of 31 moves (62 key presses in total) needed to solve the puzzle. In a previous study (Viczko et al., 2018), we found no evidence of explicit awareness of a complex series of motor movements in a procedural memory task consisting of only 13 moves; far less than what is required to arrive at the optimal solution to the ToH. Thus, the optimal sequence of movements was not likely to have been memorized or learned explicitly. Rather, the underlying cognitive strategy needed to arrive at the optimal solution to the ToH was most likely acquired implicitly, possibly through trial-and-error. This interpretation is consistent with several other studies investigating problem-solving skills (e.g.,(Anderson et al., 2005; Ashworth et al., 2014; Baker et al., 1996; Balachandar et al., 2015; Beauchamp et al., 2003; Boghi et al., 2006; Brand et al., 2010; Dagher et al., 1999, 2001; Fogel et al., 2014, 2015, 2017; Nielsen et al., 2015; Ronnlund et al., 2001; Rowe et al., 2001; Smith & Smith, 2003; Unterrainer & Owen, 2006; van den Berg et al., 2019).

Another limitation was an imbalance in the number of participants per group (i.e., N=15/group in the older age groups, N=20/group in the younger groups). This was handled in two different ways in the analyses: 1) as recommended in the FSL VBM manual, the study-specific template was generated using equal numbers of participants (randomly selected) from each group so as to not bias the template and the downstream analyses to one age group, or another, and, 2) the statistical analyses are permutation-based non-parametric statistics, which involves randomly shuffling labels for participants over 10,000 iterations. This procedure is appropriate given that there is no assumption of equal sample sizes for permutation-based tests. In addition, for all groups, the target sample size of N=15, determined *a priori*, was achieved. Thus, all hypotheses were tested with the required statistical power.

All participants were within the target age range, and below the cut-off for depression and other related inclusion criteria. However, participants were not perfectly matched for age, sex, and depression scores across groups. To control for any potential confounds, we entered these variables into the model as variables of non-interest. It should be noted that inclusion of these control variables did not alter the overall outcome or conclusions, and in fact, strengthened the effects of interest. It is also worth noting that for daytime nap protocols such as this, it is not possible to control total sleep time. Consequently, we entered sleep duration as a variable of interest to ascertain if the duration of the nap was related to grey matter in a similar manner as spindles and slow waves. This analysis revealed that there was no significant relationship between total sleep time and grey matter in young *vs*. older adults. Thus, it is unlikely that nap duration alone could account for the observed pattern of results.

4.12 Conclusions

In conclusion, the results of the present study suggest that age-related changes in sleep spindles and slow waves are differentially related to grey matter density in young and older adults in brain regions that support sleep-dependent memory consolidation for problem-solving skills.

Both sleep spindles and slow may serve as biological markers of age-related neurodegeneration of grey matter, and the associated memory consolidation deficits in older adults.

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4.14 References

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Chapter 5

General Discussion

5.1 Interpretation of Results

Sleep disruptions go hand-in-hand with cognitive impairments observed as a function of age, and may be an early warning sign for cognitive decline (Jelicic et al., 2002; Nebes et al., 2009; Schmutte et al., 2007). In North America, sleep loss has direct and indirect costs in the tens of billions of dollars (Roth, 1995). Because of Canada's aging population, age-related cognitive impairment has been identified as one of the major health challenges in the next 20 years.

To understand the impact of age on memory, and importantly, how to mitigate the consequences (e.g., as age progresses in healthy, and then, progressively, in cases of cognitive decline and neurodegenerative disease), we must first: 1) understand how sleep is involved in supporting these cognitive processes in young adults, and, 2) how this is impacted by age in healthy individuals. In the approach taken here, we investigated the effect of '*optimal aging*' on sleep and memory consolidation. The aim was to shed light on the impact of age on sleep-dependent memory processes under the 'best-case' scenario. In doing so, we assessed the behavioral, electrophysiological, and functional/structural neuroanatomical changes that impact sleep-dependent memory consolidation with age.

As such, the primary purpose of this thesis was to provide novel insights into the age-related breakdown of sleep-dependent processes that support procedural memory consolidation. This was achieved using an innovative combination of EEG, MRI, and behavioral testing in a single parsimonious design with both younger and older participants. This thesis aimed to address four main questions: 1) how aging impacts the benefit that sleep affords to procedural memory performance (Studies 1-3); 2) which sleep-specific EEG features are possible biomarkers of age-related decline for sleep-related memory consolidation (Studies 1, 3); 3) what functional (Study 2), and; 4) structural (Study 3) changes in the brain, as measured by MRI might reveal the consequences of aging on sleep and memory. The series of studies which comprise this thesis shed light on the complex interrelationships between age, sleep and problem-solving skills and their neural correlates.

In terms of behavior, consistent with our hypotheses and previous literature (Brown et al., 2009; Fogel, Albouy, Vien, et al., 2014; Spencer et al., 2007), by the end of training, older adults reached the same level of performance as younger adults. Thus, suggesting that procedural skill acquisition and strategy learning are intact. However, older adults derived a reduced benefit of sleep for problem-solving skills in terms of speed and accuracy relative to young adults, and older adults that were awake.

Study 1 (Chapter 2) investigated the electrophysiological biomarkers of age-related changes in sleep for improvements in procedural problem-solving skills. This study advanced knowledge about the function of SW-spindle coupling in both young and older adults. The current study suggested that reduced SW-SP coupling in older adults may be a possible explanation as to why sleep does not provide the same benefit to consolidation as compared to younger adults. However, interestingly, this is not consistent across all older individuals, as older individuals with more young-like SW-SP coupling tended to associate with greater offline gains in performance, whereas those with less coupling displayed lower gains. We did not find that the change in SW-SP coupling parameters differed from CTL to ToH post-training sleep as a function of age group, nor did young adults show learning-related changes in coupling, nor was the change in coupling associated with performance improvements. Thus unlike declarative memory and other forms of procedural memory that do not involve problem-solving, SW-SP coupling is not as involved. This may suggest that SW-SP coupling is not necessary for the consolidation of complex problem-solving skills. Overall, in terms of sleep architecture and microstructure, SW-SP coupling was compromised as a function of age, but whatever coupling is occurring is a marker of the extent to which older individuals will benefit from sleep in terms of offline consolidation for novel problem-solving skills. Thus, SW-SP coupling is unrelated to cognitively complex procedural memory consolidation in young adults. In older adults, while there is not a significant learning-dependent change in coupling from CTL to learning nights, the extent of the change in spindle-SW coupling was a marker of consolidation, suggesting that younger adults did not rely on coupling for the consolidation of problem-solving skills. By contrast, in healthy older adults, the extent of coupling may be important. Perhaps, older adults may be using a different means of consolidating the ToH strategy (e.g., NREM vs. REM related), or, they may be learning the skill differently, or perhaps consolidating different aspects of the task than the young. These questions remain to be addressed.

Study 2 (Chapter 3) investigated the behavioral and neuronal functional consequences of age-related differences in sleep for the consolidation of novel cognitive strategies. fMRI scans examined differences in brain activation from training to retest in young *vs.* older participants as a function of sleep. Importantly, and consistent with previous studies of other forms of motor procedural skills (Fogel, Albouy, Vien, et al., 2014; Spencer et al., 2007), we confirmed that age-related changes in sleep were detrimental to the consolidation of older adults' problem-solving skills. Specifically, our results suggested that age-related differences in sleep results in reduced hippocampal-dependent memory consolidation processes for problem-solving skills. As consolidation progresses, information is integrated into neocortical circuits and reorganized so that it can ultimately be retrieved independently of the hippocampus. A process which occurred in younger, but not older subjects. Thus, sleep may be an opportune time for consolidation to unfold uninterrupted, and perhaps, sleep may be actively involved in facilitating the strengthening and transfer of information from the hippocampus to other brain areas for more permanent storage. Our results suggest that this process is compromised with age.

Finally, Study 3 (Chapter 4) examined whether spindles and slow waves may serve as biological markers for age-related neurodegeneration of grey matter (GM), and for the related sleep-related memory consolidation deficits observed in older adults. Recently, Fogel et al. (2017) identified sleep spindles as a biological marker of age-related neurodegeneration of GM in the hippocampus, and memory consolidation deficits for cognitively simple motor procedural skills. Here, we extended these findings using a similar approach, by investigating the impact of age-related changes in sleep and GM density on cognitively complex problem-solving skills. Study 3 found that age-related changes in sleep spindles and slow waves were differentially related to GM density in young and older adults in brain regions that support sleep-dependent memory consolidation for problem-solving skills. More specifically, spindles were related to grey matter in cortical areas (e.g., somatosensory, and parietal cortex), and slow waves were related to grey matter in subcortical regions that support problem-solving skills (e.g., anterior cingulate, hippocampus and caudate). Study 3 extends knowledge about simple motor skills to more cognitively complex problem-solving skills. For the first time, Study 3 demonstrated that both spindles and slow waves (SWs) are possible biomarkers of age-related neurodegeneration of grey matter and the associated problem-solving memory consolidation deficits observed in older adults.

Overall, the three studies included in this thesis support the hypothesis that age-related changes in sleep (in particular, sleep spindles and SWs) contribute to the lost benefit of sleep for procedural memory consolidation. This research suggests that memory consolidation during sleep is an active process which transforms encoded memories from the hippocampus (temporary storage) to the neocortex (long-term storage) during sleep, ultimately allowing memories to become integrated into existing networks and independent from the hippocampus (Studies 2 & 3) (for a review, see; Diekelmann & Born, 2010). Our results suggest that this systematic transfer of information occurs in young adults but is compromised in older adults.

This series of studies was conducted in very healthy older adults, and likely represents 'optimal aging' rather than 'normal aging'. Thus, these studies have identified a very early sleep-specific marker of age-related cognitive decline. These biomarkers and related behavioral, functional, and structural changes in the brain provide early warning signs and could therefore have important diagnostic and predictive value as age and cognitive decline progress. These studies may also provide novel therapeutic targets for the treatment of different cases where the biomarkers of sleep (*e.g.,* sleep spindles, slow waves) may be implicated.

5.2 Limitations

The participants included in this series of studies, were included based on stringent screening criteria to ensure older adults were very healthy (*e.g.,* no health complications, sleep disorders, use of medications etc.). This is considered 'best-case' scenario for aging. While this is one of the strengths of these studies, it is also a limitation. As such, the generalizability of these results is limited to individuals without significant health issues. Thus, it will be important for future studies to investigate the impact of age-related changes in sleep on memory and cognition in typical aging that is more representative of the general population. Furthermore, an extension of the studies is required in more complex cases such as subjective cognitive decline (SCD), mild cognitive impairment (MCI), and other neurodegenerative diseases and dementias.

In addition, educational levels were not recorded in these studies. Future research would benefit from adding this variable to control for this factor, as it can be protective. For example, it was recently noted that dementia prevalence has fallen from 2000 to 2012 in people 65 and older and that this drop was associated with staying in school longer (Langa et al., 2017). Importantly, it is not yet fully understood which components of the pathogenic pathways involved in age-related cognitive decline may be influenced by education, as such it was not considered in this series of studies. That said, our group was comprised of exceptionally healthy individuals in terms of mental, cognitive, and physical health, and given the association with these variables and education level (and socio-economic status), it is likely that they are rather comparable to the young, University-educated samples in these studies.

Another factor to consider when working with any aging population that includes females is the effects of menopause on the interpretation of results. In these studies, this is held constant as all the women included were post-menopausal.

In addition, a napping protocol was used in the current studies to control for/mitigate the effects of time-of-day and chronotype on performance (Hasher et al., 2002; Winocur & Hasher, 1999, 2004). However, this results in limited sleep duration, and as such, we were unable to acquire enough REM sleep to examine that sleep characteristic in relation to problem-solving abilities. Much less is known about the neuroanatomical and physiological correlates of rapid eye movements during REM sleep; which are involved in the consolidation of newly acquired problem-solving skills (Fogel, Smith, et al., 2007; Mandai et al., 1989; Smith, Nixon, et al., 2004; Smith & Lapp, 1991; Smith & Smith, 2003; Smith & Weeden, 1990). Future studies employing overnight sleep protocols are necessary to directly investigate REM sleep. Importantly, tasks such as the ToH are very focused tasks that are usually only utilized in laboratory settings. Employing more ecologically sound paradigms in the future may also increase the generalizability of the results.

5.3 Future Directions

Simultaneous EEG-fMRI sleep studies would enable the investigation of whether an analogous reactivation and reorganization process occurs for the consolidation of problem-solving skills as it does for simple motor skill acquisition (Bergmann et al., 2012; Boutin et al., 2018; Dang-Vu, Schabus, Desseilles, Albouy, Boly, Darsaud, Gais, Rauchs, Sterpenich, Vandewalle, et al., 2008; Fogel, Albouy, King, Lungu, Vien, Boré, et al., 2017). Furthermore, future studies could investigate white matter fiber tracts in relation to problem-solving skills and age-related changes, especially given that the generation of spindles and slow waves depends on widespread and long-distance thalamocortical projections. These studies fill an important knowledge gap specifically focusing on acquiring problem-solving skills as a function of age, ultimately allowing future studies to investigate the breadth of the impact of targeting sleep to improve cognitive outcomes.

As such, it is expected that the advancements in this thesis will have a high impact and be of great interest to researchers, clinicians, and the public, as it will allow for more informed decision-making concerning patients' sleep deficits and cognitive decline. In addition, these studies can help clinicians provide novel therapeutic targets in the treatment of patients with cognitive decline. One such target is investigating whether spindles or slow waves can be enhanced, to restore the lost benefit of sleep for memory consolidation in elderly populations. For example, closed-loop auditory stimulation, targeted memory reactivation and pharmaceuticals can be used to enhance spindles and slow waves. Such a targeted approach would not only provide causal evidence but may also provide novel therapies for the improvement of age-related cognitive decline.

Another possible extension of these findings is whether the electrophysiological, functional, and structural signatures identified in these series of studies, may provide additional insight into the contribution of sleep to cognitive decline in neurodegenerative diseases and dementias. For example, problem-solving skills are impaired in neurodegenerative diseases e.g., Parkinson's disease (PD) (Schneider, 2007), and our group has shown that spindles in PD predict the development of dementia (Latreille et al., 2015). In addition, SCD constitutes a risk factor for later cognitive decline/dementia and is associated with an increased likelihood of Alzheimer's Disease (AD) related biomarker abnormalities, and reductions in grey matter density (for a review, see; Rabin et al., 2017). As such, SCD may represent the very earliest prodromal clinical manifestation of AD/dementia. Additionally, a reduction in spindles is a risk factor for developing SCD or MCI (Taillard et al., 2019), and may negatively impact memory consolidation. A recent study found that transcranial direct current stimulation enhanced spindle amplitude in people with MCI, and this enhancement was associated with improvements in declarative memory (Ladenbauer et al., 2017). These recent studies suggest that spindles are an ideal modifiable therapeutic target for restoring the benefit of sleep at the earliest stages of cognitive decline; however, more research is needed to explicitly test this possibility.

5.4 Conclusion

Overall, the benefit of sleep afforded to problem-solving skills is negatively impacted by aging at the behavioral, electrophysiological, functional, and structural levels. Ultimately, this research could lead to the development of novel sleep-specific interventions to be employed (*i.e.* TMR, closed-loop auditory stimulation, pharmacological interventions etc.) perhaps by experimentally manipulating these targets (*e.g.* EEG markers such as spindles, slow waves) to improve memory and cognition at the earliest stages, before significant neurodegeneration occurs.

5.5 References

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Appendices

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Appendix A: Informed Consent

The Le Royal
Mental Health - Care & Research
Santé mentale - Soins et recherche

INFORMATION SHEET AND CONSENT FORM

Project: Neural Correlates of Cognitive Procedural Memory Consolidation During Sleep
Principal Investigator: Stuart Fogel, Associate Professor, School of Psychology, University of Ottawa, 613-562-5800 ext 4295, sfogel@uottawa.ca

Thank you for your interest in this study. Before you decide whether to take part, please read the following information carefully (this sheet is for you to keep). You may ask us any questions if you would like more information.

What is this research's goal?

We are interested in how young adults learn new cognitive and motor skills. In this experiment, we investigate the brain activity related with learning a task that will require a type of memory called "cognitive procedural memory". Cognitive procedural memory helps you learn new logical strategies and perform skills. Brain activity will be recorded using electroencephalography (EEG) and functional magnetic resonance imaging (fMRI) at the Royal Ottawa Mental Health Center (ROH) Brain Imaging Centre.

Do I have to take part?

It is up to you to decide to join the study. We will describe the study and go through this information sheet. If you agree to take part, we will then ask you to sign a consent form.

You are free to withdraw at any time, without giving a reason. You can skip any questions you do not wish to answer (except for the MRI safety checklist, which is required in order to ensure your safety).

What will happen if I agree to take part?

If you decide to take part, you will be asked to come to the ROH Sleep Research Laboratory and Brain Imaging Center three separate times, including two or three nights (depending on the group you are randomly assigned to). If you agree to take part and sign the consent form, we will first ask you to complete a series of questionnaires. On two occasions you will have an fMRI scan to record your brain activity while you complete a task in the scanner. Depending on the group that you are assigned to, you might be asked to either spend an additional night sleeping in the laboratory, or you will be asked to take a nap for 2.5 hours during the day. Following these sessions, you will then complete the same task a second time.

For the fMRI sessions, you will lie in a narrow tube in the fMRI scanner and hold still for approximately an hour, and no longer than 1.5 hours. It may not be appropriate for you to be scanned if you are very claustrophobic. Because the scanner itself is quite noisy, we will give you earplugs to protect you from that noise. Throughout the experiment you will be in direct verbal communication with us. We can terminate the experiment at any point should you experience any discomfort or distress. You can also request breaks whenever you need one. In the scanner, you will complete a memory task using a keypad. You will be asked to complete the task by pressing buttons. The task may be cognitively demanding, but will not be physically tiring. In addition, before you go into the scanner, you will be asked to fill out a safety questionnaire, as well as a questionnaire about sleep quality and mood.

During your nights (~10 hours each) in the sleep laboratory, you will sleep with electrodes on your scalp and face. The placement of electrodes on the head is not painful, although there may be minor discomfort when the skin is cleaned during electrode application. The skin may be slightly reddened after the electrodes are removed. This reddening is normal and will disappear in less than an hour. The electrode gel dissolves in water; and in the morning, you will be able to take a shower after the electrodes have been removed. One of the nights in the sleep laboratory will also include sensors designed to monitor your breathing, limb movements, and oxygen level.

Compensation

You will be compensated for your time and offered free parking at the ROH. Breakfast and toiletries will also be made available on site.

If you choose to withdraw before completing the full study, you will be compensated on a per session basis as follows:

-(a) $20 for the orientation and screening/acclimatization session,

-(b) $40 for completing the baseline MRI, EEG session following the initial screening/acclimatization session ($20 for orientation + $20),

-(c) $70 for attending one experimental session ($20 for (a) + $20 for (b) + $30)

-(d) $100 for attending study completion, debriefing, and returning logs and activity monitors ($20 for (a) + $20 for (b) + $30 for (c) + $30)

Am I eligible to take part?

To be eligible to take part in this study, you must fulfill the following criteria:
- 20 to 35 years of age
- fluent in English
- right-handed
- normal or corrected-to-normal vision
- a normal sleep schedule (e.g., sleep between the hours of 10pm and 9am)
- in good health
- have a normal body mass index
- non-smoker
- non-professional typist or musician
- do not consume excessive caffeine or alcohol
- non-shift worker

And have no:
- sleep disorders
- neurological and/or psychiatric disorders (past and present)
- loss of consciousness for more than 10 minutes at any point in the past (other than under anaesthesia)
- metal in body (e.g., piercings that cannot be removed, shrapnel etc.)
- implanted devices (e.g., cardiac pacemakers, aneurysm clips, cochlear implants, medical pumps, deep brain stimulators, etc.)
- back problems
- hand or finger mobility problems

Note: Jewels, body piercings and any clothing with metal will need to be removed if you choose to take part in this study.

And not be:
- pregnant
- claustrophobic
- taking any medications known to interfere with sleep

What sort of data will be collected in this study?

We will collect simple demographic data concerning your age, gender, handedness, first language, years of education, vision, and self-reported medical history. We will also collect your evaluation of your sleep quality, your mood, and your sleep preferences. We will also collect data regarding your task performance.

Additionally, we will obtain several types of brain imaging data, which includes an anatomical picture of your brain and a series of images that will show us your brain activity while you engage in the tasks.

We will also collect EEG data during sleep, which is a harmless and non-invasive way to record the electrical activity of your brain via electrodes placed on the surface of your skin.

What is EEG?

Electroencephalography or "EEG" is a non-invasive technique that measures brain activation. EEG records brain waves through electrodes, which are small metal disks placed in direct contact with the skin. When your neurons communicate with each other, they send a bust of electricity that is picked up by the electrodes. A connected recording machine will measure the strength and duration of the electrical impulse for each brain region close to an electrode. The machine will transcribe those measures into a visual signal that can be traced on a computer screen. Your brain activity will be recorded continuously; this creates a pattern of brain activity on the screen that looks like a series of peaks and valleys, or waves. Depending on what your brain is doing, your brain waves will change as different parts of your brain become more or less activated. We will track those changes on the EEG recording to see how your brain activates while you sleep.

What is MRI?

Magnetic resonance imaging or "fMRI" is a safe and non-invasive technique. MRI does not use x-rays (such as in coaxial tomography or "CAT scans") or ionizing radiation (such as in positron emission tomography, or "PET scans").

MRI is a brain imaging technique that allows us to obtain a 3D picture of your brain using magnetic fields. Our bodies (and brains) are largely made up of water molecules (H_2O), which consist of oxygen (O) and hydrogen (H) atoms. Within the hydrogen atoms, there is a small particle called a proton. Protons act like tiny magnets. Therefore, when you lie in the strong magnetic field of the scanner, these protons will line up with the magnetic field. Then, the scanner produces short bursts of radio waves, which knock the protons out of alignment. Once the radio waves stop, the protons will realign with the magnetic field by which they send radio signals back to the scanner. The scanner feeds them back to our computer, which produces an image based on the exact location of the protons. This information can be used to create a structural image of the brain.

Functional MRI (fMRI) also records blood flow in certain regions, providing us with an indirect measure of brain activity, because we assume that more blood is needed in areas that are activated. Together with structural image, we can then look at the parts of the brain that were activated during the tasks. Please note that, depending on the group you are assigned to, you may go into a "mock scanner" instead of a functioning MRI machine.

What are the possible disadvantages and risks of taking part?

The main disadvantage is that participating will take up some of your time. EEG and MRI are safe techniques, and we will make sure that it is safe for you to go into the MRI scanner.

Moreover, you can also choose to skip any questions if you feel uncomfortable with providing an answer (except on the MRI safety questionnaire, for your own safety).

MRI scans are sometimes considered to contain some identifying information given that we could reconstruct some facial features (i.e. the shape of the head). This poses a minimal risk to preserving the anonymity of your data, even if we will associate a numerical code to your MRI scans rather than your name. Only members of the research team will have access to the scans, and they will be kept securely as described in the section beginning with: "How will you store the information that I give you?". EEG data does not contain identifying information and will also be associated with a numerical code so that your data remains anonymous.

You will lie in an MRI tube for about one hour at a time. For that reason, you should not participate in this study if you are claustrophobic or if you have back problems. The scanner is loud. We will provide you will ear plugs to ensure that the noise is kept to a safe level.
You will wear the EEG electrodes during the night. This may be slightly uncomfortable or annoying but should not interfere with your sleep through the night. Electrodes only record electrical signals of the brain, so you will not receive any electrical charge or impulse.
Lastly, the MRI scan may detect anomalies that neither you nor your doctor(s) were expecting. This is known as an Incidental Finding (see below).

Incidental Findings

If the technologist is unsure about the scan, your scan may be looked at by a Consultant Radiologist. From other published studies we know that in a small proportion of participants (about 2.5%) worrying incidental findings may occur. These results from incidental findings in young healthy volunteers are often benign, but either way, this is a good thing to know, as we may detect something that your doctor should know about at an early stage.

If this happens, a health professional of the ROH will contact you by telephone and explain these findings. All information will be made fully available to you. They will arrange the necessary next steps with you. This includes contacting your family doctor and, if appropriate, referral to a specialist for further tests.
However, this is not a diagnostic scan and we are not conducting medical research, nor are researchers trained physicians or health professionals, and therefore, there is no guarantee existing anomalies will be detected. If you prefer not to be informed of an image anomaly, you must choose not to participate in the study.

What are the possible benefits of taking part?

If you are interested in learning about the importance of sleep, about the brain and about how MRI and EEG work, this is a great opportunity to learn. Your participation will benefit the program of research and our knowledge about the function of sleep.
We cannot provide personal feedback on any of the tasks, because we are not clinicians and because the tasks are performed to satisfy research purposes. The tasks are intended to be meaningful at the group level, and not at the individual level, and so your individual test results are only meaningful when considered as part of a group.

Will I be paid for taking part in this study?

We will give you $100 to help cover any costs associated with participating and completing this study, and in acknowledgement of the time commitment and potential inconvenience to your schedule we are asking of you.

What will happen if I agree to take part, but change my mind later?

You have the right to withdraw from the study at any time during the experiment (e.g., even during MRI scanning you can press the emergency call button while lying in the MRI scanner and indicate you wish to discontinue the experiment; you can decide to signal the experimenter during the night and ask for the EEG electrodes to be removed).

How will the data be used?

The information obtained from this study will be presented at scientific conferences or in scientific journals, but your name will never appear in any public document. Only group data will be presented.

Your data may also be used in future studies as part of research in the laboratory of Dr. Stuart Fogel for the duration the data will be stored. This data includes personal characteristics, questionnaires, results on cognitive tasks, and fMRI-EEG data. The data will be anonymized, which means a numeric code will be attached to it, and no identifying information will be included (e.g. name, contact information). These data are costly to acquire, and may be useful in future research. Study information may be reviewed by members of the Research Ethics Board for quality assurance purposes.

Will my taking part in this study be kept confidential?

All information we collect about you in this experiment will be kept strictly confidential. Data will be anonymized, i.e., a code will be associated to your data and only group data will be presented. You will not be personally identified in any publications.

How will you store the information that I give you?

Any information about you that is collected during the study will be kept strictly confidential. Only the researchers will have access to this information. All information will be coded so that your identity remains anonymous. The anonymized data will be stored on password-protected hard drives in the Sleep Research Laboratory (Vanier Hall, 3047), in locked filing cabinets in locked rooms, and the Consent Form will be stored in a separate locked room (Vanier Hall, 3040).

How do I know that this research is safe for me to take part in?

All research in the University is looked at by an independent group of people, called a Research Ethics Board, to protect your safety, rights, wellbeing, and dignity. This study has been approved by the Research Ethics Board of ROH March 1st, 2017 and the University of Ottawa on August 30th, 2017.

You are under no obligation to agree to take part in this research.
If you do agree you can withdraw at any time without giving a reason.

This study is being supervised by Dr. Stuart Fogel at the School of Psychology, University of Ottawa. If you have any questions or comments on the study, you can contact Dr. Stuart Fogel at 613-562-5800 ext 4295, or sfogel@uottawa.ca . You can contact the Research Ethics Board – Protocol Officer at 550 Cumberland St., Room 154, Ottawa, (613) 562-5387, ethics@uottawa.ca. You may also contact the Chair of Research Ethics Board at the ROH, 1145 Carling Avenue, Ottawa , Ontario, K1Z 7K4; (613) 722-6521 ext 6214.

I confirm that I have read and understand the information sheet for the above study and have had the opportunity to consider the information, ask questions, and have had these answered satisfactorily. ☐

I understand that my participation is voluntary and that I am free to withdraw at any time, without giving any reason, without my medical care or legal rights being affected. ☐

3. I understand that incidental findings from my MRI scans will be reported to my family doctor. ☐

4. I know that no personal information (such as my name) will be shared outside of the research team or published in the final report(s). ☐

5. I agree to take part in the above study. ☐

One copy is for you to keep, and one is for the researcher. Please sign both.

Participant's name:……………………………………………….

Participant's signature:…………………………………….Date…………………

Researcher's name………………………………………………..

Researcher's Signature…………………………………………Date…………………

Appendix B: Description of Questionnaires

Beck Anxiety Inventory (Beck, A.T., 1988)

The BAI is a self-report inventory that contains 21 multiple-choice questions and is used for measuring anxiety in children and adults. The standardized cut-offs of the BAI are: 0–7 (overall): minimal anxiety, 8-15 (overall): mild anxiety, 16-25 (overall): moderate anxiety, 26-63 (overall): severe anxiety. A typical question asks the participant to rate the severity of a specific physiological, emotional or psychological symptom (e.g. “Do you experience nervousness? Rate the severity”).

Beck AT, Epstein N, Brown G, Steer RA (1988). "An inventory for measuring clinical anxiety: Psychometric properties". *Journal of Consulting and Clinical Psychology*. 56 (6): 893–897.

Beck Depression Inventory (Beck, A.T., 1988)

The BDI is self-report inventory, with 21 multiple choice questions. It is one of the most used psychometric tests for measuring the severity of depression. It includes statements/questions about symptoms of depression, such as: hopelessness and irritability, cognitions such as: guilt or feelings of being punished, as well as physical symptoms such as: weight loss and fatigue. A typical question provides four statements with the first expressing a normal level of the symptom (e.g. I do not feel sad), and the fourth expressing the severest degree (e.g. I am so sad and unhappy that I cannot bear it). The participant chooses the most applicable statement.

Beck, A. T., Steer, R. A., & Carbin, M. G. (1988). Psychometric properties of the Beck Depression Inventory: Twenty-five years of evaluation. *Clinical psychology review*, *8*(1), 77-100.

Circadian Rhythms Questionnaire (Horne, J.A., & Ostberg, O., 1976)

Consisting of 19 items, the self-report scale was developed to assess individual differences in morningness and eveningness – the degree to which respondents are active and alert at certain times of day. Scale items query preferences in sleep and waking times, and subjective “peak” times at which respondents feel their best.

Horne JA, Ostberg O. A self-assessment questionnaire to determine morningness-eveningness in human circadian rhythms. Int J Chronobiol. 1976;4(2):97-110. PMID: 1027738.

Edinburgh Handedness Inventory (Oldfield, R. C., 1971)

The Edinburgh Handedness Inventory is a scale used to measure a person's hand dominance, i.e. whether they are mostly right or left handed in their everyday activities. It is often used as a self-reporting measure; however, an observer can also assess the person/participant. The inventory can contain a list of 10 or 20 questions or instructions to be carried out by the individual being assessed. A typical activity may require the participant to write or draw, throw a ball, or use utensils (e.g. a toothbrush, spoon, etc.,). In a questionnaire format, the participant simply choses “left hand” or “right hand” indicating the preference for each activity.

Oldfield, RC (March 1971). "The assessment and analysis of handedness: The Edinburgh inventory". *Neuropsychologia. 9 (1): 97–113.*

Epworth Sleepiness Scale (Johns M. W.,1991)

The Epworth Sleepiness Scale (ESS) is a measure intended to assess daytime sleepiness. It is a self-report questionnaire that asks the individual to rate his/her probability of falling asleep for eight different situations that most people engage in during their day. The ESS is often used to help in diagnosing sleep disorders. A sample question asks the participant to report how likely they would “doze off” in a situation such as sitting and reading as well as while watching T.V, amongst other scenarios.

Johns, M. W. (1991). A new method for measuring daytime sleepiness: the Epworth sleepiness scale. *sleep*, *14*(6), 540-545.

Everyday Cognition Scale (Tomaszewski et al., 2008)

The Everyday Cognition (ECog) scales were developed in response to some of the limitations of existing instruments. One goal in developing the ECog was to measure relatively mild functional changes that may predate loss of independence in major activities of daily living. A second aim in developing the ECog was to assess functional abilities that are clearly linked to specific cognitive abilities, in other words, the everyday correlates of specific neuropsychological impairments.

The ECog is an informant-based measure of cognitively-relevant everyday abilities comprised of 39 items, covering six cognitively-relevant domains: Everyday Memory, Everyday Language, Everyday Visuospatial Abilities, and Everyday Planning, Everyday Organization, and Everyday Divided Attention. For each item, informants compare the participant’s current level of everyday functioning with how he or she functioned 10 years earlier. In this way, individuals serve as their own control. Ratings are made on a four-point scale: 1 = better or no change compared to 10 years earlier, 2 = questionable/occasionally worse, 3 = consistently a little worse, 4 = consistently much worse.

Tomaszewski Farias, S., Mungas, D., Harvey, D. J., Simmons, A., Reed, B. R., & Decarli, C. (2011). The measurement of everyday cognition: development and validation of a short form of the Everyday Cognition scales. *Alzheimer's & dementia : the journal of the Alzheimer's Association*, *7*(6), 593–601. https://doi.org/10.1016/j.jalz.2011.02.007

Montreal Cognitive Assessment (MoCA) (Nasreddine, Z. S., 1996)

The MoCA is a one-page 30-point test that may take approximately 10 minutes to complete. It is used to screen for and detect cognitive impairment (pre-marker of dementia). Some sections of the assessment are completed individually by the participant (e.g., drawing of a clock) whilst others require the participant to listen and repeat a set of words/numbers.

Nasreddine, Z. S., Phillips, N. A., Bédirian, V., Charbonneau, S., Whitehead, V., Collin, I., ... & Chertkow, H. (2005). The Montreal Cognitive Assessment, MoCA: a brief screening tool for mild cognitive impairment. *Journal of the American Geriatrics Society*, *53*(4), 695-699.

Napping Behavior Survey: (Milner, C. E., Fogel, S. M., & Cote, K., 2006)

The Napping survey is used to determine preference for napping (e.g., ‘‘How often would you nap if your schedule was such that you could nap every day?’’), and weekday versus weekend napping habits. Experience with napping (how often participants napped at the time of the study) was measured on a 4point scale (0 = never nap; 1 = nap once or twice a month; 2 = nap once or twice a week; 3 = nap every day). Preference for napping (how often participants would have liked to nap, if their schedule had been such that they could nap when desired) was measured on this same 4-point scale.

Milner, C. E., Fogel, S. M., & Cote, K. A. (2006). Habitual napping moderates motor performance improvements following a short daytime nap. *Biological psychology*, *73*(2), 141–156. https://doi.org/10.1016/j.biopsycho.2006.01.015

Psychomotor Vigilance Task (Dinges, D. I, 1985)

The Psychomotor Vigilance Task aims to measure the speed with which subjects respond to a visual stimulus and thus assess sustained-attention as well as reaction-time. It is often used in sleep research as literature indicates that sleep deficit correlates with deteriorated alertness, slower problem-solving, increased rate of false responding as well as declined psycho-motor skills. The purpose of the PVT is to measure sustained attention and give a numerical measure of sleepiness by counting the number of lapses in attention of the tested subject. The task is not meant to assess the reaction time, but to see how many times the button is not pressed when the light is on - as it requires the subject to press a button as soon as the stimulus (light appears). The light stimulus is on for a few seconds for a 5 to 10-minute duration.

Dinges, D. I, & Powell, J. W. (1985). Microcomputer analysis of performance on a portable, simple visual RT task sustained operations. Behavior Research Methods, Instrumentation, and Computers, 17, 652–655

Sleep Disorders Questionnaire (Douglass et al., 1994)

This questionnaire is a screening tool for physicians to assist their clinical evaluation of insomnia. It can be used to screen for a sleep disorder.

Douglass, A. B., Bornstein, R., Nino-Murcia, G., Keenan, S., Miles, L., Zarcone, V. P., Jr, Guilleminault, C., & Dement, W. C. (1994). The Sleep Disorders Questionnaire. I: Creation and multivariate structure of SDQ. *Sleep*, *17*(2), 160–167. https://doi.org/10.1093/sleep/17.2.160

Stanford Sleepiness Scale (Hoddes, E., Zarcone, V., & Dement, W., 1972)

The Stanford Sleepiness Scale (SSS) is a one-item self-report questionnaire measuring levels of sleepiness throughout the day. The scale is generally used to track overall alertness at each hour of the day and can be completed within 2 minutes. The SSS has been validated for adult populations and is used in both research as well as clinical settings to assess the level of intervention or effectiveness of a specific treatment to evaluate an individuals' progress. The questionnaire askes the participant/client to rate their degree of sleepiness while providing options such as "feeling active, vital, alert…" as well as "somewhat foggy, let down" amongst other choices.

Hoddes, E., Zarcone, V., & Dement, W. (1972). Development and use of Stanford Sleepiness Scale (SSS). Psychophysiology.

Appendix C: Cambridge Brain Science Description

Cambridge Brain Science Test Battery: https://creyos.com/features/tasks

The Creyos (formerly Cambridge Brain Sciences) suite of neurocognitive tasks are derived from traditional pen and paper tests, and accurately measure core elements of cognition like short-term memory, reasoning, attention, and verbal ability. They are trusted by healthcare clinics and researchers worldwide and have been validated by decades of scientific research.

The CBS platform is a web-based test battery, with a number of advantages over other tests of cognition, including ease of administration and the fact that the neural correlates of each subtest have been investigated using functional neuroimaging (Hampshire et al., 2012a). The CBS trials includes 12 cognitive tests that measure a broad range of cognitive abilities including reasoning, problem-solving, planning, attention, and memory.

Hampshire, A., Highfield, R. R., Parkin, B. L., & Owen, A. M. (2012). Fractionating human intelligence. *Neuron*, *76* (6), 1225–1237. https://doi.org/10.1016/j.neuron.2012.06.022

Appendix D: Supplemental Material

Supplemental Information: Study 1

Supplemental Table 1. Density (#/min NREM2), and size of sleep spindles in NREM sleep at Fz (midline frontal), and Pz (midline posterior) derivatives during the 90-min daytime nap retention interval in young and older participants.

		Young		**Older**			
		M	**SEM**	**M**	**SEM**	**t-stat**	**P**
Control							
Density	Fz	2.99	0.34	1.65	0.18	-2.865	*0.008
	Pz	3.86	0.34	2.26	0.24	-3.397	*0.002
Size	Fz	35.48	2.14	25.27	2.97	-2.840	*0.008
	Pz	37.02	2.67	52.59	15.63	1.249	0.221
Testing							
Density	Fz	2.73	0.23	1.81	0.22	-2.716	*0.011
	Pz	3.59	0.32	2.50	0.26	-2.386	*0.024
Size	Fz	34.89	2.56	22.56	1.82	-3.413	*0.002
	Pz	36.36	2.42	38.67	4.22	0.513	0.611

Abbreviations: Mean (M), standard error of the mean (SEM). * Indicates $p < 0.05$. *P*-values for paired samples t-test between spindle parameters.

A 2 (young vs. older) x 2 (control vs. testing) ANOVA was performed to assess differences in sleep spindle characteristics as a function of age and session (Supplemental Table 1). There was an effect of age for both density and size at Fz, while there was an effect of age only at Pz and not size. No significant session or interaction effects were observed. In terms of spindle density, younger subjects had significantly more spindles per number of minute at the control session (Fz: t [30] = -2.865, p = 0.008), Pz: t [30] = -3.397, p = 0.0012 and Testing (Fz: t [30] = -2.716, p = 0.011), Pz: t [30] = -2.386, p = 0.024) relative to older subjects. In terms of spindle size, younger subjects had significantly larger sleeps spindles at the control session (Fz: t [30] = -2.840 p = 0.008) and Testing (Fz: t [30] = -3.413, p = 0.002) relative to older subjects.

Supplemental Table 2. Density (#/min NREM2), and size of slow oscillation half waves during slow-wave sleep at Fz (midline frontal), and Pz (midline posterior) derivatives during the 90-min daytime nap retention interval in young and older participants.

		Young		**Older**			
		M	**SEM**	**M**	**SEM**	**t-stat**	**P**
Control							
Density	Fz	23.43	5.21	2.71	0.63	-3.051	*0.005
	Pz	16.13	4.13	0.78	0.22	-2.857	*0.008
Size	Fz	39.46	1.25	28.12	0.81	-6.541	*<0.001
	Pz	35.70	1.09	26.34	0.55	-6.322	*<0.001
Testing							
Density	Fz	23.83	4.49	2.84	0.62	-3.584	*0.001
	Pz	16.47	3.77	0.71	0.19	-3.213	*0.003
Size	Fz	38.44	1.64	29.61	1.56	-3.615	*0.001
	Pz	35.21	1.03	28.42	1.79	-3.544	*0.001

Abbreviations: Mean (M), standard error of the mean (SEM). * Indicates $p < 0.05$, corrected for heterogeneity of variance where appropriate. *P*-values for paired samples t-test between spindle parameters.

A 2 (young vs. older) x 2 (control vs. testing) ANOVA was performed to assess differences in slow wave characteristics as a function of age and session (Supplemental Table 2). There was an effect of age at Fz and Pz, but no significant session or interaction effects. Younger adults had significantly more slow waves per minute at the control session (Fz: t [30] = -3.051, p = 0.005, Pz: t [30] = -2.857, p = 0.008), and at testing (Fz: t [30] = -3.584, p = 0.001, Pz: t [30] = -3.213, p = 0.003), and significantly larger slow waves at the control session (Fz: t [30] = -6.541, p = <0.001, Pz: t [30] = -6.322, p = <0.001), and testing (Fz: t [30] = -3.615, p = 0.001, Pz: t [30] = -3.544, p = 0.001) relative to older adults.

Supplemental Information: Study 2

Table S1. Total duration (standard deviation) of each ToH testing session in seconds for the Young Nap, Young Wake, Older Nap and Older Wake conditions.

	Training	**Test**	**Retest**
Young Nap	699.38 (274.73)	396.01 (144.90)	343.98 (140.16)
Young Wake	729.87 (333.11)	390.00 (162.50)	299.99 (145.58)
Older Nap	1403.81 (766.71)	902.10 (454.86)	767.70 (339.10)
Older Wake	1199.53 (600.22)	752.18 (349.48)	823.27 (383.06)

Table S2. Sleep architecture for the experimental nap. Means (M) and standard deviations (SD) in minutes, for WASO, NREM1, NREM2, NREM3, REM, and TST in Young and Older participants.

	Older			**Young**			**Older vs. Young**		
	M	***SD***	**N**	**M**	***SD***	**N**	***t***	***P***	***d***
WASO	13.80	13.78	15	13.21	12.85	20	0.13	0.989	0.04
NREM1	7.07	4.61	15	5.63	4.52	20	0.93	0.361	0.32
NREM2	34.70	19.49	15	36.92	12.76	20	-0.41	0.686	-0.14
NREM3	10.38	11.59	12	21.09	15.45	19	-2.06	0.049*	-0.76
REM	7.33	2.93	3	8.23	4.79	15	-0.33	0.750	-0.21
TST	51.53	26.44	15	68.79	13.62	20	-2.52	0.074	0.09

Abbreviations: Wake after sleep onset (WASO), total sleep time (TST). * Indicates $p < 0.05$, corrected for heterogeneity of variance where appropriate.

Table S3. Group main effects. Changes in activation for ToH-CTRL from training to retest in young nap (YN), young no-nap (YNN), older nap (ON) and older no-nap (ONN).

L/R	Level	Region	X	Y	Z	Size	Z	p
		A: YN vs. ON						
Bilateral	Cerebral Cortex	Superior Temporal Gyrus	66	-48	20	4015	7.03	0.000
Bilateral	Cerebral Cortex	Occipital lobe (cuneus)	4	-90	18	2106	6.12	0.000
Bilateral	Cerebral Cortex	Primary motor cortex	44	-8	56	665	5.46	0.001
Bilateral	Cerebral Cortex	Dorsolateral prefrontal cortex	-12	40	56	707	5.20	0.004
Bilateral	Cerebral Cortex	Parietal cortex (precuneus)	14	-70	52	1033	5.00	0.006
Bilateral	Cerebral Cortex	Lateral prefrontal cortex	-52	26	10	387	4.71	0.019
Bilateral	Cerebral Cortex	Supplementary motor area	8	-6	78	122	4.47	0.050
Bilateral	Cerebral Cortex	Hippocampus*	-32	-6	-40	78	4.85	0.012
Bilateral	Cerebral Cortex	Cerebellum*	20	-78	-48	626	5.11	0.004
		B: ON vs. ONN						
Bilateral	Cerebral Cortex	Primary visual cortex	16	-98	10	1194	5.66	0.003
Bilateral	Cerebral Cortex	Primary motor cortex	42	-12	58	370	5.19	0.014
Bilateral	Cerebral Cortex	Supplementary motor area	12	-6	86	396	5.15	0.014
Bilateral	Cerebral Cortex	Dorsolateral prefrontal cortex*	6	46	52	63	4.70	0.046
Bilateral	Hindbrain	Cerebellum*	20	-78	-48	592	5.10	0.014
		C: YN vs. YNN						
Bilateral	Cerebral Cortex	Superior & Inferior Parietal Middle Temporal Gyrus	8	-66	58	10324	7.75	0.000
Bilateral	Cerebral Cortex	Hippocampus Putamen	66	-48	18	4086	7.21	0.000
Bilateral	Cerebral Cortex	Premotor cortex	-24	2	60	442	6.20	0.000
Bilateral	Cerebral Cortex	Inferior frontal gyrus	52	20	10	900	4.92	0.006
Right	Hindbrain	Cerebellum	24	-78	-32	105	4.56	0.022
Left	Cerebral Cortex	Orbitofrontal Cortex	12	14	-22	27	4.00	0.112

Results shown for significant activations at $p<0.05$, corrected for multiple comparisons using False Discovery Rate (FDR) whole brain correction. * Indicates bilateral activation significant on the contralateral side at $p<0.001$ (uncorrected). # Indicates significant activation at $p<0.05$ at the FDR cluster-level.

Table S4. Training session. Brain regions recruited during the training session in all participants together, and in Young *vs*. Older participants.

L/R	Level	Region	X	Y	Z	Size	Z	p
		All Participants						
Bilateral	Cerebral Cortex	Middle occipital	16	-96	8	3021	>8.00	0.000
Bilateral	Cerebral Cortex	Superior and inferior parietal	6	-66	54	2641	>8.00	0.000
Bilateral	Cerebral Cortex	Middle temporal gyrus	64	-32	-2	1569	7.19	0.000
Bilateral	Cerebral Cortex	Premotor	26	10	56	430	6.83	0.000
		Young *vs*. Older						
Bilateral	Cerebral Cortex	Middle occipital	16	-96	8	3021	>8.00	0.000
Bilateral	Cerebral Cortex	Superior parietal	6	-66	54	2641	>8.00	0.000
Bilateral	Cerebral Cortex	Premotor	-24	4	62	362	7.77	0.000
Bilateral	Cerebral Cortex	Middle temporal gyrus	64	-32	-2	1569	7.19	0.000
Bilateral	Cerebral Cortex	Posterior parietal	48	-38	58	91	6.14	0.000

Results shown for significant activations at $p < 0.05$, corrected for multiple comparisons using False Discovery Rate (FDR) whole brain correction.

Supplemental Information: Study 3

Supplemental Table 1: Bivariate correlations between behavioral performance improvements on the ToH (accuracy, speed) and sleep oscillations (fast spindles, slow spindles, slow waves) during NREM sleep in young and older adults.

	Accuracy		Speed	
	r	***p***	**r**	***p***
Young Adults				
Slow Spindle Density	0.25	0.295	0.12	0.623
Slow Spindle Size	-0.24	0.310	0.39	0.087
Fast Spindle Density	-0.15	0.524	-0.32	0.167
Fast Spindle Size	0.09	0.697	0.31	0.181
Slow Wave Density	0.26	0.275	0.32	0.169
Slow Wave Size	0.26	0.266	0.32	0.165
Older Adults				
Slow Spindle Density	0.02	0.959	0.01	0.982
Slow Spindle Size	0.21	0.445	-0.24	0.388
Fast Spindle Density	0.12	0.669	-0.04	0.879
Fast Spindle Size	0.09	0.760	-0.33	0.227
Slow Wave Density	0.28	0.351	0.08	0.793
Slow Wave Size	-0.52	0.068	0.27	0.378

Experimental Design Overview

Following the screening/adaptation session, participants returned to the laboratory on two separate occasions for both a baseline and a testing session, counterbalanced across participants to mitigate order effects. During the experimental testing session, upon arrival, participants performed eight blocks of the Tower of Hanoi (ToH) and four blocks of the Control (CTL) task while being scanned in the magnetic resonance imaging (MRI) scanner. Each block was followed by a 20-second rest period. The order of the ToH and CTL tasks were counterbalanced across participants to mitigate order effects. This training session was then followed by either: a 90-minute daytime PSG recording (Nap condition), or, a 90-minute period of wakefulness (Wake condition). All participants were then returned to the scanner and completed four retest blocks of both the ToH and CTL tasks again while being scanned in the MRI. At testing session, the ToH and CTL tasks (starting at 10:00 AM) were performed while obtaining functional MRI (fMRI) blood oxygen level dependent (BOLD) images using a block design. In addition, we obtained 8-minute awake resting state fMRI images prior to and after the training and retest on the ToH and CTL tasks.

Control Task

An adapted version of the ToH task was intended specifically to control for (*i.e.*, subtract out) brain activations associated with motor execution of movements and the visual characteristics of the ToH for the fMRI analyses reported in Toor et al. (2022). The CTL task was identical to the ToH task in every way, except that each move was prompted from one pseudorandom location to another without violating the constraints of the task. Importantly, the CTL task required the same type of motor execution as the ToH (*e.g.*, speed and number of movements per block), but the movements did not follow the sequence of movements required to learn the underlying strategy (*i.e.*, recursive logic) needed to complete the ToH. Thus, learning the strategy and reaching the optimal solution was not possible in performing the CTL task. All sensorimotor, spatial, and visual aspects of the task were the same as the ToH. Each move was prompted by the appearance of a green dot above a peg at a possible random location to identify the disk to be moved, followed by a red dot above the destination peg to complete the move. Each block of the CTL task ended when a total of 31 randomly guided moves, corresponding to the minimum number of moves it takes to complete the 5-disk ToH task were completed.

fMRI Recording Parameters

All fMRI sequences (*i.e.*, resting state and task sessions) employed multislice T2-weighted fMRI images (TR = 2.16 sec; TE = 30 ms, FA = 90º, 40 transverse slices, 3 mm slice thickness, 10% inter-slice gap, FoV = 220 x 220 mm^2, matrix size = 64 x 64 x 40, voxel size = 3.44 mm x 3.44 mm x 3 mm).

Cognitive Aptitude Battery

At the screening session, all participants completed the Cambridge Brain Sciences (CBS) test battery (Hampshire et al., 2012b). The test battery takes around 30-45 minutes to complete. The CBS tests include classic twelve cognitive tests adapted for online testing that measure a broad range of cognitive abilities including reasoning, problem-solving, planning, attention, and memory. A factor analysis based on scores from 44,600 participants (Hampshire et al., 2012b), identified that Reasoning, Verbal and Short-Term Memory (STM) abilities explain distinct and non-overlapping (*i.e.*, orthogonal) domains of cognitive abilities along with their functional neuroanatomical substrates. The Reasoning factor is best described in terms of performance on five classical tests adapted for online testing from the cognitive and neuropsychological literature, including deductive reasoning (Cattell, 1940), spatial rotation (Silverman et al., 2000), feature match (Treisman & Gelade, 1980), spatial planning (Shallice, 1982), and polygons (Folstein et al., 1975). STM is best described in terms of four tests, including visuospatial working memory (Inoue & Matsuzawa, 2007), spatial span (Corsi, 1973), paired associates (Gould et al., 2006), and self-ordered search (Collins et al., 1998). Finally, verbal ability is best captured by performance on three tests, including verbal reasoning (Baddeley, 1968), color-word remapping (Stroop, 1935), and digit span (Wechsler, 1981). See Hampshire et al. (2012) for additional details.

Baseline Session

Following the screening session, participants attended the lab for one baseline session. Participants completed four blocks of the CTL task at 10:00 AM. Unlike the Testing session, the CTL session tasks were not conducted in the MRI. At 1:00 PM, after being prepared for polysomnographic recordings, participants in the Nap condition had their sleep recorded during a 90-minute daytime nap opportunity, whereas the participants in the Wake condition remained awake while reading, and laying in a supine position under dim ambient lighting. Both Nap and Wake conditions were continuously monitored via PSG recording (*n.b.*, in part to ensure the participants in the Wake conditions did not fall asleep). At 3:00 PM, more than 30 minutes after the end of the nap opportunity (to avoid sleep inertia effects), participants completed the retest session of the CTL task comprising four blocks. The Stanford Sleepiness Scale (Maclean et al., 1992), and the Psychomotor Vigilance Test (Dinges & Powell, 1985b) were administered prior to and following both CTL sessions to obtain subjective and objective measures of sleepiness across the baseline protocol.

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Appendix E: Demographic and Neuropsychological Testing Results

	Young Subjects		Older Subjects	
	Mean	*SD*	*Mean*	*SD*
Number of Subjects	Total: 40; YN: 20		Total: 29; 15 ON: 15	
Sex	Total: 23 Females; YN: 12		Total: 20 Females; ON: 9	
Age	23.85	3.86	67.06	7.62
MOCA	Na	Na	27.02	2.07
E-Cog	Na	Na	1.49	0.40
Beck Depression	1.88	0.29	0.12	0.14
Beck Anxiety	0.21	0.34	0.90	0.12
Epworth Sleepiness Scale	1.67	0.33	0.56	0.36
Stanford Sleepiness Scale	2.57	0.75	2.21	0.85
PVT	3.23	0.34	3.20	0.27
Circadian Rhythms	51.43	3.72	64.14	8.17
Sleep Disorders				
Periodic Leg Movements	11.07	2.65	14.47	3.60
Psychiatric Sleep Disorder	13.73	3.48	13.32	2.47
Sleep Apnea	14.78	3.50	21.53	4.53