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Sleep researchers need to bring Darwin on board: elucidating functions of sleep via adaptedness and natural selection

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Summary The development of neural multifunctionality – given brain regions carrying out more than one function – conferred great efficiency on brain function at early stages of evolution. This applied to animals that led relatively simple lives with few needs for long-term memories, such as many lower invertebrates – many molluscs, echinoderms, worms, etc. As more complex lifestyles and detailed focal vision evolved, needs for self-initiated and reflexive activities increased in frequency, and recognition of many locales, conspecifics, and other forms of life became essential. These developments were accompanied by greatly expanded needs for neural processing supporting sensory and motor activities, and establishing and storing long-term memories. Since these categories of neural processing occur in largely overlapping brain regions, brain functioning would have become increasingly maladaptive, had the evolution of these more complex lifestyles not been accompanied by compensating adaptations that obviated these potentially conflicting brain activities. These adaptations consisted of: first, restful waking; second, primitive sleep; and finally, fully developed sleep, with its specialized rapid-eye-movement and non-rapid-eye-movement states, that contribute to the maintenance of great efficiency of brain function. The only animals with detailed focal vision that can achieve highly efficient brain function without sleep, are those in which demands on memory processing are greatly reduced in consequence of routine, monotonous, almost purely reflexive lifestyles, with few needs for acquiring experiential long-term memories. The best known animals in this non-sleeping category are tunas and many sharks.

Introduction

Darwin's discoveries in the field of evolution did much more than open our eyes to the long-term influences of the environment on higher plants and animals. They led to enormously fruitful reorientations of studies in all fields of biology. Viewing biological phenomena from an evolutionary perspective, frequently yields insights beyond those that are otherwise discernible. However, paraphrasing a remark of Damasio [1]: one could almost say that, until the last decade, neuroscience and cognitive science have proceeded as if Darwin never existed. In this editorial I illustrate the employment of a Darwinian approach to treat topics in the origin and functions of sleep.

Studies with the goal of identifying the selective pressures that might have given rise to sleep could cast light on its functions. Being mostly medically oriented, however, current studies of sleep have somewhat different objectives. Attention is directed primarily to mechanisms, for example, influences of various brain secretions on sleep. While significant medical progress, with great practical benefits, has been made along these lines, implications of the underlying mechanisms for sleep's functions have been tenuous or non-existent. Further, one must distinguish between the functions of sleep and the activities and benefits of sleep. Usually, the functions have been equated with the activities and benefits.

Some treatments of sleep have included evolutionary considerations, but they infrequently probed into underlying selective pressures. Almost all attention has been directed toward comparative aspects, such as the degrees to which sleep occurs in various species, and how these degrees correlate with brain structures, behavior, and ecology. Such analyses inevitably lean heavily on information gleaned from 'endpoints' of evolution, perhaps millions of years removed from the selective pressures of origin, and often arrived at along different routes.

Taken at face value, these endpoints can be misleading.

Even before beginning to attack the problem of the basic or primitive function of sleep, one can anticipate that it will be expressible in terms of maintaining the overall high efficiency of brain operation. No one would doubt that the waking brain operates at a high level of efficiency, with urgent responses of the organism having highest priority. Accordingly, the provision of a suitably modified alternative vigilance state – sleep – in some animals, very likely functioned to maintain an overall high level of efficiency of brain operation by subsuming non-urgent activities that could not be performed efficiently during a single, continuous waking state.

Schwartz's admonition and Rauschecker's 'fundamental dogma'

In addressing the problem of sleep's basic or primitive function, that is, the function that provided the evolutionary selective pressure for sleep's origin, we take a cue from Schwartz's [2] admonition to sleep researchers. Certain phenomena that characterize a given state, "...may mirror aspects of the mechanism for generating the state and its attendant phenomenology rather than the function of the state" (original italics). This caution is highly relevant for sleep studies, because some researchers assume that a sufficient knowledge of the neurological and physiological mechanisms that initiate, maintain, and terminate sleep, will reveal sleep's basic function. However, the proposed basic function discussed below is only remotely related to sleep's neurological (brainstem activating systems) and physiological control mechanisms [3]. The latter are manifested chiefly by cyclic alterations in brain neuromodulatory substances (such as acetylcholine and serotonin) during vigilance states, that is, rapid-eye-movement (REM) and non-rapid-eye-movement (NREM) sleep, and active and restful wakefulness [4].

It is a property of brain evolution, driven by the adaptive advantages of efficiency, that any given region of the brain typically carries out more than one function. It is this adaptation that largely underlies the ‘fundamental dogma’ of neuroscience, as characterized by Rauschecker [5], in recognition of long-term memory being stored by means of synaptic modifications in the same widely-separated assembly of brain structures that process and analyze the events and relations to be remembered [6]. In a striking example of such neural multi-functionality, one not only becomes blind to colors (achromatopsia), after severe damage to brain regions that process colors, some of those so afflicted cannot even remember that colors exist [7].

Restful waking, detailed focal vision, and conflicting brain activities

As suggested elsewhere [3], restful waking probably was the vigilance state that preceded primitive sleep’s evolution. It would have evolved in many animals that previously were active continuously. For greatest effectiveness, periods of restful waking likely were relatively lengthy and spent in safe retreats. Inasmuch as daily light-dark cycles provide natural limiting conditions for alternate periods of activity and inactivity, at its inception, restful waking in any given species probably was channeled largely into lengthy daytime or nighttime periods.

One can assume that vertebrates already were engaging in daily cycles of activity and restful waking when selective pressures for primitive sleep arose. The evolutionary progression toward primitive sleep would have begun when animals with simple lifestyles evolved increasing complexity and detailed focal vision (vision that recreates a complex scene). Such vision requires enormous amounts of brain processing [8] – the combining of a very great number of incredibly specific bits and pieces of visual features – vastly more, and exceptionally more complex, than that of any other sensory modality.

Despite its complexity and enormous requirements, visual processing is carried out largely at a low level without visual attention (but not without potential interference with other waking brain activities). Without focussing attention on any specific region of a scene, one becomes aware of the space-filling presence of almost limitless numbers of objects, of all sizes shapes and colors, in all imaginable relationships – with everything in view at the same time. In those ancient times when detailed focal vision was acquired, animals would have been engaging increasingly in multifarious activities and wide-ranging movements. In such a lifestyle, lifelong retention of greatly increased stores of memories would have been crucial.

It has been proposed that, in animals achieving detailed focal vision, with large stores of memories, the parallel processing capacity of the brain was becoming excessively taxed because of conflicts between the enormous demands of complex visual analysis and needs for split-second control of movements, on the one hand, and learning and memory processing, on the other [3]. The brains of these animals could no longer meet crucial, largely unpredictable hazards and routine needs, while at the same time meeting needs to acquire, establish, and reinforce large stores of long-term memories, with all neural activities in given categories overlapping in corresponding dedicated brain regions. In other words, an adaptation (neural multifunctionality) that had conferred great efficiency before the evolution of detailed focal vision, would have become increasingly maladaptive as a more complex visual lifestyle evolved, had not compensating adaptations evolved in parallel, namely, restful waking, at first, and then primitive sleep.

Primitive sleep obviated potentially conflicting brain activities

Thus, the selective pressure for the origin of primitive sleep may have been the need to

ameliorate the above developing conflicts by achieving a more profound state of brain unresponsiveness to external occurrences during memory processing than exists during restful waking. By relieving the brain of extensive needs to process and respond to environmental, chiefly detailed visual, inputs during a portion of the 24-h cycle, memory processing could have proceeded without impediment during that portion. As a result, those mnemonic activities of the brain that could be delayed with minimal survival risk, primarily the establishment of new memories and the reinforcing of existing long-term memories, apparently came to be carried out during the new portion, namely, primitive sleep [3]. It is a reasonable assumption that primitive sleep in our reptilian ancestors during those early times was closely akin to the sleep of present-day reptiles.

Key, overt, adaptive changes that accompanied selection for primitive sleep probably were: (a) to close eyelids that previously were transparent and purely protective, but were in the process of becoming increasingly opaque; and/or (b) to retire to secure quarters, often in dim light or darkness. With the exclusion of light and of the need to process complex visual inputs, and with correspondingly decreased attentiveness to other sensory inputs, the sleeping brain would have been almost totally occupied with those previous waking activities that could be delayed with minimal survival risk.

Some workers felt that sleep would have subjected animals to greater risks than if they spent the same periods awake. But whether risks were increased was not the determining circumstance. The critical consideration, vis-a-vis natural selection, was whether primitive sleep's adaptive advantages outweighed the greater risks entailed. The proposed adaptive advantages were the maintenance of great efficiency of brain function, both awake and asleep—highly efficient sensory processing and responding when awake, and highly effective memory processing when asleep. Primitive sleep would have compensated for a gradually

developing conflict, namely, the need to accomplish all these interrelated brain activities during a continuous waking state. In this connection, Moorcroft [9] made a general suggestion similar to that proposed here and earlier [3,10], namely, that sleep provides a time when certain activities “can occur most easily and most efficiently.” In a similar vein, Maquet [11] suggested that “[s]leep could be a privileged period for memory consolidation.....”

Consolidating visual discriminations requires REM and NREM sleep

In the very early stages of sleep’s evolution, the brain functions that now occur independently during waking and sleep probably occurred in competition with one another. However, there is compelling evidence that the conflicts now have become unresolvable during wakefulness. Some memory establishment (known as “consolidation”) that involves detailed visual discriminations cannot occur during waking. It absolutely requires sleep [12, 13]. This unequivocal establishment of a specific vision-related activity that requires sleep lends strong support to the foregoing proposals for the role of detailed focal vision in sleep’s origin. Further studies have revealed an even more specific dependence. NREM sleep, alone, is not sufficient. It must be followed by REM sleep [14]. Other strong support for the proposals comes from findings that sleep occurs only in animals with complex image-forming eyes, as opposed to mere eye spots and light-sensitive pigment cups and tubes, and that to sleep, many animals must block their vision, either by closing their eyelids or other means [3].

REM sleep, fast waves, and states of awareness

In the light of recent findings concerning the actions of brain waves, one aspect of the evolution of primitive sleep can be dealt with on a more explicit basis. Over 20 years ago, von

der Malsburg [15] proposed his 'cell assembly' hypothesis, according to which the thoughts, perceptions, and actions of conscious activity are brought about through the mobilization and synchronous activation of the widely-separated brain circuits that participate in the particular events. Experimental studies in following years, most notably by G. Buzsáki, R. Eckman, C.M. Gray, R. Llinás, W. Singer, and M. Steriade, implicated fast brain waves (≥ 14 –200 cycles/s) in this assembly and activation process. It is thought that, on a time scale of 10–30 ms, these waves coordinate and synchronously bind outputs of the widely-separated component circuits of the events – mostly circuits for cognition, the senses, and detecting and effecting motion. The accompanying expression of the assembled, bound contents of these circuits in higher vertebrates can be regarded as the neuronal correlate of consciousness.

If the above-described conflicts that led to selection for sleep's origin arose from the waking need to acquire and maintain large stores of memories of new and old waking experiences, the new vigilance state of primitive sleep should have provided the unrestricted opportunity to fulfill this need. Since the fast waves that activate and bind component circuits of memories are thought to produce awareness during waking, it follows that fast waves could not have been present during the evolving vigilance state of primitive sleep.

Accordingly, at the neurophysiological level, the selective pressure for primitive sleep would have favored a progressively reduced presence of fast waves during restful waking, culminating in sleep. Indeed, this is what happens when we fall asleep, often described merely as an overt increase in the threshold for responses or arousal. During the new state of primitive sleep, only waves of frequency less than 14 cycles/s would have been present. Memory reinforcement during primitive sleep, in whatever degree, would have had to be accomplished by these "slow waves." The more complex matter of memory consolidation during sleep is treated elsewhere [16].

At the present time, sleep in mammals and birds is partitioned into two major states. In humans, these occur in alternation roughly every 90 min. During REM sleep, although fast waves are present and accomplish assembly and activation of events, and reinforcement of circuitry, our awareness of the events is only 'non-conscious,' that is, as dreams. Several of the known differences from waking conditions, not necessarily mutually exclusive, that result in the expression of events only as dreams during REM sleep, are: atonia in large muscle masses; a high (but not complete) degree of perceptual isolation from external stimuli; the circumstance that all events of REM dreams originate within the brain; and the condition sleep researchers refer to as "reduced behavioral responsiveness."

During most of NREM sleep, slow waves predominate. These primarily reinforce individual circuit components (fragments) of memories, which are inherently unable to penetrate consciousness. The small amounts of lower amplitude fast waves (e.g., "ripples"), that are present during NREM sleep, apparently give rise to the lesser numbers of NREM dreams, including those that are described as 'thoughtful' [16,17].

These proposals for the origin and function of primitive sleep do not preclude subsequent or concomitant evolution of secondary functions that may have become essential. Indeed, for birds and most mammals, secondary functions of sleep come into play, as well as deep-seated rhythmical changes engaging many physiological systems [18, 19].

Vertebrates that never sleep

The lifestyles of vertebrates that never sleep are fully consonant with the above proposals. Thus, as would be expected, since genetically blind cold-blooded vertebrates that live in caves can have no visual processing conflict, they have no need for sleep. Although the majority of

fishes sleep, many that possess detailed focal vision, such as tunas and many sharks, do not. Rather, they swim continuously. Their lack of sleep can be attributed to an existence in which needs for processing sensory information, predominantly visual, and for long-term experiential memories are greatly reduced. These reductions owe to the following aspects of their behavior and ecology: (1) their visual input is greatly reduced or absent during lengthy periods of both diurnal and nocturnal activity; (2) their practice of schooling greatly reduces needs for environmental sensory information, particularly visual; (3) being maintained through frequent or almost continuous use, their circuitry for most inherited memories needs no supplemental reinforcement; and (4) leading a comparatively routine, monotonous existence in essentially featureless, open waters, they acquire, and have need to reinforce, relatively few experiential memories. Analogous circumstances could account for the ability of migrating birds to fly for days without rest or sleep [20, 21].

Earliest vertebrate sleep

With the knowledge that the occurrence of sleep in fishes is dependent upon their behavior and ecology, as also is proposed for land vertebrates, and that marine vertebrates preceded land vertebrates, it is likely that the earliest vertebrate sleep occurred in fishes. Prominent modern-day fishes with detailed focal vision that sleep are many teleosts (bony fishes) that occupy complex coral reef habitats. Teleosts, however, date back only about 235 million years to the early Triassic period. For that reason, the earliest primitive sleep in marine forms with detailed focal vision might have occurred much earlier, say in small, shallow-water or, possibly, reef, sharks – the earliest jawed fishes – during or later than the Ordovician period, about 450 million years ago [20].

On evolutionary approaches to sleep

In this editorial, I have sought to illustrate the utility of an evolutionary approach – always seeking and mindful of differential adaptedness and underlying selective pressures – to guide research into the origin and functions of sleep. It is of paramount importance in such pursuits to recognize that physiological and behavioral adaptive responses to many types of selective pressures are basically highly conservative, usually occur gradually and continuously, and typically are restricted to modifying or co-opting existing substrates, rarely effecting new mechanisms. It is equally important to be mindful of the often-overlooked circumstance that, though counterexamples unequivocally invalidate mathematical and logical theorems, they do not enjoy the same power of discrimination in the much more complex biological realm. Otherwise, since biological counterexamples are by no means rare (for example, sighted fishes that do not sleep), one may be too easily diverted from pursuing valid lines of analysis. Evolutionary processes sometimes achieve adaptations that, on the face of it, appear to be unattainable.

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