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Overnight improvements in two REM sleep-sensitive tasks are associated with both REM and NREM sleep changes, sleep spindle features, and awakenings for dream recall

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ABSTRACT

Memory consolidation is associated with sleep physiology but the contribution of specific sleep stages remains controversial. To clarify the contribution of REM sleep, participants were administered two REM sleep-sensitive tasks to determine if associated changes occurred only in REM sleep. Twenty-two participants (7 men) were administered the Corsi Block Tapping and Tower of Hanoi tasks prior to and again after a night of sleep. Task improvers and non-improvers were compared for sleep structure, sleep spindles, and dream recall. Control participants ($N = 15$) completed the tasks twice during the day without intervening sleep. Overnight Corsi Block improvement was associated with more REM sleep whereas Tower of Hanoi improvement was associated with more N2 sleep. Corsi Block improvement correlated positively with %REM sleep and Tower of Hanoi improvement with %N2 sleep. Post-hoc analyses suggest Tower of Hanoi effects—but not Corsi Block effects—are due to trait differences. Sleep spindle density was associated with Tower of Hanoi improvement whereas spindle amplitude correlated with Corsi Block improvement. Number of REM awakenings for dream reporting (but not dream recall per se) was associated with Corsi Block, but not Tower of Hanoi, improvement but was confounded with REM sleep time. This non-replication of one of 2 REM-sensitive task effects challenges both 'dual-process' and 'sequential' or 'sleep organization' models of sleep-dependent learning and points rather to capacity limitations on REM sleep. Experimental awakenings for sampling dream mentation may not perturb sleep-dependent learning effects; they may even enhance them.

1. Introduction

1.1. REM and NREM sleep stages in memory consolidation

Despite strong and growing evidence supporting a role for sleep in the consolidation of new memories, the contribution of specific sleep stages remains controversial (see reviews Diekelmann & Born, 2010; Ellenbogen, Payne, & Stickgold, 2006; Walker & Stickgold, 2010). Many findings support 'dual-process' models which stipulate that REM and NREM stages of sleep facilitate different memory systems, most commonly, hippocampally- vs. non-hippocampally-mediated memories, or non-declarative vs. declarative memories (e.g., Maquet, 2001). To illustrate, in the case of REM sleep, associated improvements have been demonstrated for mirror-tracing (Plihal & Born, 1997), complex logic, word priming, emotional memory (Baran, Pace-Schott, Ericson, & Spencer, 2012; Gujar, McDonald, Nishida, & Walker, 2011; Wagner, Fischer, & Born, 2002; Wagner, Gais, & Born, 2001), and visuospatial working memory (see Smith, 1995 for review), while in the case of NREM sleep, associated improvements have been demonstrated for paired-associate learning (Plihal & Born, 1997), facial recognition (Clemens, Fabo, & Halasz, 2005), face-name, face-scene and face-city associations (Bergmann, Molle, Diedrichs, Born, & Siebner, 2012; Clemens et al., 2005; Ruch et al., 2012), and spatial maze learning (Meier-Koll, Bussmann, Schmidt, & Neuschwander, 1999).

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In contrast, many results support alternative models according to which both REM and NREM sleep are required for memory consolidation. These alternatives include ‘sequential’ or ‘2-stage’ models that require a succession of REM and NREM stages (Buzsaki, 1989; Fogel, Smith, & Beninger, 2009; Giuditta, Mandile, Montagnese, Piscopo, & Vescia, 2003), and ‘sleep organization’ models requiring an intact organization of NREM-REM cycles through the night of sleep (Ficca & Salzarulo, 2004). Some supportive findings include the facts that in humans visual discrimination learning is associated with changes in both NREM and REM sleep on the same night (Stickgold, Whidbee, Schirmer, Patel, & Hobson, 2000), and that in rats avoidance learning is followed by increases in both REM sleep theta power and NREM sleep spindle density (Fogel et al., 2009). Such alternative models also account more parsimoniously for results not easily explained by dual-process approaches, e.g., that declarative memory can at times be associated with REM (rather than NREM) sleep (Tilley & Empson, 1978) and that non-declarative memory can at times be associated with NREM (rather than REM) sleep (Doyon et al., 2009; Morin et al., 2008; Smith & MacNeill, 1994; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002).

Clarifying the role of sleep stages in memory consolidation is further complicated by the multiplicity of macro- and micro-structural sleep measures and their differential associations with different learning tasks within and between experiments. Memory improvements have been linked not only to changes in the relative proportions of REM sleep (Baran et al., 2012; Gujar et al., 2011), Stage 2 (N2) sleep (van der Helm, Gujar, Nishida, & Walker, 2011), and Stages 3 and 4 (N3) sleep (Lau, Tucker, & Fishbein, 2010), but also to particular sleep features such as EEG spindles (Barakat et al., 2011; Fogel & Smith, 2011), theta waves (Popa, Duvarci, Popescu, Lena, & Pare, 2010), alpha and beta EEG power (Yordanova, Kolev, Wagner, Born, & Verleger, 2012), slow (<1 Hz) EEG oscillations (Dickson, 2010; Marshall, Helgadottir, Molle, & Born, 2006), and rapid eye movement density (Smith, Nixon, & Nader, 2004). Even different attributes of each measure have found to be differentially related to learning; to name a few: REM density vs. duration (Fogel et al., 2009), early vs. late night REM or NREM sleep (Stickgold et al., 2000), spindle density vs. duration (Bergmann et al., 2012), or variations in cortical topography of EEG changes (Murphy et al., 2011). Thus, it is not unusual to find that two different sleep measures are associated with cross-night improvements on two different learning tasks. To illustrate, one study reported that among the same participants, overnight improvements on a face recognition task were associated with NREM sleep time, whereas improvements on a face-name associates task were linked to an increase in localized stage N2 sleep spindles (Clemens et al., 2005). More recent models of sleep-sensitive learning have attempted to deal with this complexity (Stickgold & Walker, 2013), but more research is clearly needed.

Thus, despite burgeoning evidence supporting a role for sleep in memory consolidation, the contribution of specific sleep stages, or combinations of sleep stages, to memory remains contentious. Different models have been proposed to account for the variety of findings but none is predominant. A promising strategy for examining the sleep stage/memory type question is the use of several tasks with known sleep-dependent effects in conjunction with the assessment of multiple sleep variables concurrently. The present protocol employs such a strategy in administering two validated tasks for which overnight improvement is dependent upon REM sleep (Smith, 1995) but which index different cognitive and brain systems: the Corsi Block Tapping Task (CBT) (Milner, 1971) and the Tower of Hanoi (ToH) (Cohen, Eichenbaum, Deacedo, & Corkin, 1985). These tasks are both non-verbal in nature and both draw upon working memory capacity. However, the CBT is a visuospatial working memory task sensitive to hippocampal functioning (Toepper et al., 2010) while the ToH is a problem-solving, executive function task sensitive to frontal lobe functioning (Milner, 1971; Welsh, Satterlee-Cartmell, & Stine, 1999). Dual-process models would lead to the expectation that both of these tasks will demonstrate an association with overnight REM but not NREM sleep. Alternative 2-stage or sequential models might predict that the two tasks will be associated with both REM and NREM sleep measures.

1.2. Dream mentation sampling as a possible experimental artifact

Some research has demonstrated memory consolidation to be followed by changes in dream mentation that is sampled from either REM (De Koninck, Christ, Rinfret, & Proulx, 1988; Fiss, Kremer, & Lichtman, 1977; Pantoja et al., 2009) or NREM (Wamsley, Tucker, Payne, Benavides, & Stickgold, 2010) sleep. Compared with the sleep studies described above, dream mentation research is less common (see reviews in Smith, 2010; Wamsley & Stickgold, 2011) in part because the awakening of participants for mentation sampling disturbs the associated sleep physiology and may thus perturb sleep-related memory benefits. However, it is also possible that awakenings from sleep will enhance memory; studies with rats have found that sequences of REM and NREM sleep that include transitions to wakefulness are associated with the fast learning of avoidance reactions (Piscopo et al., 2001). Given the paucity of information about the effects of night awakenings and of recalling dream mentation on memory in humans, our protocol was designed to assess whether these factors were associated with disruption or enhancement of REM sleep-dependent effects on performance for two tasks.

2. Methods

2.1. Participants

Thirty-seven healthy volunteers were recruited by advertisements in newspapers and by word of mouth. They reported themselves to be free of sleep, psychiatric, and physical illnesses, to have normal sleep schedules, and to be free from medications. They were reminded several days prior to participating to abstain from alcohol for at least 24 h, and from caffeine for at least 6 h, prior to arriving at the laboratory. The sleep study sample ($N = 22$) comprised two cohorts. Sixteen participants (4 men, 12 women) spent 2 nights each in the sleep laboratory with cognitive testing on night 1. Six additional participants (3 men, 3 women) spent 1 night each in the laboratory with the same cognitive testing on that night. The two cohorts did not differ in age or on any sleep or cognitive test measures and were combined to form a sample (mean age: 25.0 ± 5.0), of whom 15 were women (mean age: 25.1 ± 5.5) and 7 were men (mean age: 24.6 ± 4.2). The waking state control sample ($N = 15$) consisted of 11 women and 4 men with a mean age of 24.9 ± 5.6 yrs. The sleep and wake groups did not differ in age. All participants gave written informed consent; the study was approved by the hospital ethics review board.

2.2. Procedures

2.2.1. Cognitive testing

Participants in the sleep sample arrived at the sleep laboratory at least 2 h prior to their normal bed times. A polysomnographic (PSG) recording montage was applied and 2 cognitive tasks were administered 30 min before lights out (T1-S). These were the Tower of Hanoi (ToH) task (Cohen et al., 1985) followed by the Corsi Block Tapping (CBT) task (Milner, 1971). For the ToH, participants were told that a pyramid of 5 disks should be moved from