

Towards an Evolutionary Theory of Sleep and Dreams

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Abstract

Despite the importance of sleep and dreams for the understanding of human consciousness, science is yet to achieve a consensus about their functions and intricate phenomenology. This paper outlines an evolutionary theory that is compatible with several basic observations regarding sleep and dreams. The theory proposes that slow-wave (SW-) sleep evolved from mere rest in early reptiles as a prolonged and quiescent offline state able to promote calcium-dependent memory consolidation. This cognitive role is performed by increased reverberation of waking patterns of neuronal activity during SW-sleep. Rapid-eye-movement (REM-) sleep, a second offline state, characterized by high cerebral activity and maximum sensory disconnection, evolved in early birds and mammals as a post-SW-sleep mini-state, lasting just a few seconds. Despite its short duration, REM-sleep is capable of boosting memory consolidation by activating genes linked to synaptic plasticity. At some point, mammals evolved extended single REM episodes, prolonging the non-stationary neuronal reverberation that characterizes REM-sleep to promote memory restructuring rather than memory stabilization. Dreams as vivid narratives that unfold in time arose as a by-product of neuronal reverberation during extended REM-sleep. Due to such non-stationary reverberation, dreams are hyper-associative strings of fragmented memories that simulate past events and future expectations, enacting possible solutions for cognitive challenges facing the dreamer. Though probabilistic, dream simulations can at times yield accurate predictions of future events. Under increased brain metabolism, it is possible to experience an enhanced REM-sleep state in which dream events are under partial or total

voluntary control. The cognitive potential of such 'lucid' dreams remains uncharted territory for science.

Introduction

“Macrobius and Artemidorus [sustained that] dreams were divided in two classes. The first was believed to be influenced only by the present (or the past), and was unimportant in respect to the future; it included the [...] insomnia, which directly reproduces a given idea or its opposite (e.g., hunger or its satiation), and the phantasmata, which elaborates the given idea fantastically (as e.g. the nightmare) [...]. The second class of dreams, on the other hand, was determinative of the future. To this belonged direct prophecies received in the dream (oraculum), (...) the foretelling of a future event (visio), (...) and the symbolic dream, which requires interpretation (somnia).” Gruppe apud Freud (1900).

What are dreams, and why do we dream? More than a century after the publication of “The Interpretation of Dreams”⁽¹⁾, a scientific consensus about these two essential questions concerning human consciousness is yet to be achieved. While depth psychology focuses on dream meaning and wish fulfillment⁽¹⁻⁷⁾, experimental psychology scrutinizes sleep-dependent learning in search of less subjective dream purposes⁽⁸⁻²²⁾. Neurophysiology, on the other hand, tends to the investigation of the systemic, cellular and molecular mechanisms related to sleep⁽²³⁻³⁴⁾ and its cognitive functions⁽³⁵⁻⁵³⁾. Due to their different methods, each of these fields of investigation has, to a large extent, established a dream phenomenology of their own.

The gap separating the neural processes underlying sleep from a comprehensive account of subjective dreaming has produced dream models that are outright incompatible with fundamental observations available to any introspective dreamer or psychoanalyst. One example of such dissociation is the notion that the bizarreness and hyper-associativeness of dreams can be trivially explained by random neuronal activation of the neocortex during the rapid-eye-movement (REM) phase of sleep. According to this anti-Freudian theory^(54, 55), dreams arise from stochastic deep brain inputs to the neocortex, evoking a succession of neuronal firing patterns that correspond to randomly-assembled memory fragments. The model proposes that such process has the function of erasing irrelevant memory traces, cleaning up storage space to allow the formation of new memories. A corollary of this theory is that dream content is intrinsically

meaningless. This conclusion undermines the very significance of dream interpretation as a relevant window into human consciousness⁽¹⁾.

The 'random cortical activation' theory did not survive confrontation with the fact that dreams can be remarkably repetitive, especially when major trauma has occurred. Indeed, recursive nightmares are an important symptom of post-traumatic stress disorder, which is characterized by disturbed, hyper-aroused REM-sleep^(56, 57). For instance, shark attack survivors usually go through a period of shark-related nightmares that may continue for several months following the injuries. Even more compelling is the situation lived by war veterans, who dream about battle events for decades after the end of combat⁽⁵⁸⁻⁶⁰⁾. Given the colossal number of neurons and synapses in the human neocortex, it is impossible to explain the activation of nearly identical neuronal firing patterns over several consecutive dreams by way of random neocortical activation.

If it is true that some neurobiological theories of dreaming conflict hopelessly with some basic dream phenomena, the psychoanalytical tradition has been faulted and even ridiculed for ignoring that most adult dreams lack wish-fulfillment, for failing to deal with the fact that memory consolidation is facilitated by sleep, and for being absolutely unconcerned with the evolution of sleep and dreams.

It is time for a synthesis. A satisfactory theory of dreaming must first account for all the available dream phenomenology, and not selected parts of it. Second, it must distinguish the several functions of the different sleep and dream states. Third, it must include an evolutionary description of how these functions evolved.

2. The evolution of SW-sleep

To begin delineating a satisfactory theory of dreams and sleep, let us first turn to the issue of the phylogenetic origin of the two sleep states. When, why and how did sleep evolve? Extant fish and amphibians fall short of having proper sleep, rather displaying intermittent and opportunistic rest periods that occur whenever permitted by the lack of environmental threats^(61, 62). The primary functions of rest are the conservation of energy and the replenishment of metabolites depleted during waking. With very few exceptions, all animals display intermittent rest in alternation with periods of activity. While rest is

unpredictable and mostly determined by external variables, sleep is an endogenous state of deep-quiescence tightly regulated by circadian mechanisms tuned to variations of ambient light. All extant reptile, avian and mammalian species investigated to date^(61, 63, 64) display a periodic state of inactivity and generalized sensory-motor shutdown called slow-wave (SW-) sleep. Judging by the pattern of SW-sleep occurrence in extant higher vertebrates, it is likely that SW-sleep began to evolve in the Carboniferous period (360 Myr B.P.), which witnessed the ecological pilgrimage of vertebrates from water to dry lands⁽⁶⁵⁾. It is interesting to consider the ecological pressures that might have driven the evolution of SW-sleep. Fish inhabit an aquatic medium that allows them to rely heavily on electroreception, magnetoception and olfaction to survive^(66, 67). The conquest of the terrestrial environment required a drastic change of the vertebrate sensory environment, as land dwellers in general depend heavily on visual and auditory information to survive. It is fair to assume that the absence of light during night-time, by forcing proto-reptiles to hide from predators in burrows, caves or nests⁽⁶⁶⁾, was a strong constraint on the evolution of early reptile SW-sleep.

How relevant was this step? While SW-sleep more than fulfills primary rest functions related to energy conservation and metabolite turnover, it also enhances an additional biological function of immense behavioral impact: learning. During SW-sleep, waking patterns of neuronal activity reverberate in several forebrain areas including the hippocampus and the neocortex^(37, 38, 40, 41, 43-47, 50-53), likely reflecting the absence of sensory interference^(53, 68). Such reverberation has been proposed to promote the amplification and consolidation of memories by way of calcium-dependent mechanisms^(33, 69-72). By focusing endogenous brain activity on recently utilized neuronal networks, SW-sleep increases the contrast between what will or will not be remembered so as to effectively amplify selected memories. While the body rests and saves energy, SW-sleep promotes learning by repetition.

It is conceivable that the cognitive function of SW-sleep evolved as a mere epiphenomenon of the adaptation to a marked circadian regulation of rest behavior. Still, it is tempting to speculate that the proto-reptilian evolution of an offline brain state able to enhance memory consolidation played a significant role in the rapid reptilian radiation

during the Permian (286-248 Myr B.P.), leading to the long Mesozoic (248-65 Myr B.P.) age of reptile supremacy.

3. The evolution of REM -sleep

Although ancestral reptiles first evolved proper sleep, modern reptiles sleep less than most mammals. Even more remarkable, most reptiles lack rapid-eye-movement (REM)-sleep⁽⁶³⁾, an ubiquitous state among birds and mammals that is characterized by eye-closure, increased cerebral activation and total absence of muscle movements, except for occasional localized muscle twitches⁽²³⁻³²⁾. Why did reptiles fail to further develop REM-sleep? A possible key may be found in the temporal order of the two sleep states, and their differential susceptibility to fear. Under normal circumstances, in men and mice alike, REM-sleep can only follow SW-sleep but the opposite never occurs^(23, 30-32). Furthermore, REM-sleep can only occur after a fair amount of SW-sleep has taken place^(23, 30-32). Importantly, rats exposed to fear conditioning have a strong suppression of subsequent REM-sleep, but not SW-sleep⁽⁷³⁾. The appearance of ever more implacable predator dinosaurs over the Mesozoic certainly turned life on the dry land increasingly threatening over time. Could predation have prevented the ancestors of modern reptiles to sleep well? Maybe the myth of the dragon that sleeps with one open eye has its ethologic foundation in the fact that some reptiles display uni-hemispheric sleep⁽⁷⁴⁾, a strange split-brain state also present in birds⁽⁷⁵⁾, and shown to be positively correlated with predation risk⁽⁷⁶⁾.

Or perhaps, quite contrary, the cognitive advantage provided by reptilian SW-sleep far exceeded the need for more animal intelligence in the rich and stable Pangaeian environment, a vast Eden populated by relatively harmless protein-rich invertebrates and abundant edible vegetation. The fact of the matter is that reptiles did not have to outsmart anybody else for over 200 million years. Whether the mightiest and most intelligent of the large Jurassic predators ever evolved REM-sleep is an unsolvable mystery. We do know, however, that the mass extinction at the end of the Cretaceous (65 Myr B.P.) allowed for the ecological spawn of birds and mammals, warm-blooded vertebrates characterized by having REM-sleep⁽⁷⁷⁾ and a superior capacity for learning⁽⁷⁸⁻⁸⁵⁾. A link

between these features is suggested by the fact that REM-sleep upregulates the expression of *zif-268*⁽⁴²⁾, a learning-related gene capable of triggering the experience-dependent strengthening of synaptic connections⁽⁸⁶⁻⁹¹⁾. *Zif-268* gene expression is upregulated during REM-sleep and downregulated during SW-sleep, so that a single night of sleep witnesses several stop-and-go gene upregulation cycles⁽⁴²⁾. *Zif-268* promotes synaptic changes on the post-synaptic terminal in response to pre-synaptic excitation^(92, 93). As a consequence the SW-REM-sleep cycle produces a propagation of *zif-268* gene expression across several brain areas⁽⁴⁹⁾.

By occurring during REM-sleep in the absence of sensory interference, *zif-268* upregulation likely increases the durability of memories already amplified by SW-sleep. Most importantly, the propagation of synaptic changes across SW-REM-sleep cycles may increase the reach and strength of memories over time. Although a single cycle involving both phases suffices to consolidate certain short-term memories⁽²¹⁾, it is the repetition of several cycles during a night that may truly promote deep memory transformations, gradually propagating them through several brain areas⁽⁶⁸⁾, and thus anchoring them ever more solidly in the neuronal matrix so as to cause a cumulative increment of learning at each night of sleep⁽⁹⁴⁾. Memory propagation may also be at the roots of the progressive disengagement of the hippocampus from mnemonic processes after initial acquisition⁽⁹⁵⁻⁹⁷⁾, promoting a net exodus of memories from the hippocampus to the neocortex due to the much larger coding capacity of the latter. It may be hard to determine today how important the acquisition of REM-sleep was for the ecological success of birds and mammals, but certainly its addition to SW-sleep made for much faster, stronger and durable learning.

4. The evolution of extended REM -sleep

When it comes to REM-sleep differences between mammals and birds, time is of essence. While most mammals display a few long REM-sleep episodes per 24-hour cycle, with episode duration of up to hundreds of minutes, birds exhibit hundreds of ultrashort REM-sleep episodes in a single night, with duration smaller than 20 seconds⁽⁹⁸⁻¹⁰¹⁾. Why did birds fail to develop long REM-sleep? A clue may be found in the fact that, during

REM-sleep, despite the lack of sensory inputs, great portions of the forebrain become as active as during waking. Such high levels of activity fail to become overt behavior (and therefore interrupt sleep) because inhibitory glycinergic neurons in the pons effectively block most of the muscle activity during REM-sleep⁽¹⁰²⁾. Thus it is conceivable that the need to keep residual muscle tonus while perching was the ecological constraint for the small duration of avian REM-sleep episodes⁽⁹⁸⁻¹⁰¹⁾. The current evidence indicates that plasticity-related gene expression, possibly the primary cognitive function of REM-sleep, is uncorrelated with time spent in REM-sleep^(42, 49, 103), and reaches maximum levels even when REM-sleep episodes are cut very short⁽¹⁰⁴⁾. What sort of selection pressures drove the elongation of individual REM-sleep episodes in mammals? Do extended REM-sleep episodes contribute to learning in any special way?

The molecular and cellular sleep-dependent mechanisms described so far are involved in the stabilization and strengthening of already-acquired memories. There is however another form of learning, more spectacular and mysterious. The insight, also known as abduction, corresponds to the creation of new memories and ideas not trivially derived from pre-existing memories. Although insight may occur during waking⁽¹⁰⁵⁾, it is greatly facilitated by sleep⁽¹⁰⁶⁾. Several notorious examples of sleep-dependent insight can be drawn from both science and art⁽¹⁰⁷⁾. Kekulé dreamt with a snake eating its own tail and thus discovered the circular structure of benzene. Mendeleev, the discoverer of the periodic table, visualized his breakthrough concept in a dream. Intense dreams very much inspired artists like Dürer, Blake, Dalí, Frida Kahlo and many others.

While the biological mechanisms underlying sleep-dependent insight still remain unknown, the available subjective reports of the phenomenon point to an important role of dreams⁽¹⁰⁷⁾. In support of this hypothesis, mounting evidence indicates that extended REM-sleep harbors very non-stationary neuronal reverberation, in contrast with highly-stationary reverberation during SW-sleep^(37, 53, 108, 109). In principle, such ‘noisy’ reverberation during REM-sleep may promote memory restructuring, assembling “new memories” from fragments of pre-existing ones. In other words, insight may derive from a shuffling or recombination of relevant memory traces during REM-sleep. Evidence in favor of this hypothesis comes from psychological experiments in which subjects were woken up from either SW- or REM-sleep and immediately asked to resolve anagrams.

The results indicate that REM-sleep promotes more flexible cognitive processing than SW-sleep, suggesting that memory restructuring is indeed facilitated by REM-sleep⁽¹¹⁰⁾.

5. The evolution of dreams as simulations of past and future

Human dreams are subjective narratives composed of familiar and unfamiliar beings, things and places, interacting around a self-representation of the dreamer that mostly observes an unfolding plot. Dreams vary in intensity, ranging from confused and faint impressions to complex time-evolving narratives made of vivid imagery. Although dreams tend to be dominated by visual imagery, they can also involve combinations of auditory, olfactory, tactile, gustatory, motor, vestibular and linguistic modalities. Dreams can sometimes be extremely pleasant or just the opposite, but are usually characterized by a mix of emotions. Dreams are also hyper-associative, linking characters, places and actions in bizarre ways. While normal dreams usually lack in logical coherence, remarkably meaningful dreams do occur to most people at least a few times in life. As noted by Freud, dreams often involve elements of the experience of the preceding day(s), which he called 'day residue'⁽¹⁾. Dreams can also anticipate events of the coming day(s), particularly when subjects undergo extreme anxiety and expectation. A good example is provided by the dreams of students before difficult exams, which often contain detailed anticipatory simulations of the expected challenges, either in content and/or context. Freud also observed that dream narratives sometimes fulfill wishes of the awoken subject, simulating the realization of specific desires. Although the prevalence of overt wish fulfillment in the dreams of normal adults is low, it is relatively common in young children⁽¹¹¹⁾.

Dreams may have first evolved as a collateral effect of extended REM-sleep, and are likely present in all the mammals that possess such trait. Any pet owner knows that cats and dogs seem to act out dreams during sleep. More controlled evidence of dreaming in non-human mammals was obtained by lesions of the brainstem nuclei that promote muscle atonia during REM-sleep⁽¹¹²⁾. Cats with such lesions sleep quietly through SW-sleep, but upon entering REM-sleep become suddenly agitated by vigorous species-specific behaviors, such as meowing and pouncing. What do cats dream about? What is

the purpose of dreams? What are the neural bases of dreaming, and which selection pressures shaped dream evolution?

Dreams are caused by intense and non-stationary memory reverberation during extended REM-sleep, with the neocortex lightened up at high neuronal firing rates and oscillatory frequencies predominantly above 30 Hz⁽¹¹³⁾. The qualitative feeling of “quasi-reality” in dreams derive from the fact that memory reverberation during REM-sleep occurs at an intensity and oscillatory spectrum comparable to those of waking⁽³³⁾. Such high levels of excitation cause the reverberating memories that comprise dreams to appear bright and vivid to the self-representation, and variations in neural activity levels explain the dynamic range of vividness that characterizes normal dreaming. Likewise, the simultaneous occurrence of neuronal reverberation in multiple forebrain sites during REM-sleep^(44, 53, 114) explains the wide variation in dream modality. There is also a compelling relation between the low stationarity of neuronal reverberation during REM-sleep and the fragmentation, condensation and bizarreness of dreams. Far from being random^(54, 55), dream narratives highlight waking events according to how recent, novel and behaviorally significant they were. Dreams seldom occur during SW-sleep^(29, 115). Instead, the subjective experience of SW-sleep consists of low-intensity but coherent thoughts resembling waking reasoning⁽¹¹⁶⁾. The coherence of such ‘mentation’ likely reflects the high stability of neuronal reverberation during SW-sleep^(37, 53, 108). By the same token, the lack of intense imagery during SW-sleep probably reflects the decreased cortical activity and slow oscillations below 4 Hz that characterize memory reverberation in this state^(32, 33).

If dreams first arose as a by-product of neuronal reverberation during extended REM-sleep, what (if any) the functions of dreams are? So far I have proposed that sleep states co-evolved with learning-related neural mechanisms so as to acquire increasingly important cognitive roles. It is therefore plausible that dreams, just like sleep states, were also selected for their adaptive value for learning. This may not be apparent in most people’s dreams, but normal human dreaming is arguably a good model of normal mammalian dreaming. Humans organized in complex societies face minimal behavioral challenges, in comparison with the constant game of life and death experienced by freely ranging animals. The stakes are high in Mother Nature’s realm: vital resources are scarce,

and populations of nearly all species suffer predation. Contrary to humans, most animals face the perspective of being eaten alive on a daily basis. A single mistake when facing a novel situation can be fatal, and a second should be avoided at any cost. Animal behavior in the wilderness is definitively selected for fast and effective learning. The evolution of dreams in early mammals was certainly shaped by a tough environment in which uncertainty was the rule, and every day involved struggle for survival. For non-human mammals, every day is examination day: an A-grade, when they manage to eat, sleep and mate; a B-grade, when they simply eat and sleep; a C-grade, when they suffer hunger or wounds from predation; a D-grade, when predation leads to their death; and a F-grade, for slow and painful death. Given this set of possibilities, one should expect freely ranging mammals to possess a very limited dream repertoire, consisting of actions to avoid predation, food cache maps, mating, and a few other adaptive behaviors. In comparison, the life of modern middle-class humans involves much less obvious anxieties. Non-human predators are very rare, law enforcement restricts conspecific predation and, however, stressful school and workplace examinations may be, they do not involve physical pain and possible mutilation. Nutritious food can be acquired in large quantities at grocery stores, health care is provided quickly after accidental injuries, and we inhabit permanent, safe and solid shelters.

To conceive how dreams evolved in non-human mammals, we must look towards the kind of dreams that humans have when confronted with primeval challenges. Two inter-related types of dream are of special interest here: dreams that follow attempts of predation upon the dreamer; and, dreams that anticipate predation on the dreamer. With regard to the first case, we know that major psychological and physical trauma usually triggers extremely vivid and repetitive nightmares (e.g., shark attack dreams). The excessive reverberation of traumatic memories during sleep stems from the overwhelming emotional strength of those memories at the time of encoding. It is as if the brain was stuck with a problem that has no answer, which is often the case in irreversibly mangled human patients. As to the second case, dreams that predict possible predation in the future are usually rare in humans, except during wartime. A more familiar example to most people can be found in the anticipatory dreams preceding

school exams, which simulate potentially dangerous events from the point of view of the dreamer.

We now come to the central hypothesis of the theory, namely that mammalian dreams are probabilistic simulations of past events and future expectations. The main function of such simulations would be to test specific novel behaviors against a memory replica of the world, rather than the real world itself. This hypothesis is a generalization of the threat simulation theory of dreaming⁽¹¹⁷⁾, since learning during dream simulations can occur by example or counter-example, i.e., dreams may either simulate actions that lead to a desirable outcome and therefore should be performed in the real world, or actions that lead to undesirable consequences and therefore should be avoided in the real world. In other words, I propose that nightmares evolved as a way to negatively modulate particularly dangerous behavior simulations, while blissful dreams correspond to the association of pleasure reward with dream simulations of especially adaptive behaviors, such as finding mates and food. In all animal species studied so far, REM-sleep is much more abundant in juveniles than in adults^(63, 118). This observation seems to reflect the fact that naïve individuals rely heavily on simulation-based learning processes to survive in unpredictable and dangerous environments.

According to the view presented here, the function of dreams is to trim and shape the memories acquired during waking, in a cyclic process of creation, selection and generalization of conjectures about the world. This aspect of future prediction, or more exactly future guessing, is probably the explanation for the ancient belief in the premonitory powers of dreams. Indeed, despite their stochasticity, dreams sometimes yield very accurate predictions of future events. This is a very rare phenomenon in modern human society, but dream soothsayers prospered during all of the antiquity^(4, 119), and dream interpretation continues to play an important role in many so-called “primitive” cultures⁽¹²⁰⁻¹²³⁾. As human life became gradually easier and complex, dreams lost their predictive power but acquired a diversified symbolic repertoire. In modern humans, dreams are no longer under the influence of life-or-death events, but are rather dominated by a myriad of minor frustrations, challenges and expectations. In the absence of highly eventful recent experiences, it is not surprising that normal human dreams tend

to mix recent though somewhat trivial elements of waking life with old, but strongly encoded, memories of childhood⁽¹⁾.

6. The evolution of lucid dreams

One remarkable feature of dreams is that they are never observed by dream characters other than the self-representation. Under normal circumstances, dreamers have limited control of their dream actions, and no control whatsoever of other dream characters and scenes, which display a large degree of autonomy. It seems obvious from these facts that the self-representation is just one among the many memories activated during REM-sleep, woven into dream narrative by the idiosyncratic probabilities of memory association in each individual. Dreams, conceived by Freud as “a conglomerate of psychic formations”⁽¹⁾, seem to reflect the fragmented activation of the very stuff the unconscious is made of, i.e. latent memories⁽¹²⁴⁾. The very limited volitional power of the self-representation during dreams likely reflects the deactivation during REM-sleep of the dorsolateral prefrontal cortex^(125, 126), a brain region essential for the planning, execution and evaluation of goal-directed behaviors^(127, 128).

Although most people report no awareness of being dreaming while dreams takes place, it is possible for one to be aware of dreaming without waking up, a state called lucid dreaming⁽¹²⁹⁻¹³³⁾. Lucid dreams occur during REM-sleep episodes of greatly increased metabolism, characterized by increased eye movement density, heart rate, and respiration rate⁽¹³⁴⁾. During lucid dreams it is possible for the dreamer to assume partial or total control of the unfolding dream narrative^(131, 132), which indicates that the self-representation is more dominant in lucid dreams than in regular ones. This suggests that activity in the prefrontal cortex is enhanced during lucid dreams, by mechanisms yet unknown. Despite the abundance of subjective reports on the use of lucid dreams to improve performance on a variety of real life skills⁽¹³⁵⁻¹³⁸⁾ the cognitive potential of such dreams also remains to be investigated by science. The use of lucid dreams for conscious simulation-based learning, if confirmed and made accessible to the general public, may

yet come to represent a breakthrough of enormous impact for the evolution of human consciousness.

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