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Is sleep's 'supreme mystery' unraveling? An evolutionary analysis of sleep encounters no mystery; nor does life's earliest sleep, recently discovered in jellyfish

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Summary. Biotelemetry has revealed daily 15-h behavioral sleep periods in a cubomedusan jellyfish, *Chironex fleckeri*. Its sleep is expected to be phylogenetically most primitive, since jellyfish possess only two germ layers. They belong to the phylum Cnidaria, the simplest multicellular organisms with an organized nervous system. Cubomedusae have a complex visual system with 24 eyes of four different types, each type specialized for a different task. Input to these eyes during visually guided fast-swimming predation requires enormous amounts of neural processing, possibly nearly saturating the capacity of their comparatively simple nervous system. These heavy neural demands may account for the need for fifteen hours of sleep. *C. fleckeri* is the only animal known for which sleep may be either present or absent, dependent on lifestyle. Limited knowledge of behavior of some other cubomedusae suggests that they also possess this faculty. The finding of sleep in *C. fleckeri* supports current proposals of sleep's origin and basic function. Evolutionary analyses link sleep to a conflict produced by excessive processing demands on multifunctional neural circuitry for detailed focal vision by complex lensed eyes. The conflict arises between the enormous demands of complex visual analysis and needs for split-second control of actions, on the one hand, and non-urgent processing of memories of ongoing and stored events, on

the other. Conflict is resolved by deferring the non-urgent processing to periods of sleep. Without sleep, selection would favor the evolution of circuitry dedicated to single or but few tasks, with corresponding lesser efficiency. Had complex lensed eyes of medusae originated as a consequence of selection for increased mating success of males pursuing females, it could have occurred before the evolution of fast-swimming bilateral (three-germ-layered) prey. But if it was a consequence of selection for increased prey-hunting success, the origin of such eyes probably awaited the coexistence of bilateral prey.

Introduction

The recent finding of behavioral sleep in the cubomedusan jellyfish *Chironex fleckeri* focuses attention on the role of vision because, quite remarkably, cubomedusae have 24 eyes (ocelli), eight of which are of a complex camera-type like the lensed eyes of vertebrates. I conclude in the following that these eight eyes, if not all 24 ocelli, play an essential role in *C. fleckeri's* need for behavioral sleep (hereafter abbreviated merely as “sleep”). For that reason an appropriate starting point for this Editorial is Darwin’s studies of eye evolution.

Upon advancing his theory of natural selection Darwin [1] sought to anticipate and deflect possible objections by acknowledging that “If any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down”. The vertebrate eye was the obvious potential counterexample, and Darwin was at great pains to present evidence that such an “organ of extreme perfection and complication” could have evolved by natural selection.

This observation is consistent with present knowledge that changes in eye design follow evolutionary changes in lifestyle relatively rapidly [2,3].

Darwin's choice of the eye to buttress his theory hinged on its great complexity, exceeded only by the brain. But he also was greatly interested in eyes beyond considerations of complexity. He defined the prototypical eye as consisting of two cells only, a photoreceptor cell and a pigment cell. One primitive example of each of these exists in some flatworms. Darwin's remarkable evolutionary insights are enhanced by his concepts of eye evolution. These are closer to the mark [4] than those espoused only decades ago by the great evolutionist, Ernst Mayr [5], who proposed multiple independent origins of eyes. In current views "all bilaterian eye types go back to a single root, a Darwinian prototype" [4].

It is no coincidence that, beyond direct roles in vision, complex lensed eyes have another profound influence on the lives of most organisms possessing them, namely, the need for sleep. Had Darwin also directed his great analytical powers toward the "supreme mystery", as many researchers characterize sleep, the mystery might long ago have neared solution.

An evolutionary analysis of sleep's basic function

Before turning to the remarkable implications of the recent finding of sleeping box jellyfish, I consider current views on sleep's basic function arrived at through an evolutionary analysis [6]. The jellyfish findings both support these views and reveal the need to generalize them. As ancient animals evolved detailed focal vision (DFV; vision that recreates a complex scene) it was proposed that their simple lifestyles were

becoming increasingly complicated. Concurrently their restful waking was deepening into sleep [3, 7]. DFV requires enormous amounts of neural processing (see [3]), vastly more and more complex than for any other sense. Despite this complexity it proceeds without visual attention but not without potential interference with other ongoing brain activities.

This potential exists because in the course of neural evolution, driven by the adaptive advantages of efficiency, any given neural circuitry typically has come to serve more than one function. In achieving this capability, long-term memories of events came to be stored in the same neural regions that process the events, analyze them, and control responses to them [8]. An illustrative example of circuit multifunctionality (see, also, below) is provided by circuits for color vision. People not only become blind to colors (achromatopsia) after certain brain injuries, some patients lose all concept of what a color is [9].

While circuit multifunctionality was highly adaptive for relatively simple lifestyles, it was susceptible to losing its adaptedness in a more complex existence. For example loading circuitry with a demanding new waking function might interfere with the simultaneous accomplishment of its other functions. Just such circumstances were proposed to underlie sleep's origin, with the "demanding new waking function" being DFV [3, 6, 7].

As increasingly complex lifestyles evolved, animals acquiring DFV also would have developed greater discriminative abilities and engaged in many new activities, including fast wide-ranging movements and rapid actions and responses. In such lifestyles maintenance of increasing numbers of memories for the long term would have become

crucial, such as, memories of locations, predators and prey encountered there, etc. But with increasing numbers of memories being stored in given circuitry possibilities for conflict with processing of other functions served by that circuitry also would have increased.

Reflecting on these considerations it appeared likely that the parallel processing capacity of some regions of these animals' brains was becoming severely taxed. Specifically, this would have traced to conflicts between the enormous demands of complex visual analysis, and needs for split-second control of actions, on the one hand, and learning and maintaining long-term memories of these demands and actions, on the other. The circuit multifunctionality that conferred increased efficiency, before the evolution of DFV, would have become increasingly less efficient as visual lifestyles became more complicated, had not compensating features evolved in parallel.

These features are thought to have been, first, restful waking, subsequently sleep and, with the acquisition of warm-bloodedness, sleep's non-rapid eye- movement and rapid-eye-movement phases specialized for different aspects of memory processing [10]. The former phase is specialized for reinforcing component circuits of memories, each usually stored at a different site in the brain. For a visual memory, these would include circuits for shape, size, orientation, color, texture, position, or motion. The latter sleep phase – sleep researchers' "proverbial riddle wrapped in a mystery inside an enigma" – is specialized for reinforcing fully formed memories, including linking the memories' distributed components together [6, 10]. Without neural multifunctionality these components, for example shape, would have to be stored in separate 'dedicated' circuits for shape, possibly one for each memory.

Evolution of this second vigilance state – sleep – fully remediated the developing conflicts described above. By relieving multifunctional circuitry of the need to process memories fully during waking activities, the circuits' urgent functions could proceed without or with lesser impediment. Lacking sleep's relief, multifunctional circuits would have been selected against, that is, selection would have favored replacing them by larger numbers of dedicated circuits with single, or fewer tasks, not involving nor being interfered with by memory processing. However, these 'dedicated' circuits would have required more neural tissue to accomplish the same amount of neural processing, with corresponding losses of efficiency. Accordingly from an evolutionary perspective, in terms of benefits to neural circuitry, sleep shielded neural multifunctionality from exposure to adverse selection and lesser efficiency. Instead of selecting for additional dedicated neural circuits, those aspects of memory processing that could be delayed with minimal survival risk, were deferred to the sleep state.

Supporting this close nexus between sleep and DFV is the circumstance that, in many birds and marine mammals, half of the brain instantly falls asleep or awakens when one set of eyelids close or open. Avian sleep is so closely associated with eyelid closure that it is asserted that the eyelids "close only in sleep" (see [3]). Moreover, sleep occurs only in animals with complex lensed eyes and, in order to sleep, many animals block their vision. Once this link between sleep and the enormous processing needs of DFV was uncovered, tentative conclusions about sleep's antiquity could be drawn for the first time, as detailed in the following section. These conclusions also provide perspectives for the discussion of box jellyfish sleep.

In the following, it will be assumed that the same considerations that led to the need for sleep in three-germ-layered (triploblastic) organisms apply to the two-germ-layered (diploblastic) cubomedusae. Within this paradigm, in certain circumstances most vertebrates need sleep to accommodate neural processing of input from only two camera-type eyes, despite possessing a comparatively massive brain. How much greater, then, might be the need for sleep in box jellyfish in comparable circumstances, with 12 times as many 'eyes', four times as many being of camera type, and only a comparatively simple nerve net and nerve ring to serve their enormous needs to process light input?

Antiquity of sleep

Vertebrate sleep might have occurred at least 450 My (million years) ago in the earliest jawed fishes living in complex habitats. Invertebrate sleep had an even more ancient origin. Among mollusks only cephalopods sleep. Like vertebrates many of them have large camera-type eyes. Ancestors of the chambered Nautilus date back to the Silurian period (435 My ago), when they were top predators. Their lifestyle may have been sufficiently complex to require sleep. This might have applied even earlier, in the Cambrian period (543 My ago) in free-swimming trilobites *Opipiteuter* whose large eyes, with 360° vision, dominated the head. Horseshoe crabs of the same period also might have slept. They were dominant Cambrian predators that possessed 10 eyes, two of them compound [6].

In these examples the postulated occurrence of sleep is based either on analogies with living relatives, or on fossil remains indicative of the possession of lensed eyes. All

the above examples concern fast-moving marine predators inhabiting more or less complex environments, in which vision played a dominant role. Indeed, it has long been recognized that “.....the highest selective premium on superior eyes exists for actively motile predators.....” [2], while “[a] common feature of all organisms with lensed eyes is a fast-moving free-swimming habit and moderate to large size” [11], together with a predatory lifestyle.

Even with knowledge of the lifestyle and properties of marine organisms that sleep or their ancestors that are thought to have slept, it was unexpected to find sleep in the tropical inshore, highly venomous box jellyfish, *C. fleckeri* [12], despite similarities of lifestyle. This jellyfish belongs to the class Cubozoa in the Phylum Cnidaria, members of which are diploblastic and include the simplest organisms with an organized multicellular nervous system. Within the group *C. fleckeri* is commonly described as being of relatively large size, a fast-moving visual predator inhabiting complex habitats [13].

Although cnidarians are at least 600 My old, few jellyfish are found in the fossil record and those only from relatively recent times. Some are found as very fine sedimentary compressions, others as sand infillings of the gut cavity, principally *Brooksella* of the middle Cambrian [14]. The only recognized fossil cubomedusan *Anthracomedusa turnbulli* dates to the Pennsylvanian (323–290 My ago). With its square shape and clusters of tentacles it was likely within the same family (Chirodropidae) as *C. fleckeri* [13].

***C. fleckeri* medusae**

Cubomedusae have a complex active behavior. Unlike most other jellyfish they are extremely efficient fast (variously reported as 0.2–0.5 m/s maximum speed by *C. fleckeri*), agile swimmers most of whom can change direction in just a few swim contractions [15]. Attention is confined to the most pertinent aspects of the anatomy, visual apparatus, and capabilities of *C. fleckeri* medusae. Except for size these aspects are thought to be very similar in all cubomedusae.

Cubomedusae possess four sensory stalks, the rhopalia, suspended beneath the umbrellar bell (a box-shaped body, 16–24 cm in diameter in *C. fleckeri*) lying in indentations of the bell's tissue. Rhopalia lie midway between the pedalia, which lie at the bell's corners and from which the tentacles extend. A nerve ring connects the rhopalia to one another and to the four pedalia [14, 16]. Each rhopalium contains a statocyst and a cluster of six eyes of four different types, each type specialized for a specific task.

There are two slit eyes, two pit eyes, and two different-sized complex camera-types, the most highly evolved among the Cnidaria. Both camera types possess corneas, lenses, pupils, retinas, photoreceptor cells similar to those of vertebrates, and pigment layers. Both the pit and the slit eyes face laterally inward toward the bell's center, as does the larger of the camera types. The smaller one is directed upward toward the bell's apex. Since rhopalial stalks can swing, twist, and turn, and the bell is largely transparent, the surrounding view is multidirectional and virtually unobstructed [17]. Being sensitive to orientation, the statocysts allow sensing and orientational control of each rhopalium and its eyes [15].

Although, details of neural processing of visual input are unknown, accounts of cubomedusan behavior – the most complex among medusae – leave little doubt that they see, in the sense of forming and processing a retinal image [18], possibly uniquely [19]. Evidence that retinal images may be underfocused, because only a small vitreous space lies between the retina and lens [20, 21] was not obtained in normally behaving animals, and may be misleading. Further, other animals are known in which eyes focus images onto a retina close to the lens (see Sivak 1976 in [17]). But underfocusing might be adaptive, with the lensed eyes acting as low-pass filters [21]. It should be emphasized, however, that although cubomedusae have a complex active behavior and are extremely efficient, agile swimmers, there is no unequivocal evidence that they can focus sharply on, or stalk, individual prey.

The above description of *C. fleckeri* reinforces the likelihood that a high degree of visual processing is needed in some circumstances. When these include the need for high-speed swimming and split-second actions and responses one can anticipate an offline need for sleep, regardless of whether retinal images are sharp. The circumstance that cubomedusae lack a single bilateral, ganglionic nerve center (the brain of bilateral organisms) but instead possess a diffuse nervous system and a nerve ring, appears to rule out point-by-point mapping from the retina to a locus in the nervous system, as implied by DFV. Accordingly it is desirable to broaden previously published proposals concerning the need for sleep [3, 6, 9], to its hinging on the enormous computational requirements of complex lensed eyes, irrespective of possession of DFV. Unless a significant degree of complex retinal processing occurs (see [3]) the cubomedusan

nervous system must be at least as complex as the visual system whose input it analyzes.

Sleep in *C. fleckeri*

The tropical box jellyfish *C. fleckeri* is seasonal, typically occurring in large numbers during the warmer months of the year [22]. In the pioneering, but as yet not replicated, study by Seymour et al. [12], telemetered data were continuously monitored during the long-day, austral summer months (late December through early February). Although local sunset was 18:30–19:00, high mountains at the study site, caused the light to diminish 2.5–3 h earlier. The data obtained from radio transmitters glued to juvenile individuals revealed markedly diurnal behavior.

During 9 h of daylight (06:00–15:00 h) in the wild, hunting *C. fleckeri* moved rapidly in straight lines in darting fashion, by a jet-like propulsion, with overall individual displacements of about 212 m/h. At night, however, individual displacements amounted to less than 10 m/h. Isolated sleeping jellyfish lay motionless on the sea floor for 15 h (15:00–06:00; 27–28° C), “with no bell pulsation occurring and with tentacles completely relaxed and in contact with the sea floor”. When mildly disturbed, they rise, “swim around for a short period, and then fall back into an inactive state on the sand” [12]. The characteristic posture, motionless periods, and their resumption after mild disturbances, are behaviors highly indicative of sleep [3].

Although observed unsystematically (i.e., not for continuous, lengthy periods) over many decades, only telemetry revealed that *C. fleckeri* sleep. Since field observations of other cubomedusan behavior have been limited and unsystematic, sleep in others also

may have gone unrecognized. There have, however, been many observations of jellyfish motionless or at rest, (i.e., not engaged in volitional activity).

Complicating the situation, studies of captive *C. fleckeri* reveal that the need for sleep is facultative (in the sense of being dependent upon lifestyle, rather than volitional). This is not unexpected of sleep in its most primitive manifestation, as seen in *C. fleckeri*, since sleep likely evolved from rest [3]. Moreover, other wild populations of *C. fleckeri* have been observed swimming at night, at times when the telemetered individuals would have been at rest, for example, in an area illuminated by pier lights [20]. Additionally, a single mature (rather than juvenile) individual tracked for over 30 h by telemetry in late April had a completely different movement pattern and slept for only 2 h (Seymour; personal communication).

Not only does knowledge of sleep in *C. fleckeri* further support the above proposals, so also do the conditions in which they do not sleep, or sleep or rest very little. A hand-fed captive subadult “swam continuously in the upper water column” of a tank for 9 months. Other hand-fed individuals maintained in good condition for lesser periods also swam continuously, except for limited periods of digestion and rest, when they settled to the bottom [20].

Because these and other captive individuals were either hand fed, or prey were readily available, there was lesser need for such neural processing as supports high-speed swimming and maneuvering during predation. In these circumstances, little or no interference would be expected between neural processing for limited feeding activities, and limited learning and memory processing. Accordingly there would be little or no need for sleep.

In field conditions, in which *C. fleckeri* acquire food without much need to engage in high-speed activity, there also may be little or no need for sleep. For example, in some circumstances *C. fleckeri* swimming near the surface periodically sample lower waters by sinking passively to the bottom. If successful they rest, apex downward, allowing the tentacles to fall into the bell. After all captured food is removed from the tentacles, they rise to the surface and resume swimming [22]. The extent to which these animals rest (beyond motionless periods during digestion) or sleep is undocumented.

Further continuously monitoring studies of cubomedusae will be needed to answer the questions already raised by those of Seymour et al. [12], such as the influences of age, season, prey, feeding methods, etc., on the need for sleep. Existing studies of other cubomedusae are suggestive in this regard, but none rules out the possibility of facultative sleep, dependent on lifestyle. The food acquiring tactics of other cubomedusae may or may not be sufficiently demanding of neural processing to require lengthy periods of rest or sleep. In another example suggestive of sleep, when the sea is disturbed, *Carybdea alata*, rest motionless on the bottom, but when it is calm at night, they rise to the surface and feed [23].

In accord with the need for sleep by *C. fleckeri* that feed by vigorous predatory activity, the relatively small medusae of *Carybdea rastonii* (bell about 2.5 cm high; in the family Carybdeidae) were often observed to be resting on the bottom in both the field and the laboratory. This 'rest' phase (including digestion) is essential for engaging in the following complex stereotypical feeding. After capturing prey with the tentacles, *C. rastonii* engage "in a stereotypical feeding pattern characterized by an increase in swimming speed vertically upward for a few seconds, followed by a 180° turn and a total

cessation of bell pulsation. The pedalia flex inward 90° and the tentacles and attached prey [brine shrimp, mysids, and small fish] fall into the bell as the medusa drift downward". If interrupted, the pattern is repeated [19].

On the other hand, consistent with the above facultative, lifestyle proposal regarding the need or lack thereof for sleep in cubomedusae, Satterlie [24] found that medusae of *C. rastonii* swim "continuously in the laboratory and in the ocean without intermittent swim and rest periods.....with no apparent variation in swimming regularity or frequency" in the laboratory at night. Feeding mode was not specified but, like that of captive *C. fleckeri*, it may have been relatively non-demanding of neural processing, and not requiring sleep.

Could selective pressures for complex lensed eyes and sleep have preceded the origin of bilateral organisms?

For selective pressures for complex lensed eyes and sleep to have preceded the origin of bilateral (three-germ-layered) organisms, they would have had to be exerted within the phylum Cnidaria, itself. But the most likely need for high-speed hunting within the phylum would have been as a mating tactic. Though most cubomedusae broadcast their gametes [13], males of the cubomedusan, *Tripedalia cystophora* do, indeed, pursue and catch females to mate with them [16, 25, 26].

There is no firm answer to the question in the above heading. Complex lensed eyes and sleep might have originated in ancestors of cubomedusae through selective pressures on the visual system induced by males pursuing females. I would suggest, rather, that they originated as a result of these ancestors hunting bilateral prey. In a

comparable situation, convergent evolutionary similarity of cephalopod eyes to vertebrate eyes is thought to owe to the eventual existence of fast, adept vertebrate predators on cephalopods, and as prey for cephalopods [27].

Overview

Behavior of medusae seemingly provides a window into the basis for sleep's earliest function and evolution, as proposed above. Possessing the first organized nervous system, following those proposals, an implication is that neural multifunctionality exists in cnidarians, and played a role in the evolution of sleep. Since both sleeping and non-sleeping medusae exist, the presence of complex lensed eyes, the more complex lifestyles, and the greater needs for neural processing in those that sleep, become implicated in the need for sleep.

Perhaps, the three paramount implications of these findings are: (1) sleep appears to be a more basic phenomenon than heretofore realized, closely tied to conflicting neural processing needs; (2) even at its simplest level, sleep probably functions to maintain the high efficiency of neural multifunctionality by shielding it from adverse selection; and (3) at their most primitive level in medusae, rest and sleep appear to be facultative, in the sense of being dependent on the imposed lifestyle.

The finding of behavioral sleep in *C. fleckeri*, of the family Chirodropidae, raises the question of its existence in other, perhaps all, cubomedusae. This seems likely in view of possibly similar, or at least not contradictory, field and laboratory behavior of *C. rastonii*, a member of the only other family, Carybdeidae.

Neural processing of cubomedusan visual information from 24 ocelli, and coordinating it with the guidance of rapid movements, are both highly demanding activities. Since this is achieved with one of the simplest of multicellular nervous systems, one can suspect that the degree to which these activities monopolize the totality of neural processing potential during active predation by *C. fleckeri*, exceeds that in other organisms.

The influence of lifestyle on the need for sleep in cubomedusae closely parallels circumstances among vertebrates. Thus, many pelagic fishes (e.g., some sharks) with simple lifestyles in monotonous open-sea environments, with few needs for experiential memories and few intrinsic (inherited) memories to process, are perpetually active. Contrariwise, some closely related forms (other sharks) inhabiting complex inshore habitats and coral reefs, with great dependence on experiential memories, need sleep [7]. The *C. fleckeri* findings not only parallel this result at a vastly simpler level of the animal kingdom, they do so, unprecedentedly, in members of the same species. As we have seen, in the one lifestyle, exemplified in captivity with food provided, *C. fleckeri* sleeps little or not at all, whereas telemetered individuals, in the particular field conditions studied, slept 15 h.

In essence, the condition determining the need for sleep in cubomedusae appears to be the degree to which the demanding neural processing needs for incoming 'visual' information and visually guided actions saturates their processing capacity. Accordingly, it can be suggested that, even the neural processing needs for vision with complex lensed eyes may be too restrictive a condition on the mode of light reception, as regards the need for a second vigilance state.

Taking the broadest view in unraveling the “supreme mystery”, one can suspect that circumstances in cubomedusae constitute extremes of those that lead to the need for a second vigilance state in other medusae. Even lesser neural processing demands that monopolize the capacity for light-sensing and responding in nervous systems of lesser capacity, might lead to a requirement for rest or sleep. Supporting this view, the following observations confirm rest – possibly sleep – in medusae of *Aurelia aurita*, in the class, Scyphozoa, which have only two tiny, non-lensed ocelli, of different composition (see [17]), on each of their eight rhopalia. “In the dark, the medusae were quiescent, with bell contraction rates reduced or absent.....on still nights medusae covered the surface.....animals were almost motionless.....” [28].

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