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Mentation during sleep onset theta bursts in a trained participant: A role for NREM stage 1 sleep in memory processing?

Philippe Stenstrom^{1,2}, Kieran Fox³, Elizaveta Solomonova^{1,2} and Tore Nielsen^{1,4}

¹ Sleep Research Center, Hôpital du Sacré-Coeur de Montréal, Montreal, Canada

² Department of Psychology, Université de Montréal, Montreal, Canada

³ Department of Psychology, University of British Colombia, Vancouver, Canada

⁴ Department of Psychiatry, Université de Montréal, Montreal, Canada

Summary. NREM stage 1 sleep, known as a brief interval of transition from wake to sleep, is characterized by neurophysiological events and subjective sensory experiences that suggest the stage may be involved in memory processing. To examine this possibility, we conducted multiple awakenings with a trained participant during short bursts of theta activity defining the 5th sub stage of NREM stage 1 sleep (NREM1 Φ). Awakenings provided frequent reports of vivid dreaming containing coherent scenes—as opposed to isolated objects often associated with general sleep onset imagery. Analyses of the temporal and semantic aspects of the memories associated with this imagery suggest that multiple memories are selected for incorporation in NREM1 Φ imagery on the basis of their semantic proximity and temporal remoteness. Analyses also demonstrate a remarkable pattern in about a third of dreams in which distinct, semantically related memories dating from as little as 10 minutes to as much as 15 years ago were bound in close temporal and spatial proximity within the novel contexts of the imagery. This offline manipulation of semantic information, observed here at a phenomenological level, bears a resemblance to processes thought to underlie *integrative encoding*, i.e., the encoding of an association between events that were not experienced together but which are subsequently combined because they contain at least one overlapping element. This preliminary study provides evidence consistent with the notion that hippocampal-mediated memory processing occurs during the theta bursts found at sleep onset.

Keywords: Sleep onset; Dreaming; Theta; Hippocampus; Memory; NREM sleep; REM sleep

"I turned the chair to face the fireplace and slipped into a languorous state. Again atoms fluttered before my eyes. Smaller groups stayed mostly in the background this time. My mind's eye, sharpened by repeated visions of this sort, now distinguished larger figures in manifold shapes. Long rows, frequently linked more densely; everything in motion, winding and turning like snakes. And lo, what was that? One of the snakes grabbed its own tail and the image whirled mockingly before my eyes. I came to my senses as though struck by lightning; this time, too, I spent the rest of the night working out the results of my hypothesis."

Friedrich Kekulé, on his discovery of the molecular structure of benzene, (Translated in Rothenburg, 1998).

Corresponding address:

Email: tore.nielsen@umontreal.ca

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1. Introduction

Recent years have seen a surge in research examining relationships between memory and sleep. But despite a wealth of findings clarifying the roles of stages 2, 3 and 4 NREM and stage REM sleep in memory consolidation, our knowledge of the first stage of sleep, NREM stage 1 (NREM1), in relation to memory processes is lacking. As a brief, transitory state, NREM1 sleep may seem trivial or uninteresting; however, it is characterized by a highly dynamic brain state whose neurophysiology is likened by some to a hybrid of wake, NREM and REM sleep (see Table 1). For example, recent studies (Bódizs, Sverteczki, Lázár & Halász, 2005; Bódizs, Sverteczki & Mészáros, 2008) have shown hippocampal activity during NREM1 that is characteristic of REM sleep. Rather, the impediment to studying NREM1 sleep is that it is the gateway to sleep and thus it does not lend itself well to current experimental paradigms that have been fruitful in investigating the role of sleep for learning and memory in humans. Nonetheless, one study (Lahl, Wispel, Willigens & Pietrowsky, 2008) found enhanced retention of word lists after 5 min naps containing minimal amounts of stage 2 sleep, leading the authors to suggest that the task was processed during NREM1.

While studying memory processing during NREM1 may present particular challenges, its proximity to wakefulness makes it an ideal stage for probing the phenomenological contents of mental activity. Methods of collecting sleep mentation have recently been used to clarify learning and mem-

Tore A. Nielsen, PhD, Dream and Nightmare Laboratory, Sleep Research Center, Hôpital du Sacré-Coeur de Montréal, 5400 Gouin Blvd West, Montréal, Québec, Canada, H4J 1C5



ory processes during NREM sleep (e.g., Wamsley & Antrobus, 2009; Wamsley, Perry, Djonlagic, Reaven, & Stickgold, 2010; Stickgold, Malia, Maguire, Roddenberry, & O'Connor, 2000), with one study (Wamsley, Tucker, Payne, Benavides, & Stickgold, 2010) finding a strong link between dreaming of a task in NREM sleep and increased sleep-dependent learning. These studies support the notion that mentation during NREM sleep reflects memory processing, and may provide a unique perspective by which offline memory processing can be examined (see Wamsley and Stickgold, 2010).

It is well known that vivid visual imagery is experienced at sleep onset—and only remembered if the individual is awakened at this time. Early studies examined this imagery specifically in terms of its similarity to REM sleep dreaming (Foulkes & Vogel, 1965; Foulkes, Spear, & Symonds, 1966; Vogel, Barrowclough, & Giesler, 1972; Foulkes & Schmidt, 1983; Rowley, Stickgold & Hobson, 1998). More recent studies have either focused on the EEG correlates of sleep onset dreaming without considering its relationship to memory and learning (Germain & Nielsen, 1997; Hayashi, Katoh, & Hori, 1999; Hori, Hayashi, & Morikawa, 1993; Nielsen et al., 2005) or examined it in relation to a pre-sleep task without specifying EEG or other associated physiological correlates (Stickgold et al., 2000; Wamsley et al., 2010). The present study is an exploratory attempt to consider all of these factors together with a single, highly trained participant; i.e., to examine the imagery and memory processes associated with a sub-stage of NREM1 with distinct EEG correlates. The objective is to evaluate NREM1 dream reports for evidence of memory processing that may be active at this time, specifically, 1) the presence of hippocampallymediated, declarative memories, and 2) chronological and semantic patterns of memory representation.

The target NREM1 sub-stage is one of nine EEG patterns first defined by Hori et al. (1993b) and illustrated in Table 1. Beginning with relaxed wakefulness characterized

Table 1: EEG patterns defined	by Hori et al (1993b)
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Stage	sub stages ¹	EEG Signa- ture	EEG Signature Wave- form	Subjective State	Recall of Mentation	Eye move- ments	Hip- pocampal activity
Wake	1	Alpha wave train	mumummumm	Awake	?	?	?
	2	Alpha wave intermittent (>50%)	MMMMMMMM ~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	Awake	?	?	?
NREM 1	3	Alpha wave intermittent (<50%)	Mmmmmm Mmmm	?	?	Slow and short lasting ²	Dimin- ished⁵
	4	EEG flattening (<20 μV)	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	Wake: 62% Sleep: 16% Not sure: 22% ¹⁰	82% ¹⁰	?	?
	5	Theta ripples	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	Wake: 43% Sleep: 40% Not sure: 17% ¹⁰	85%10	Wake-like slow saccades ²	?
	6	Vertex sharp wave (<200 µV)	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	?	?	Wake-like slow saccades ²	?
	7	> 1 Vertex sharp wave (<200 μV)		?	?	Oculomotor slowing ²	?
	8	Incomplete spindle	malando	?	?	Oculomotor slowing ²	Higher than wake⁵
NREM 2	9	Complete Spindle	man and the many the	Sleep	43%11	Minimal activity	Active ⁴
NREM 3-4		Delta	Manna	Sleep	43%11	Minimal activity	Dimin- ished⁴
REM		Theta	Mar	Sleep	82% ¹²	Wake-like rapid saccades ³	Active ^{6,7,8} Higher than wake ⁹

¹ Hori et al. 1994.; ² Porte et al., 2004; ³ Ogawa et al., 2009; ⁴ Kaufmann et al. 2006; ⁵ Picchioni et al. 200; ⁶ Only PET data available for this area in REM; ⁷Maquet et al. 1996; ⁸ Nofzinger et al. 1996; ⁹ Braun et al. 1997; ¹⁰ Unpublished findings from 104 Hori sub-stage 4 and 135 Hori sub-stage 5 reports from 27 healthy participants (Nielsen et al. 2005); ¹¹ Nielsen, 2000 (average from 29 studies); ¹² Nielsen, 2000 (average from 33 studies)

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by alpha wave trains (sub-stage 1) and intermittent alpha >50% (sub-stage 2), a reliable sequence (Doerfling, Ogilvie, Murphy, & Lamarche, 1996) of sub-stages characterizes NREM1: intermittent alpha <50% (sub-stage 3), EEG flattening (sub-stage 4), theta waves (sub-stage 5), solitary humps or solitary vertex waves (sub-stage 6), hump trains or vertex waves (sub-stage 7), humps or vertex waves with incomplete spindles (sub-stage 8) and spindles (sub-stage 9). The latter sub-stage typically signals the onset of NREM stage 2 sleep.

Of particular interest to learning and memory is NREM1 sub-stage 5 (NREM1Φ), characterized by clearly visible low voltage theta waves, following which dream-like experiences are reported with very high frequencies (Germain & Nielsen, 1997; Hori et al., 1993; Nielsen et al., 2005). Cortical theta is reliably associated with learning and memory (see Mitchell, McNaughton, Flanagan, & Kirk, 2008 for review) and is involved with declarative memory consolidation during REM sleep in humans (Fogel, Smith, & Cote, 2007). Importantly, theta is thought to underlie the interactions between hippocampus and neocortical areas (Buzsaki, 2006; Miller, 1991) that form the basis of episodic memory encoding and retrieval, i.e., the ability re-experience an event in some perceptual detail (Tulving, 2002). However, the relationship between hippocampal and scalp EEG theta is not well understood in humans (Mitchell, McNaughton, Flanagan, & Kirk, 2008) and therefore a link between hippocampal theta and sleep onset theta bursts as measured by EEG is speculative.

Dreaming has also been described as a function of hippocampal-neocortical interactions that are constrained and modulated by the unique neurophysiology of REM sleep (Johnson, 2005; Nielsen & Levin, 2007; Nielsen & Stenstrom, 2005; Paller & Voss, 2004; Payne & Nadel, 2004; Sil'kis, 2010; Stickgold, 2002; Stickgold, Hobson, Fosse, & Fosse, 2001). We have argued (Nielsen & Stenstrom, 2005) that the hippocampus plays a critical role in dream construction by binding neocortical memory traces together to create the "here and now" experience of dreaming. Consistent with evidence described earlier that REM-related processes such as hippocampal theta occur at sleep onset (Bodizs, et al., 2005; see Nielsen, 2000 for review) and are associated with sleep onset imagery (Nielsen et al., 2005), we expect that hippocampal processes will also be involved in the theta-rich sub-stage of NREM1Φ dreaming.

The notion of hippocampal involvement in sleep onset imagery, and in dreaming more generally, is nonetheless contested. The seemingly chaotic and isolated nature of dreaming is taken by some authors to indicate that dream imagery is generated with an absence of hippocampal input (Payne & Nadel, 2004). Moreover, the finding that densely amnesiac, hippocampal-lesioned patients report sleep onset imagery similar to that of controls suggests that dreaming at sleep onset does not utilize the hippocampally-mediated declarative system (Stickgold et al., 2001).

The issue of hippocampal involvement in NREM1Φ has not been clarified by fMRI (Kaufmann et al., 2006; Picchioni et al., 2008) and MEG (Ioannides, Kostopoulos, Liu, & Fenwick, 2009) studies examining NREM1 because the NREM1 sub-stage has not been studied in isolation. Nonetheless, one fMRI study of NREM1 sleep found an increase of hippocampal activity from the first to the last 30 sec of the NREM1 period (Picchioni et al., 2008). It remains an open question whether this increase in hippocampal activity occurs before, during or after the theta bursts of sub-stage 5. Because the hippocampus and theta activity are central to memory processes, their co-activation at sleep onset would be consistent with a possible role for this stage in memory consolidation.

The current study explores a novel methodological approach to this question by probing specific phenomenological qualities of NREM1Ф imagery for evidence of processes that are known to be hippocampally mediated. Imagery was analyzed for the presence of scene construction (Hassabis & Maguire, 2007) a process shown to be critically dependent on the hippocampus (Hassabis & Maguire, 2009). The notion of scene construction as a hippocampally-mediated process rests on findings that patients with hippocampal lesions are severely hindered in remembering past experiences (Squire, Stark, & Clark, 2004) and imagining new situations (Hassabis, Kumaran, Vann, & Maguire, 2007). Similarly, fMRI studies with healthy participants demonstrate that the hippocampus is involved with recreating past experiences and imagining future experiences (Addis, Pan, Vu, Laiser, & Schacter, 2009; Addis & Schacter, 2008; Addis, Wong, & Schacter, 2007), as well as imagining fictive scenarios (Hassabis, Kumaran, & Maguire, 2007). Together these findings converge in demonstrating that the hippocampus is critically involved in scene construction, i.e., binding disparate elements of an imagined situation within a spatial framework (Hassabis & Maguire, 2007).

Accordingly, evidence of scene construction in NREM1 Φ images would be consistent with hippocampal involvement at this time. While sleep onset imagery is claimed by some to be associated with isolated objects (Mavromatis, 1987; Stickgold et al., 2000), we have observed complex, spatially embedded, hallucinatory activity associated specifically with the NREM1 Φ sub-stage in several subjects (unpublished findings). To further examine this effect, a participant trained in self-observation was awakened multiple times from discrete episodes of NREM1 Φ sleep during two non-consecutive nights. The participant provided detailed reports of the immediately preceding imagery; these were assessed for the presence or absence of scene construction.

We also examined the temporal and semantic characteristics of memories that the participant associated to this imagery ('memory sources') as evidence of memory processing during NREM1Φ. Previous research has demonstrated a reliable temporal pattern of memory source incorporation into night dreams (for review see Nielsen, 2004) that is characterized by a predominance of memory sources from 1-2 days prior to the dream (day residue effect) and 5-7 days prior to the dream (dream lag effect) as compared to 3-4 days prior to the dream (Blagrove, Henley-Einion, Barnett, Edwards & Seage, 2010; Nielsen, Kuiken, Alain, Stenstrom, & Powell, 2004; Nielsen & Powell, 1989; Powell, Cheung, Nielsen, & Cervenka, 1995). The dream lag effect has been explained as due to cellular-level hippocampal memory consolidation processes (Nielsen & Stenstrom, 2005) and has not yet been investigated in sleep onset dreaming. Thus, the participant in the present study was required to provide detailed reports of potential memory sources of NREM1Ф dreams. On the assumption that REM-like processes occur during NREM1Φ, we predicted that the temporal pattern of dream incorporations previously found for REM sleep dreaming (day residue and dream lag effects) would also be found at sleep onset.

That REM processes occur during NREM1 Φ may also indicate that imagery at this time will, in a manner similar to REM dreams (Fosse et al., 2003), not replay complete episodic episodes. While NREM stage 2 dreams contain a large number of episodic elements compared to SWS and REM sleep (Baylor & Cavallero, 2001), no study to date has examined the extent to which NREM1 dreams are characterized by the presence/absence of episodic replay. To address this, the present participant provided ratings of *episodic integrity*, defined as the degree to which each NREM1 Φ dream consisted of a replay of a previous experience. We predicted that NREM1 Φ dreams will not be episodic replays but, like REM sleep dreams, will consist of novel associations between distal memories.

Our specific hypotheses concerning the imagery reported following NREM1 Φ awakenings were as follows:

H1) NREM1Φ dreams will be constructed as scenes, i.e., will contain items situated in a three dimensional environment forming a coherent scene, as opposed to items not well integrated within an environment or missing an environment altogether.

H2) Memory sources for NREM1 Φ dreams will be influenced by similar temporal factors as sources for REM sleep dreams, i.e., the day-residue and dream-lag effects. Thus, memory sources will originate in events occurring 1 or 2 and 5, 6, or 7 days, as opposed to 4 or 5 days, prior to occurrence of the dream.

H3) NREM1 Φ dreams will not consist of the replay of whole episodic memories but, like REM dreams, will feature multiple memory sources from unrelated memories.

2. Method

A single male participant (author KF, age 23) in good mental and physical health was previously habituated to the laboratory environment, had good dream recall, and had not used medications, drugs or alcohol at least 1 month prior to the experiment. He had been practicing dream recall and identifying memory sources of his dreams several years prior to the first night. He previously underwent 2 sessions of NREM1 Φ awakenings (5 and 10 awakenings each; not reported here) according to the methods described below. He was aware that an objective of the current study was to identify memory sources, and was aware of the day-residue and dream-lag effects, but was unaware of the hypothesis concerning scene construction.

The participant slept two non-consecutive nights in a sleep laboratory with EEG recordings made from C3, C4, O1 and O2 electrodes applied according to the standard 10-20 system. We awakened the participant repeatedly throughout the entire night between the hours of 11 PM and 7 AM and exclusively during NREM1 Φ sleep, i.e., when at least 5 sec had elapsed of Hori sub-stage 5 characterized by low voltage theta (5-7Hz) wave ripples with an amplitude of 20 μ V to 50 μ V (Hori, Hayashi, & Morikawa, 1993a). The sleep stage was determined in real time by an experienced polysomnographer and was verified by a second experimenter. When the stage criteria were met, the experimenter called the participant by his first name through an intercom preset at a comfortable volume. In every case the participant immediately responded to their name.

The participant gave a detailed verbal report of each ex-

perience that had immediately preceded the call; he sometimes made drawings of the imagery for clarity. This report was followed by a report of any distinct memory sources he could identify for specific dream elements. A distinct memory source was defined as an object, person, setting or sound whose waking-life source the participant could unambiguously recall. He stated the approximate time in days, months or years since that memory had occurred. Memory sources were later classified by the experimenter into one of 4 temporal bins: 0-3 days, 4-30 days, 1-11 months and 1 year or more.

The participant then verbally responded to scales measuring the presence of self (yes or no), perspective (first person, third person or both), self movement (yes or no), movement other than self (yes or no), presence of emotions (yes or no), intensity of emotions (1 to 9; 1 = not at all intense, 9 = extremely intense), valence of emotions (1 to 9; 1 = very negative, 5 = neutral, 9 = very positive), and type of emotion (open-ended). The participant also rated dream reports for the extent to which they reflect an actual memory, i.e., episodic integrity (1 to 9; 1 = not at all like a replay of a memory, 9 = entirely like a replay of a memory) and the extent to which the dream was bizarre (1 to 9; 1 = not at all bizarre, 9 = extremely bizarre).

Two days following each experimental night the participant and one author (PS) examined the dream reports to identify recurring elements, defined as semantically similar elements in the dream.

Finally, two independent judges evaluated the presence of scene construction in the dream; drawings made by the participant were also available for this task. Transcribed dream reports were classified into three bins: 1) presence of scene construction: imagery containing clear evidence of items well integrated within a three dimensional environment; 2) absence of scene construction: reports containing no evidence of items integrated within a three dimensional environment; and 3) ambiguous reports: imagery containing unclear evidence that items were integrated within a three dimensional environment. Items were defined as either an object or a person.

3. Results

The participant was awakened 16 times during Night 1 and 18 times during Night 2 for a total of 34 awakenings with reports. Three awakenings produced only 'thought-like' activity (i.e., no imagery) and were discarded. The remaining 31 reports contained hallucinatory activity (pseudo-sensory imagery) that defined 'dreaming' for the present study.

The participant reported himself as being awake for 44 % of awakenings, as sleeping for 28% and as "not sure" for the remaining 28% (ratios very similar to those obtained from 27 other subjects in our lab; unpublished data, see Table 1). A majority of awakenings gave rise to visual imagery (N = 31; 100%) composed of a three dimensional environment in which the participant was present (N = 24; 77%) and viewing the scene from a first person perspective (N = 24; 77%). In no case did the participant report seeing himself. While for about half of the reports the participant was engaged in motor activity (N=14; 45%), in most cases something in the environment was moving (N = 28; 90%). Emotions were present in most (N = 21; 67%) reports and were of generally low intensity (M = 3.90, SD = 1.70). A balanced mix of positive (N = 6, e.g., exhilaration of flying with a flock of geese) and negative (N = 5; e.g., fear of falling off a building; anxiety

over another dream character being injured) emotions was reported.

3.1. Scene construction

The two judges agreed on the categorization of the imagery in regards to the presence of scene construction in all cases but three, and resolved the discrepancies after discussing the matter with the participant. In most cases (N = 26; 84%) dreams were judged to be constructed as scenes, i.e., objects were well integrated within a three dimensional environment. In only four dreams (13%) was there no evidence of scene construction whatsoever: in one case there occurred an environment but no object ('protagonist traveling through space'); in the 3 other cases (9%) an object occurred without an environment (e.g., 'a cube floating in darkness', the participant's headphones appearing isolated from any environment). In two other cases (6%) the dream began with simple objects that evolved into 3D scenes (e.g., simple geometric shapes bouncing around becoming slowly integrated into a full scene); these were considered as examples of scene construction. In another case (3%) both an object and a background was present but there was insufficient information to determine whether they were well integrated within a three dimensional environment (e.g., an isolated white cube that seemed to have emerged from a body of water).

3.2. Episodic replay

Only one dream was described as highly episodic, i.e., the near replay of a past event, and even this dream contained discrepancies with the actual event. The event in question was the participant sitting on a ski slope with friends 1 month prior to the experiment (score: 9 out of 9 for episodic integrity). Dreams were described as containing varying degrees of episodic integrity, with an average rating of 3.81 (SD = 2.24) on the 1-9 scale. Four dreams contained no bizarre elements at all, with an average bizarreness score of 4.52 (SD = 2.47) on the 1-9 scale. Bizarreness scores were negatively correlated with episodic integrity scores (r30=

.594, p = .0001) and positively correlated with the number of memory sources contained in each dream (r30= .638, p = .0001). The number of memory sources negatively correlated with episodic integrity (r30= -.363, p = .045)

3.3. Memory Sources

A total of 81 distinct memory sources were reported for 31 dreams; at least one memory source (and as many as 5) was identified for each dream, with an average of 2.6 (SD = 1.1) memory sources per dream. Six dreams (19%) produced memories from immediately prior to sleep (e.g., lab technician, EEG amplifier), 16 (52%) produced memories from 1-12 months and 16 (52%) produced memories from 1+ years ago (see Figure 1). The most distant source was 15 years ago. Surprisingly, not a single occurrence of memory sources from 4 to 13 days ago was reported.

Memory sources from immediately prior to sleep always occurred within the first four awakenings on both nights (N1, 11:32-12:58 AM; N2, 11:56-12:34 AM), while years-distant sources never appeared until at least the 4th awakening on Night 1 (12:58-5:41 AM) and the 3rd awakening on Night 2 (12:34-5:15 AM), suggesting that time-of-night/circadian factors influenced reported memory sources. Indeed, a strong correlation was found between time-of-night and the temporal distance of the memory sources (in days, log transformed) (r (82) = .347 p = .001).

Twenty-one dreams (67%) produced memories from the last 1-11 months, however, only 3 of these dreams produced memory sources exclusively from 1-11 months ago. The other 18 dreams produced additional memories from the last few days, from years ago, or from both. Six reports (19%) produced memory sources from both the last 3 days and more than 1 year ago.

3.4. Semantic elements

Recurring semantic elements (n = 18), ranging from general themes (e.g., China) to specific objects (e.g., a white cube), were identified for several dreams within a single night. In

Table 2. Example of a recurring science fiction theme spanning multiple dreams on Night 1

Time of awakening	Memory source	Semantic aspects of memory sources	Temporal aspects of memory source
12:22 AM, Dream # 3	Situation and environment from the movie "2001: A Space Odyssey (1968)"	Particular type of high speed space travel	Movie seen 14 days ago
03:09 AM, Dream # 10	Situation and environment from the movie "Fire in the Sky (1993)"	Examination by aliens in space ship	Movie seen 8 months ago
04:55 AM, Dream # 14	Objects from the movie "Time Cop (1994)"	Particular shape of time travel portal	Movie seen 3 years ago
05:22 AM, Dream #15	Environment from book "The Mind's Eye (2005)"	A virtual grid superim- posed on a moonscape	Book read 14 days ago
05:41 AM, Dream #16	Object from comic "Battle Angel"	Particular shape of space ship	Comics read 3 months ago

Note: All space themes occurred during Night 1; no space theme occurred during Night 2

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contrast, only 2 recurring elements (Buddhism and University) were found across the two nights, and these referred directly to ongoing, long-term concerns of the participant. Overall, recurring elements appeared in from 2 to 5 (M = 2.47, SD = .70) different dreams and could be traced to specific memories 77% of the time (n = 14). When the memory sources of recurring elements could be identified, in all cases they could be traced to distinct and unrelated memories sometimes separated by several years. For example, the theme of 'outer space' recurred in 5 dreams on N1: memory sources were identified as three science fiction films seen 14 days, 8 months, and 3 years prior to the experiment, and two science-related books read 14 days and 3 months prior (see Table 2). The three films, for example (2001: A Space Odyssey, Time Cop, and Fire in the Sky), were viewed months or years apart, are totally unrelated to one another (e.g., not sequels, or featuring same director or actors), and were themselves produced over a period of nearly 30 years (1968 - 1994). Yet the common theme of futuristic technology and advanced forms of space-time travel was culled from all three films and recurred throughout a single night of NREM1 dreams alongside similar themes taken from books. Recurring elements were always distributed equally throughout the night, and were separated by an average of 3.82 (SD = 2.37) dreams between reappearances.

Recurring elements could also be found *within* single dreams. In 32% (n = 10) of dreams, memory elements with similar semantic properties yet stemming from different memories separated by from 2 days to 15 years appeared simultaneously in a single dream (see Table 3). In most cases (8/10), semantically related items came from memories that were separated by from 1 to 15 years (M = 4.21, SD = 5.03). The two remaining dreams were particular in that semantically related items stemmed from the same location (McGill University Campus); the dreams were only 10 minutes apart and the memories 3 months apart.

4. Discussion

To investigate the possibility that memory processing occurs during NREM1 sleep a trained participant was awakened 34 times from episodes of NREM1 sub-stage 5 sleep (with theta activity) across two non-consecutive nights for mentation reports. A majority of awakenings (31/34; 91.2%) resulted in detailed reports of vivid visual images that were constructed as integrated scenes and linked to a variety of memory sources.

4.1. Evidence of scene construction

A vast majority of recalled dreams (84%) were judged to be composed of multiple items (objects or persons) that were coherently integrated within a defined spatial context, i.e., a three-dimensional environment. They are thus similar in nature to other imaginative activity in which item-in-context associations are visualized as scenes, namely, remembering a past event (episodic memory), thinking about a future event, or imagining a novel event (Addis, McIntosh, Moscovitch, Crawley, & McAndrews, 2004; Addis et al., 2009; Addis & Schacter, 2008; Addis et al., 2007; Hassabis, Kumaran, & Maguire, 2007; Hassabis, Kumaran, Vann et al., 2007; Weiler, Suchan, & Daum, 2010). This type of scene construction is thought to reflect the hippocampally mediated process of binding together disparate neocortical traces into a coherent whole (Hassabis & Maguire, 2007, 2009) and, in this respect, our theta-linked NREM1Φ hypnagogic dreams may well be hippocampally mediated like these other forms of mentation.

This finding appears to contradict previous reports that densely amnesic patients with bilateral hippocampal lesions report imagery similar to that of controls during unspecified NREM1 or Stage 2 sleep (Stickgold et al., 2000). However, because in the latter study the reported imagery consisted of pre-sleep task-related Tetris blocks dissociated from any sort of environment, and thus did not involve scene construction as defined by Hassabis and Maguire (2007), the hippocampus need not have been involved in production of the imagery. In fact, because the theta ripples characterizing NREM1Φ are short in duration and account for only a fraction of each NREM1Φ episode, it is possible that previous studies investigating sleep onset cognition have not awakened participants at a time when the hippocampus was active. Indeed, sleep onset imagery is commonly described as containing isolated objects (Mavromatis, 1987) and it is possible that imagery during theta bursts is unusual in its complexity precisely because of involvement of the hippocampus.

While the structure of NREM1Φ dreaming was character-

Table 3. Examples of semantically related elements within a single dream

Time of awak- ening	Common Semantic Element	Description of elements included in the dream	Temporal aspects of memory source
Night 1 Dream #10 3:09AM	Body modification. Participant was on an operating table in a situation with visual and scene elements from 3 movies.	Body reconstruction from the movie "The Fifth Element (1997)"	2 months ago
		Autopsy from the movie "Fire in the sky (1993)"	8 months ago
		Torture from the movie "The Cell (2000)"	6 years ago
Night 2 Dream #13 4:00AM	<u>Pets.</u> Three pets from 3 time periods present in the backyard of childhood home.	Pet cat	2 months ago
		Pet rabbit	12 years ago
		Teddy bear	15 years ago



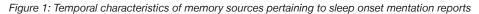
ized by scene construction in much the same manner as episodic memory recall is, these dreams did not consist of replays of episodic memories. Instead, most were described as bizarre and as containing a wide range of elements relating to multiple memory sources. In fact, only 1 dream (3.2%) was considered highly episodic, and only 5 dreams (16%) were not considered bizarre, with most featuring moderate levels of bizarreness (4.5 on a scale of 1 to 9) and moderate levels of episodic integrity (3.8 on a scale of 1 to 9). Furthermore, the degree of episodic integrity was found to be negatively correlated with the degree of bizarreness and the number of memory sources identified in a dream. Along with the finding of a positive correlation between the number of memory sources and bizarreness, these results suggest that dreams of low episodic integrity containing a number of distal memory sources will, guite reasonably, be rated as bizarre.

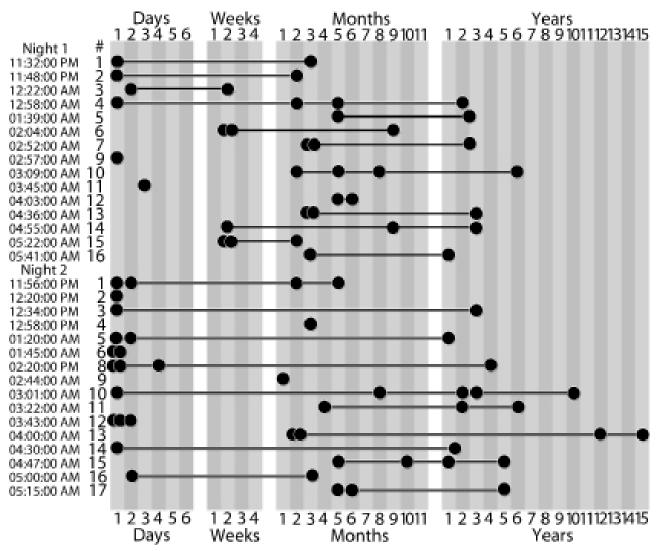
4.2. Temporal aspects of memory sources

The predominance of recent memories during the first 4 awakenings and of distant memories from the 3rd awakening

onward is consistent with previous findings that early-night REM dreams are constructed from more recent memory sources, and late-night REM dreams from more temporally distant sources (Verdone, 1965). This may indicate that either circadian or sleep-dependent processes underlie the recent/remote quality of memory source selection for both REM sleep and NREM1 Φ dreaming and further supports the claim that sleep onset NREM imagery may be modulated by changes in REM propensity (see Nielsen, 2010 for review). However, it is difficult to distinguish circadian effects from those entailed by sleep deprivation due to the multiple sleep onset awakenings performed in the current study.

In most cases, multiple memory sources linked to single dreams were separated by at least one month (see Figure 1). The intriguing possibility that memory sources within a single dream are targeted predominantly on the basis of distal temporal relationships is suggested by 1) the preponderance of reports eliciting memories from *both* 1-11 months ago and some other time period (less than 4 days, more than a year ago) and 2) the negligible number of dreams with *only* 1-11-month-old memories.





Note: Circles represent memory sources situated in time (X axis) for mentation reports occurring across two nights (Y-axis). Black lines connecting circles indicate sources are from the same dream.

We expected to find peaks in dream memory sources arising from 1-2 days ago (day residue) and 5-7 days ago (dream lag) based on previous studies for nocturnal dreams (Blagrove, 2010; Nielsen, 2004). However, although a clear day-residue effect was found, with 16 reports (52%) containing a memory source from 1 day prior, there was a total absence of a dream lag effect (0%). In fact, there was a curious lack of any memory sources from 5 to 13 days ago, suggesting an important difference between REM and NREM1Φ dream-incorporation mechanisms.

4.3. Recurring semantic elements

Unexpectedly, a large number of memory sources were found to be semantically related. Previously, Cippoli et al., (1988) found interrelated elements in stage 2 and REM dreams within single nights. Here we report that during multiple sequential NREM1 Φ episodes recurring elements are often related on a semantic level and most of these elements can be traced to episodic memories.

Eighteen recurring semantic elements were identified, ranging from simple objects (e.g., obelisk), personal items (e.g., pet animals), and landmarks (e.g., Asian temples), to more general themes (e.g., torture). With the exception of two semantic elements relating to pervasive personal concerns (Buddhism, University life), recurring semantic elements were specific to a single night. For example, the semantic element 'science fiction' was present in 5 dreams distributed across Night 1 and entirely absent on Night 2 (see Table 2). The fact that elements recurring across several dreams are not grouped together but are well distributed across the night suggests that multiple instances of semantically related elements across multiple dreams are not simply a function of semantic priming.

A third of all dreams contained semantically related items from distal memories. These items were isolated from their original context, i.e., dissociated from the memory of the event of which the items are a part, and integrated together in a novel scene that was vividly perceived. This offline manipulation of memory items bears a resemblance to integrative encoding, the hippocampally-mediated process by which overlapping items from separate events "are integrated into a linked mnemonic representation" (Shohamy & Wagner, 2008, p. 378). While the hippocampus has been demonstrated to enable associative inference between overlapping elements of two events that were not experienced together (Greene, Gross, Elsinger, & Rao, 2006; Heckers, Zalesak, Weiss, Ditman, & Titone, 2004; Preston, Shrager, Dudukovic, & Gabrieli, 2004), Shohamy and Wagner (2008) demonstrated that overlapping elements from separate episodes are encoded to provide a rich network of associations that cut across multiple events. While these studies limit distinct episodes to the duration of the experiment lasting only a few hours, here we find merged in a single scene semantically related items from memories that occurred months to years apart and that arose in entirely different contexts. That evidence of this phenomenon occurred in a third of all reports suggests that NREM1Φ dreaming may be involved in linking common elements from memories spanning several years (the oldest memory source was a toy animal from 15 years ago that the participant had not thought of since that time).

4.4. Similarities between NREM1Φ sleep and REM sleep

A century after Freud observed that past events are readily incorporated into dreaming, it is still unknown why certain memories are selected for incorporation, why specific elements within these memories are targeted for incorporation and what role the incorporation of such elements may play in offline memory processing. Here we provide preliminary evidence that during NREM1 sleep with theta waves, memory sources are selected on the basis of both distal temporal relationships and proximal semantic relationships, a finding consistent with the hypothesis put forth by Walker & Stickgold (2004) that the recombination of previous memories during REM sleep facilitates novel inferences.

Indeed, both REM and NREM1Φ dreams seem to form links between loosely associated items. For example, previous research suggests that the REM sleep state is characterized by a cognitive bias towards employing weak, as opposed to strong, semantic associations (Walker, Liston, Hobson, & Stickgold, 2002). Similarly, one study found that REM sleep is associated with increased performance on a creativity task; specifically, it served to prime associative networks and integrate unassociated information (Cai, Mednick, Harrison, Kanady, & Mednick, 2009). Along the same lines, we find that a third of the NREM1 Φ dreams featured semantically related items stemming from episodic memories that were separated by several years and bound together in spatial and temporal proximity within the imagery. Such modification of semantic information suggests that this stage of sleep may be involved in cross-episode integration on the scale of decades. These exploratory results thus provide evidence for the possibility that offline memory processes occur during NREM stage 1 sleep just as they do during REM sleep.

4.5. Use of trained participants for the study of dreaming

For this study, the finding of patterns within the temporal and semantic characteristics of memory sources was largely due to the excellent quality of the image reports and associated memory sources. We have previously argued for the need to employ trained participants to counter difficulties inherent in gaining access to subtle features of dream experience (Nielsen & Stenstrom, 2005). Although dreams can be difficult to remember, recent evidence suggests that remembering the details of dreams is a learnable skill. We demonstrated that providing participants with training to remember dreams and to identify their memory sources increases these abilities (Solomonova et al., 2008). The current study demonstrates that a motivated participant, habituated to laboratory awakenings and trained and practiced in recalling dreams and memory sources can produce well remembered and detailed dream reports, the analysis of which may lead to a more nuanced understanding of the mind in sleep.

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References

- Addis, D. R., McIntosh, A. R., Moscovitch, M., Crawley, A. P., & McAndrews, M. P. (2004). Characterizing spatial and temporal features of autobiographical memory retrieval networks: a partial least squares approach. Neuroimage, 23, 1460-1471.
- Addis, D. R., Pan, L., Vu, M. A., Laiser, N., & Schacter, D. L. (2009). Constructive episodic simulation of the future and the past: distinct subsystems of a core brain network mediate imagining and remembering. Neuropsychologia, 47, 2222-2238.
- Addis, D. R., & Schacter, D. L. (2008). Constructive episodic simulation: temporal distance and detail of past and future events modulate hippocampal engagement. Hippocampus, 18, 227-237.
- Addis, D. R., Wong, A. T., & Schacter, D. L. (2007). Remembering the past and imagining the future: common and distinct neural substrates during event construction and elaboration. Neuropsychologia, 45, 1363-1377.
- Baylor, G. W., & Cavallero, C. (2001). Memory sources associated with REM and NREM dream reports throughout the night: a new look at the data. Sleep, 24, 165-170.
- Blagrove, M., Henley-Einion, J., Barnett, A., Edwards, D., & C.H. Seage (2010) A replication of the 5-7day dreamlag effect with comparison of dreams to future events as control for baseline matching. Conscious Cogn, doi:10.1016/j.concog.2010.07.006.
- Bódizs, R., Sverteczki, M., Mészáros, E. (2008). Wakefulnesssleep transition: emerging electroencephalographic similarities with the rapid eye movement phase. Brain Res Bull, 76, 85-9.
- Bódizs, R., Sverteczki, M., Lázár, A. S., & Halász, P. (2005). Human parahippocampal activity: non-REM and REM elements in wake-sleep transition. Brain Res Bull, 65,169-76.
- Braun, A. R., Balkin, T. J., Wesenten, N. J., Carson, R. E., Varga, M., Baldwin, P., et al. (1997). Regional cerebral blood flow throughout the sleep-wake cycle. An H2(15)O PET study. Brain, 120, 1173-1197.
- Buzsaki, G. (2006). Rhythms of the Brain. Oxford: Oxford University Press.
- Cai, D. J., Mednick, S. A., Harrison, E. M., Kanady, J. C., & Mednick, S. C. (2009). REM, not incubation, improves creativity by priming associative networks. Proc Natl Acad Sci U S A, 106, 10130-10134.
- Cipolli, C., Fagioli, I., Baroncini, P., Fumai, A., Marchio, B., & Sancini, M. (1988). The thematic continuity of mental experiences in REM and NREM sleep. Int J Psychophysiol, 6, 307-313.
- Doerfling, P., Ogilvie, R. D., Murphy, T., & Lamarche, C. (1996). Applying the Hori sleep scoring system to the examination of the sleep onset process in insomniac and normal sleepers. Sleep Research Online, 25.
- Fogel, S. M., Smith, C. T., & Cote, K. A. (2007). Dissociable learning-dependent changes in REM and non-REM sleep in declarative and procedural memory systems. Behav Brain Res, 180, 48-61.
- Fosse, M. J., Fosse, R., Hobson, J. A., & Stickgold, R. J. (2003). Dreaming and episodic memory: a functional dissociation? J Cogn Neurosci, 15, 1-9.
- Foulkes, D., & Schmidt, M. (1983). Temporal sequence and unit composition in dream reports from different stages of sleep. Sleep, 6, 265–280.
- Foulkes, D., Spear, P. S., & Symonds, J. D. (1966). Individual differences in mental activity at sleep onset. Journal of Abnormal Psychology, 71, 280–286.

- Foulkes, D., & Vogel, G. (1965). Mental activity at sleep onset. Journal of Abnormal Psychology, 70, 231–243.
- Germain, A., & Nielsen, T. A. (1997). Distribution of spontaneous hypnagogic images across Hori's EEG stages of sleep onset. Sleep Research Online, 26.
- Greene, A. J., Gross, W. L., Elsinger, C. L., & Rao, S. M. (2006). An FMRI analysis of the human hippocampus: inference, context, and task awareness. J Cogn Neurosci, 18, 1156-1173.
- Hassabis, D., Kumaran, D., & Maguire, E. A. (2007). Using imagination to understand the neural basis of episodic memory. J Neurosci, 27, 14365-14374.
- Hassabis, D., Kumaran, D., Vann, S. D., & Maguire, E. A. (2007). Patients with hippocampal amnesia cannot imagine new experiences. Proc Natl Acad Sci U S A, 104, 1726-1731.
- Hassabis, D., & Maguire, E. A. (2007). Deconstructing episodic memory with construction. Trends Cogn Sci, 11, 299-306.
- Hassabis, D., & Maguire, E. A. (2009). The construction system of the brain. Philos Trans R Soc Lond B Biol Sci, 364, 1263-1271.
- Hayashi, M., Katoh, K., & Hori, T. (1999). Hypnagogic imagery and EEG activity. Percept Mot Skills, 88, 676-678.
- Heckers, S., Zalesak, M., Weiss, A. P., Ditman, T., & Titone, D. (2004). Hippocampal activation during transitive inference in humans. Hippocampus, 14, 153-162.
- Hori, T., Hayashi, M., & Morikawa, T. (1993). Topographical EEG changes and hypnagogic experience. In R. D. Ogilvie & J. R. Harsh (Eds.), Sleep Onset: Normal and Abnormal Processes (pp. 237-253).
- Ioannides, A. A., Kostopoulos, G. K., Liu, L., & Fenwick, P. B. (2009). MEG identifies dorsal medial brain activations during sleep. Neuroimage, 44, 455-468.
- Johnson, J. D. (2005). REM sleep and the development of context memory. Med Hypotheses, 64, 499-504.
- Kaufmann, C., Wehrle, R., Wetter, T. C., Holsboer, F., Auer, D. P., Pollmacher, T., et al. (2006). Brain activation and hypothalamic functional connectivity during human nonrapid eye movement sleep: an EEG/fMRI study. Brain, 129, 655-667.
- Lahl, O., Wispel, C., Willigens, B. & Pietrowsky, R. (2008) An ultra short episode of sleep is sufficient to promote declarative memory performance. J Sleep Res, 17, 3-10.
- Maquet, P. (2000). Functional neuroimaging of normal human sleep by positron emission tomography. J Sleep Res, 9, 207-231.
- Mavromatis, A. (1987). Hypnagogia: the Unique State of Consciousness Between Wakefulness and Sleep. London: Routledge and Kegan Paul.
- Miller, R. (1991). Cortico-hippocampal Interplay and the Representation of Contexts in the Brain. Berlin: Springer-Verlag.
- Mitchell, D. J., McNaughton, N., Flanagan, D., & Kirk, I. J. (2008). Frontal-midline theta from the perspective of hippocampal "theta". Prog Neurobiol, 86, 156-185.
- Morikawa, T., Hayashi, M., & Hori, T. (1997). Auto power and coherence analysis of delta-theta band EEG during the waking-sleeping transition period. Electroencephalogr Clin Neurophysiol, 103, 633-641.
- Nielsen, T. (2000). A review of mentation in REM and NREM sleep: "covert" REM sleep as a possible reconciliation of two opposing models. Behav Brain Sci, 23, 851-866; discussion 904-1121.
- Nielsen, T., & Levin, R. (2007). Nightmares: a new neurocognitive model. Sleep Med Rev, 11, 295-310.
- Nielsen, T., & Stenstrom, P. (2005). What are the memory sources of dreaming? Nature, 437, 1286-1289.

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- Nielsen, T., Stenstrom, P., Takeuchi, T., Saucier, S., Lara-Carrasco, J., Solomonova, E., et al. (2005). Partial REM-sleep deprivation increases the dream-like quality of mentation from REM sleep and sleep onset. Sleep, 28, 1083-1089.
- Nielsen, T. A. (2004). Chronobiological features of dream production. Sleep Med Rev, 8, 403-424.
- Nielsen, T. A., Kuiken, D., Alain, G., Stenstrom, P., & Powell, R. A. (2004). Immediate and delayed incorporations of events into dreams: further replication and implications for dream function. J Sleep Res, 13, 327-336.
- Nielsen, T. A., & Powell, R. A. (1989). The 'dream-lag' effect: a 6-day temporal delay in dream content incorporation. Psychiatr J Univ Ott, 14, 561-565.
- Nielsen, T. (2010). Ultradian, circadian, and sleep-dependent features of dreaming. In: Principles and Practice of Sleep Medicine, 5th, edited by M. Kryger, T. Roth, and W. C. Dement, New York:Elsevier, 2010, p. 576-584.
- Ogawa, K., Abe, T., Nittono, H., Yamazaki, K., & Hori, T. (2009). Temporal coupling of rapid eye movements and cerebral activities during REM sleep. Clin Neurophysiol, 120, 18-23.
- Paller, K. A., & Voss, J. L. (2004). Memory reactivation and consolidation during sleep. Learn Mem, 11, 664-670.
- Payne, J. D., & Nadel, L. (2004). Sleep, dreams, and memory consolidation: the role of the stress hormone cortisol. Learn Mem, 11, 671-678.
- Picchioni, D., Fukunaga, M., Carr, W. S., Braun, A. R., Balkin, T. J., Duyn, J. H., et al. (2008). fMRI differences between early and late stage-1 sleep. Neurosci Lett, 441, 81-85.
- Porte, H. S. (2004). Slow horizontal eye movement at human sleep onset. J Sleep Res, 13, 239-249.
- Powell, R. A., Cheung, J. S., Nielsen, T. A., & Cervenka, T. M. (1995). Temporal delays in incorporation of events into dreams. Percept Mot Skills, 81, 95-104.
- Preston, A. R., Shrager, Y., Dudukovic, N. M., & Gabrieli, J. D. (2004). Hippocampal contribution to the novel use of relational information in declarative memory. Hippocampus, 14, 148-152.
- Shohamy, D., & Wagner, A. D. (2008). Integrating memories in the human brain: hippocampal-midbrain encoding of overlapping events. Neuron, 60, 378-389.
- Sil'kis, I. G. (2010). Paradoxical sleep as a tool for understanding the hippocampal mechanisms of contextual memory. Neurosci Behav Physiol, 40, 5-19.
- Solomonova, E., Nielsen, T., Stenstrom, P., Lara-Carrasco, J., Brochu, K., & Ross, M. (2008). Enhanced dream reports and better identification of dream memory sources following training in an introspective technique. Paper presented at the International Association for the Study of Dreaming.
- Squire, L. R., Stark, C. E., & Clark, R. E. (2004). The medial temporal lobe. Annu Rev Neurosci, 27, 279-306.
- Stickgold, R. (2002). EMDR: a putative neurobiological mechanism of action. J Clin Psychol, 58, 61-75.
- Stickgold, R., Hobson, J. A., Fosse, R., & Fosse, M. (2001). Sleep, learning, and dreams: off-line memory reprocessing. Science, 294, 1052-1057.
- Stickgold, R., Malia, A., Maguire, D., Roddenberry, D., & O'Connor, M. (2000). Replaying the game: hypnagogic images in normals and amnesics. Science, 290, 350-353.
- Stickgold, R., Wamsley, E. (2010). Why we dream. In: Principles and Practice of Sleep Medicine, 5th, edited by M. Kryger, T. Roth, and W. C. Dement, New York:Elsevier, 2010, p. 628-637.
- Rothenburg, A. (1995). Creative Cognitive Processes in Kekulé's Discovery of the Structure of the Benzene Molecule.

The American Journal of Psychology. Vol. 108, pp. 419-438.

- Rowley, J., T, Stickgold, R., Hobson, J., A. 1998. Eyelid movement and mental activity at sleep onset. Conscious Cogn, 7, 67-84.
- Tulving, E. (2002). Episodic memory: from mind to brain. Annu Rev Psychol, 53, 1-25.
- Verdone, P. (1965). Temporal reference of manifest dream content. Percept Mot Skills, 20(Suppl):1253-1268.
- Vogel, G. W., Barrowclough, B., & Giesler, D. D. (1972). Limited discriminability of REM and sleep onset reports and its psychiatric implications. Archives of General Psychiatry, 26, 449–455.
- Walker, M. P., Liston, C., Hobson, J. A., & Stickgold, R. (2002). Cognitive flexibility across the sleep-wake cycle: REMsleep enhancement of anagram problem solving. Brain Res Cogn Brain Res, 14, 317-324.
- Walker, M. P. & Stickgold, R. (2004). Sleep-dependent learning and memory consolidation. Neuron, 44, 121-133.
- Wamsley, E. J. & Stickgold R. (2010). Dreaming and offline memory processing, Current Biology, 20, 1010-1013
- Wamsley, E., Tucker, M., Payne, J., Benavides, L., & Stickgold, R. (2010). Dreaming of a learning task is associated with enhanced sleep-dependent memory consolidation. Current Biology, 20, 850-855.
- Wamsley, E. J., & Antrobus, J. S. (2009). The expression of trace conditioning during non-REM sleep and its relation to subjective experience. Neurobiol Learn Mem, 92, 283-291.
- Wamsley, E. J., Perry, K., Djonlagic, I., Reaven, L. B., & Stickgold, R. (2010). Cognitive replay of visuomotor learning at sleep onset: temporal dynamics and relationship to task performance. Sleep, 33, 59-68.
- Weiler, J. A., Suchan, B., & Daum, I. (2010). Foreseeing the future: Occurrence probability of imagined future events modulates hippocampal activation. Hippocampus, 20, 685-690.