

A neuro-cognitive model of sleep mentation and memory consolidation

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Summary. Previous research has found evidence of relationships among sleep states and memory consolidation. However, no dominant models of sleep mentation (dreaming) account for the relationship between sleep and memory, despite the fact that the underlying neural processes of offline memory consolidation and sleep mentation happen simultaneously (and are therefore produced by the same brain state). In addition, experimental brain research contradicts what dominant neurological models of sleep mentation predict. Here a model of dream generation that agrees with empirical findings on dreams, and which is based on the neural process of memory consolidation during sleep, is proposed. The implications of the model are such that it suggests sleep state mentation may actually be a by-product (or readout) of the consolidation of memories produced by non-random cortical/sub-cortical reactivation during REM and Non-REM sleep (processes which are known, and are necessary for normal human memory function).

Keywords: REM dreams; NREM dreams; dream recall frequency; neurological substrates

1. Introduction

Previous research has found evidence of relationships between memory consolidation and sleep, as well as dreams (Smith, 2008; DeKoninck, Christ, Hebert, & Rinfret, 1990). However, dominant neurological models of dream generation are inconsistent with experimental findings that have arisen in recent years. In addition, no dominant models of dream generation account for the relationship between dreams and memory function (Wamsley, Tucker, Payne, Benavides, & Stickgold, 2010), nor do they account for the fact that dream content is often found to hold dreamer-specific meaning (DeCicco, 2007). Despite significant research contributions in the area, the way in which dreams are generated (as well as their purpose) has remained almost entirely elusive. Herein a model of dream generation is proposed that concurs with empirical observations of dream characteristics, and which suggests that dreams may actually be a by-product (or readout) of the processes of memory consolidation occurring during sleep – processes that are necessary for normal memory function within the human brain (Peigneux & Smith, 2011; Smith, 2008).

Major unanswered questions concerning sleep state mentation (dreaming) involve the concepts of the purpose of dreams and their production by the brain – what are the physiological functions served by dreams (if there is a function), how are they generated by the brain, and do they contain information which is meaningful for the dreamer? A number of recent studies have found evidence that supports a variety of perspectives on dream meaningfulness and the

reflection of individuals' waking day lives in their dreams (Dale, DeCicco, & Miller, 2013; DeCicco, 2007). However, there is a lack of definitive support for any particular perspective in terms of explaining the origin of dreams; even the dominant neurological models of sleep mentation, while revolutionary in their time, are unable to explain more recent experimental observations (Hobson, 1988; Solms, 1997).

2. Neurological Theories of Dream Generation

Research suggests that dreams may contain meaningful information which is dreamer-specific (i.e. dreams contain information meaningful to the dreamer rather than random information that could produce meaningful insight when analyzed by another person; DeCicco, 2007). However, neurological theories of dreams have proposed models that do not allow specific meaning for imagery in dreams – instead, it is often suggested that the brain makes sense out of images generated by random cortical activations (Hobson, 1988). In terms of explaining dream generation in neurological terms, two major perspectives emerge as dominant theories in the field.

The first (and more prevalent) example is J. Allan Hobson's Activation-Synthesis hypothesis (Hobson, 1988), which explains dream imagery as the brain's interpretation of random activations of the cortex caused by brainstem activity. In *The Dreaming Brain*, Hobson (1988) outlines this process and explains that REM-Sleep (Rapid Eye Movement Sleep; a sleep state characterized by 7-10 Hz brainwave activity, as well as repetitive and rapid conjugate movement of the eyes) activation is capable of activating almost every neuron in the brain in a stereotyped fashion. The activation-synthesis theory suggests that this provides stimulation of neuronal pathways that would otherwise not be activated on a day-to-day basis. Without this activation, Hobson suggests that we would lose those memories and functions (because the underlying neural pathways would atrophy). Structures in the brainstem/pons stimulate cells

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in the visual cortex (as well as other cortical areas). These stimulations are random, and the dream is considered to be the result of the brain interpreting and “making sense” of randomly produced visual events. In this view, sleep mentation images are not implicitly meaningful – it is the rational component of the brain that applies meaning to the random imagery that is generated (Hobson, 1988).

In addition to activation-synthesis, another similar model (often considered as the successor to activation-synthesis) was proposed by Hobson (2009). This model suggests that REM sleep may constitute a proto-conscious state (a virtual-reality world produced within the brain during sleep that is of use to the development and maintenance of waking consciousness). This model, termed the AIM model, relies on three processes: A (Activation; the level of energy of the brain and its constituent circuits), I (Input-Output Gating; the facilitation or inhibition of sensory information from the outside world), and M (Modulation of the chemical microclimate of the brain by neurons in the brainstem). The AIM model describes REM sleep as being similar to wakefulness – however, during wakefulness, input-output gating is “open,” allowing the perception of external stimuli. During REM sleep, however, high levels of A but low levels of I and M result in brain activity (and thus mentation) in the absence of access to sensory information from the external world. Dreaming is therefore proposed to be the subjective experience of a brain state similar to waking consciousness.

While the activation-synthesis and AIM models have powerful implications for explaining dreams, findings suggest the models may not accurately represent empirical observations of sleep mentation characteristics. For example, truly random cortical activations (as defined in the activation-synthesis model) do not allow for the possibility of recurrent nightmares (a phenomenon frequently reported, often following experiences of trauma). Neither activation-synthesis nor the AIM model account for the existence of NREM dreams; in addition, both activation-synthesis and the AIM model rely on the brainstem as a major component necessary for dream generation. The second dominant neurological viewpoint in terms of dream generation is incompatible with Activation-Synthesis and the AIM model – however, it has been supported by experimental findings.

This second perspective, introduced by Solms (1997), utilized the brain scans of lesioned patients to examine the brain areas which are critical for dream generation. The results of Solms’ (1997) investigations have shown that when individuals had damage to the brainstem, 81% of participants still reported a “preservation of the subjective experience of dreaming.” These findings are in contradiction to Hobson’s (1988; 2009) perspective, which would predict that the mechanism responsible for generating sleep state mentation must involve the functioning brainstem. However, Solms (1997) has not provided an extensive alternative theory of dream generation other than to suggest that intact temporo-parietal-occipital and medial prefrontal areas are important.

With regards to neural activation during sleep, recent research has demonstrated that one major pillar of the activation-synthesis theory (random cortical activations) has further inconsistencies with experimental findings that are not addressed by the more recent AIM model. One imaging study conducted using positron emission tomography (PET) to look at cerebral blood flow revealed that following the learning of a serial reaction time task, brain activity dur-

ing REM sleep was significantly higher for those who had learned the task than those who had not – however, activation during REM sleep was of the *same* brain areas that had increased activation during the learning of the task (Maquet et al., 2000). This suggests that cortical activation during REM sleep is in fact not random, but rather is influenced by experience (i.e. memories acquired during the day are strengthened in the same areas of the brain at night during REM sleep, so that the specific brain areas activated during REM are influenced by pre-sleep memory acquisition). This pattern of neural reactivation during sleep has also been found in Slow Wave Sleep (SWS – a Non-REM sleep state defined by 1-3 Hz/Delta brainwave activity); also using cerebral blood flow measurements, similar patterns of reactivation have been shown in the hippocampus (the amount of hippocampal reactivation expressed during SWS was found to be associated with improvement on the learned task the next day; Peigneux et al., 2004). Furthermore, this pattern has been demonstrated repeatedly using multiple research techniques in both humans and animals (Euston, Tatsuno, & McNaughton, 2007; Hoffman & McNaughton, 2003; Maquet et al., 2000; Peigneux et al., 2004; Wilson, 1994). These findings collectively suggest that brain activity during REM and Non-REM (NREM) sleep is influenced by pre-sleep memory acquisition. In addition, dreams also appear to reflect memory processes (Maquet et al., 2000; Peigneux et al., 2004; Wamsley et al., 2010), and may therefore be linked with this process of reactivation.

With regards to previous theories of dreaming, it must be noted that no current model of dreams accounts for the apparent relationship between dreams and memory. While it may be the case that a proto-conscious state arises during REM sleep, the actual purpose of this state has not been addressed sufficiently. In support of the idea that REM sleep may provide the construction of a proto-conscious state, one historical research study conducted using the lesion method in cats demonstrated that when REM sleep paralysis is inhibited, animals appear to act out their dreams (Jouvet & Delorme, 1965). This suggests that the existence of such an internal world during REM sleep is very likely – however, the purpose of such a system and the way in which these brain processes relate to the memory processes of the brain that exist during sleep has not been explained.

3. Sleep & Memory

Turning to a non-neurological theory of dreams (that is firmly based on experimental observation), the continuity hypothesis suggests that information from waking day life is reflected in dream imagery (Schredl & Hoffman, 2003). This well-documented dream phenomenon indicates that dream imagery is not random, but instead is a reflection of waking day experiences had by the dreamer. As an extreme example of this, one recent study suggests that among individuals commonly experiencing nightmares, those who had experienced trauma generally developed more depressive symptoms and experienced more traumatic events in their dreams (David, Pruiksma, Rhudy, & Byrd, 2011). Previous research has indicated that sleep may play a significant role in the consolidation of newly acquired memories. The purpose of dreaming in relation to empirical findings associating memory consolidation and the processes of the sleep-state brain, however, has remained largely unexplored – despite the fact that these two processes (memory consolidation and dreaming) occur simultaneously.

REM/NREM Dreams

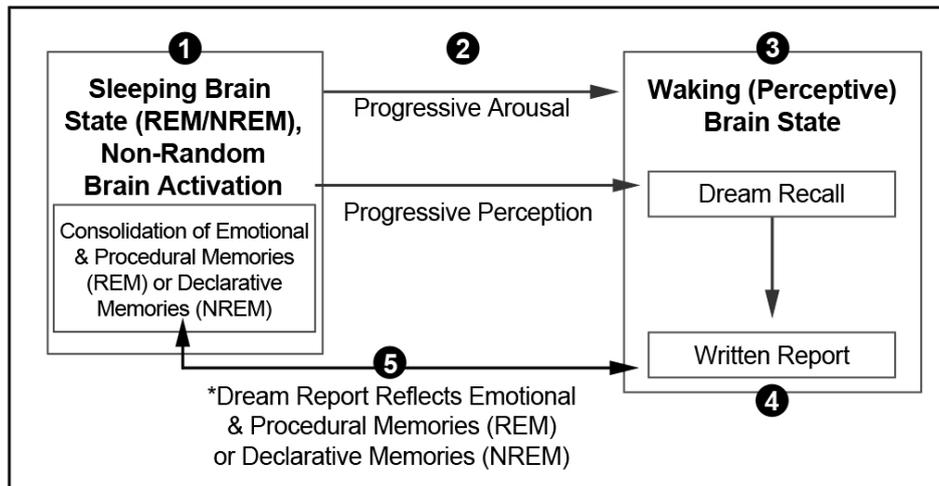


Figure 1. Model of REM/NREM Dream Production based on memory consolidation during sleep.

Recent research suggests that REM preferentially supports the consolidation of emotionally significant - as well as procedural - memories (Diekelmann, Wilhelm, & Born, 2009; Nishida, Pearsall, Buckner, & Parker, 2009; Payne, Chambers, & Kensinger, 2012; Vandekerckhove & Cluydts, 2010;). Reviews of experimental findings also suggest the idea that SWS is more specifically implicated in the consolidation of declarative memories (Diekelmann, Wilhelm, & Born, 2009; Smith, 2008).

Similarly to the memory functions of the brain, mentation also differs between REM and NREM brain states. REM dreams have been characterized by one study as having a “dream-like” quality - bizarre imagery, movement, and emotions to name some (Monroe, Rechtschaffen, Foulkes, & Jensen, 1965). The same study also found that NREM dreams can be characterized as more “thought-like.” More recent research has also noted differences between REM and NREM mentation, especially in terms of recall frequency, with a higher frequency of dream recall reported following REM sleep (Foulkes, 1966; Nielsen, 2000). Mentation following REM sleep seems reflective of emotional experience and procedural (implicit) learning, while NREM mentation is more reflective of factual (declarative) memories (Cavallero, 1993; Cicogna, Cavallero, & Bosinelli, 1986; Monroe et al., 1965; Nielsen, 2000).

While research has strongly suggested a role for sleep in memory consolidation (Maquet, 2001; Rasch, Büchel, Gais, & Born, 2007; Stickgold, 2005; Wilson & McNoughton, 1994), fewer experimental investigations have noted associations between dreams and memory. One investigation showed that French immersion students who experienced incorporation of the French language into their dreams earlier and who had more verbal communication in their dreams overall showed more significant progress in their learning of the French language (DeKoninck et al., 1990). In addition, one more recent investigation found that when participants were presented a memory task, improved performance on the task at re-test was associated with task-related dream imagery (Wamsley et al., 2010). These findings further suggest that dreams reflect memory processes.

All of the aforementioned investigation results suggest that dreams are not just a replay of experiences, but are instead a reflection of those waking-day experiences that the brain is actively consolidating during sleep into a more stable form. A comprehensive theory of dreams must account for the possibility of recurring dreams, the question of why dreams seem to contain information which is meaningful for the dreamer, continuity, and the relationships that have been discovered between sleeping brain states and the neurological processes of memory consolidation. In addition, it should also agree with imaging studies demonstrating how neural activity changes during sleep (in comparison to the normal/waking day), and must therefore account for the apparent non-random brain activation during REM and NREM sleep (Maquet et al., 2000; Peigneux et al., 2004).

4. Neuro-Cognitive Model of Dream Generation

According to the culmination of evidence from previous research, it is proposed that the dream-experience is simply a reflection of the neural processes associated with memory consolidation, and exists as a natural by-product (or read-out) of those processes during the brain’s transition from an unconscious/sleeping state to a conscious waking state.

In keeping with this way of conceptualizing the generation of dreams, meaningfulness in dreams should naturally emerge as a common characteristic of dream imagery since most dreams recalled are from REM sleep - the sleeping brain state associated with emotional memory consolidation (Foulkes, 1966; Nielsen, 2000; Smith, 2008). The functional aspect of the proto-conscious state described by the AIM model may also be explained by memory consolidation processes, since REM sleep is also implicated in the consolidation of procedural memories (Peigneux & Smith, 2011; Smith, 2008). One additional aspect of dreams not considered by previous models is the fact that dreams appear to only be recalled from the transition between sleep and wakefulness (i.e. dreams do not seem to be recalled from throughout the entire night in the absence of an arousal).

The proposed model suggests that dreams may be defined as the experience of perceiving the processes of memory consolidation during the brain's transition from sleep to wakefulness. The model consists of five components (see Figure 1): 1) The brain during sleep is consolidating a stage-dependent memory type, and non-random cortical/sub-cortical reactivation within the sleeping brain is influenced by pre-sleep memory acquisition; 2) during arousal, perception begins as the brain transitions from a sleeping state to a waking/perceptive state – it is during arousal (between the sleeping and waking states, while cortical/sub-cortical reactivation and memory consolidation are shutting down in some parts of the brain and the waking/perceptive brain state is simultaneously beginning in others) that both memory consolidation and waking perception briefly coexist within the brain; 3) stage-dependent memory consolidation is experienced as dream recall; 4) dream recall is submitted as a written report of subjective experience; 5) the written dream report reflects the consolidation of a stage-dependent memory type.

Traditionally, the processes of sleep mentation and memory consolidation have been studied independently, and therefore considered as two separate and independent processes. However the fact that these two processes occur simultaneously suggests that the underlying neurological bases for these two phenomena must also be occurring at the same time, and may therefore be linked together (and noted in research findings as two different observable activities of the same single underlying brain process).

This way of conceptualizing neurological dream generation allows for the possibility of recurring dreams, and explains dreams as the by-product of the already-known processes of neural reactivation during different sleep states that facilitate the consolidation of newly acquired memories into a more stable, long term form. In addition, this approach further accounts for both the qualitative difference between REM and NREM mentation noted by previous research (Monroe, Rechtschaffen, Foulkes, & Jensen, 1965; Cavallero, 1993; Cicogna, Cavallero, & Bosinelli, 1986; Monroe et al., 1965; Nielsen, 2000) and the continuity hypothesis of dreams (since stage-dependent cortical/sub-cortical reactivation facilitates the consolidation of newly acquired material from an individual's prior waking experience). Research has also demonstrated that the frequency of incorporation of memory sources into dreams is influenced by the emotional significance of the experience (Schredl, 2006); this bias toward the incorporation of emotionally significant memories can also be explained by the proposed model, since most dreams are recalled from REM - the sleep stage associated with emotional memory consolidation (Peigneux & Smith, 2011; Smith, 2008).

While the AIM model and activation-synthesis (Hobson, 1988; Hobson, 2009) do not account for the occurrence of NREM dreams, the processes of neural reactivation during both REM and NREM have already been confirmed in different (stage-dependent) areas of the brain using functional brain imaging and other techniques in both humans and animals (Maquet et al., 2000; Peigneux et al., 2004; Wilson, 1994; Hoffman & McNaughton, 2003; Euston, Tatsuno, & McNaughton, 2007).

The existence of a proto-conscious state within REM sleep may also possibly be accounted for by the fact that procedural memory consolidation is associated with REM rather than NREM sleep (Peigneux & Smith, 2011; Smith,

2008) – however, the stage dependent processes of reactivation allow for both REM and NREM dreams while also explaining the qualitative difference between the two that have been noted by previous research findings (Monroe, Rechtschaffen, Foulkes, & Jensen, 1965; Cavallero, 1993; Cicogna, Cavallero, & Bosinelli, 1986; Monroe et al., 1965).

While this model offers an approach to explaining many of the observable characteristics of both sleep mentation and brain activity during REM and NREM sleep, challenges arise in terms of designing practical experiments that can link brain reactivation during sleep to sleep mentation. However, one recent study demonstrated that, by using functional brain imaging, it is possible to decode visual imagery during sleep using computer learning models (Horikawa, Tamaki, Miyawaki, & Kamitani, 2013). This experimental approach has already demonstrated that brain activation during sleep relates to the production of visual imagery in a very specific way. However, in order to conclusively determine whether this brain activation both facilitates memory consolidation and produces visual imagery simultaneously, a more extensive experimental protocol is necessary.

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