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REVIEW ARTICLE

Vertebrates that never sleep: Implications for sleep's basic function

J. Lee Kavanau*

University of California, Department of Biology, Los Angeles, CA, USA

ABSTRACT: A major activity of the brain of most vertebrates during waking behavior is the processing of sensory information, preponderantly visual. This processing is not fully compatible with the brain's spontaneous oscillatory activity that maintains (refreshes) infrequently used circuits that store inherited and experiential information (memories). Great reduction in sensory input and processing during sleep permits the refreshment of memory circuits to occur unimpededly. Accordingly, sleep may have evolved as ever augmenting needs for processing visual information during waking behavior by brains of great complexity conflicted increasingly with needs to refresh memory circuits. The lack of a need for sleep by genetically blind fishes that live in caves, and sighted fishes that swim continuously, is consistent with this thesis, as their needs for processing of sensory information, predominantly visual, are either greatly reduced or nil. Reduced requirements for processing sensory information by continuously swimming fishes owe to the following aspects of their behavior and ecology: (1) visual input is greatly reduced or absent during lengthy periods of nocturnal activity; (2) schooling greatly reduces needs for sensory information, particularly visual; (3) being maintained through frequent use, circuitry for most inherited memories needs no refreshment; and (4) inasmuch as they lead a comparatively routine existence in essentially featureless, open waters, pelagic species acquire, and have need to refresh, relatively few experiential memories. Analogous circumstances could account for the ability of migrating birds to fly for days without rest or sleep.   © 1998 Elsevier Science Inc.

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INTRODUCTION

Efforts to identify sleep's basic function are complicated by ancillary benefits in mammals and birds, such as bodily rest and rejuvenation, physiological restoration, regulation of hormonal secretions, and reinforcement of the immune system [29,140]. Such efforts can be more sharply focused by identifying the ecobehavioral property common to all nonsleeping vertebrates:

they spend much or all of their lives under conditions of reduced, minimal or nil visual input and, for many of them, also with reduction of other sensory inputs.

These findings raise the possibility that the selective pressure for the evolutionary origin of sleep was a conflict between the brain's waking needs for processing sensory information, predominantly visual, with its needs to refresh memory circuits for infrequently used functions. The conflict might have arisen as nonsleeping animals acquired increasingly complex brains, behavior, and visual competencies, together with ever enlarging stores of experiential and inherited memories. If under selective pressure, the brain were to achieve a more profound state of unresponsiveness to sensory inputs than usually occurs during restful waking, namely the state of sleep, circuit refreshment could have proceeded unimpededly. Evidence consistent with this thesis is presented in this article.

Nonsleeping vertebrates encompass a wide range. Almost all of them swim continuously. A few rest most of the time. Some are genetically blind, others have excellent visual acuity, still others have great visual sensitivity at low light levels but their acuity is poor. They cover the gamut from being color blind to having four-pigment color vision and a greater diversity of visual pigments than all other vertebrates combined. Some can occlude their pupils, others have only limited ocular control over ambient light reception.

Adult weights range from several g to hundreds of kg. Some hunt by day, some by night, others take food at any time. Some inhabit shallow waters and coral reefs, others are pelagic, range far into the great ocean basins, and migrate between the continents. Some are strict ectotherms (loosely speaking cold-blooded), others are "partially warm-blooded", maintaining their bodies at temperatures above external ambient values.

With the exception of some salamanders, all nonsleeping vertebrates considered here are fishes. Several studies indicate that a frog and three reptiles also do not sleep, engaging only in restful waking [12]. Inasmuch as they provide less clear-cut examples, they are not considered further. As employed here, "restful waking" or "rest" is characterized minimally by behavioral quiescence,

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  * Address for correspondence: J. Lee Kavanau, University of California, Department of Biology, 405 Hilgard Avenue, Los Angeles, CA 90095-1606, USA. Fax: (310) 206-3987; E-mail: lkavanau@biology.ucla.edu

characteristic postures, vigilance, reduced or absent complex visual processing, and unaltered sensory thresholds. It usually is engaged in only under conditions of relative safety, in which there is little need for close monitoring of sensory information.

REFRESHMENT OF MEMORY CIRCUITS AND PROCESSING OF EXOGENOUS INFORMATION

Spontaneous, endogenous activities of the brain during sleep are treated here, with a discussion of the basis for the conflict between these activities and exogenously-induced processing of sensory input, chiefly complex visual information. Examples are drawn largely from mammals [56–58].

Spontaneous Brain Activities During Sleep

In 1966, Roffwarg et al. [108] proposed that spontaneous, repetitive activations of circuitry in the central nervous system (CNS) of the human embryo during rapid-eye-movement (REM) sleep facilitate the development and maintenance of inherited (genetically programmed) memory circuits. They suggested that such activations during REM sleep maintain (refresh) inherited circuitry throughout life. Subsequent investigators extended the concept to include refreshing of circuits storing experiential information [46,100,124].

Functional and "nonutilitarian" "dynamic stabilization." The concept provided the basis for a paradigm of "dynamic stabilization" (DS) of neural circuitry [55]. According to it, synaptic efficacy in circuits storing inherited and experiential memories is maintained both by frequent use ("functional DS") and by activations induced by spontaneous oscillatory brain activity ("nonutilitarian" DS). The spontaneously induced activations are referred to as being "nonutilitarian" because they customarily do not trigger circuit functions—usually inhibited by temporarily increased thresholds for activation.

Spontaneous oscillatory activity. It has long been suspected that self-generated, spontaneous brain oscillations play a fundamental role in brain activity [65]. The major function of many of these oscillations during sleep may be the nonutilitarian DS of synapses in infrequently used circuitry. Although it was proposed initially that the oscillations play this role during REM sleep, it now is recognized that they also act during nonrapid-eye-movement (NREM) sleep [11,125–127]. Concerning the lethal effects of sleep deprivation in mammals [29], it can be suggested that these owe, not so much to the cessation of nonutilitarian DS of memory circuits, but to the deleterious influences of the loss of some of the ancillary benefits of sleep referred to previously.

Examples of spontaneous oscillatory activity (nonutilitarian DS) that may refresh circuits are: the theta rhythm (4–10 Hz) of REM sleep, which may refresh hippocampal circuits [94,98,110]; irregular sharp spikes (1/50–3 Hz) of NREM sleep, which may refresh circuits targeted by the hippocampus [11,15]; cyclic trains of single spikes or rhythmic spike bursts in thalamocortical axons resulting from spindle oscillations (7–14 Hz wavelets occurring every 3–10 s), delta oscillations (1–4 Hz), and continuous synaptic bombardment from the intrinsic cortical networks that generate the slow sleep oscillation (~ 0.3 Hz) of NREM sleep, which may refresh synapses in cortical association circuits [126,127]. Accordingly, the refreshing activations apparently have their origin primarily in low frequency oscillations below the beta band (14–30 Hz) (for a treatment of the evolution of sleep and its NREM and REM phases, see [57,58]).

The need for spontaneous neural activations to refresh memory circuits probably is of very ancient origin. This is suggested by the finding that "coordinated spontaneous activity . . . is a fundamental feature of the most primitive nervous systems" [10]. Inasmuch as

basic aspects of mechanisms that achieve short-term and long-term synaptic efficacy tend to be evolutionarily conservative, one expects the primordial basis for long-term maintenance of memories to exist in some "simple" nervous systems, and this coordinated spontaneous activity appears to be the underlying mechanism.

Not only are spontaneous, stereotypic activations of synaptic terminals, synapses, and neural pathways in the embryo and fetus needed to achieve circuit development, maturation, fine-tuning, and maintenance [14,45,48,54,75,79,108], they also are essential in synaptic remodelling through selective eliminations [103]. Silent "trial" synapses are maintained only if they are functionally relevant to developing circuits, with the connections used most frequently becoming established "permanently" [16]. As the sense organs mature, however, specific inputs at specific times are essential for normal sensory and related cortical development, as the brain comes to depend increasingly on exogenous activations from sensory experiences [54,86,90,122].

Sensory Dominance of Visual Input Processing

The essence of waking brain function in the absence of volitional activity is the processing of sensory input, the great preponderance of which normally is visual. Wide regions of cortex, including many cortical fields, apparently interact during even simple visual tasks [51]. Of over 52 areas of macaque monkey (*Macaca fascicularis*) neocortex, 25 are devoted solely to visual processing, including visuomotor performance. Another seven areas process visual information but are multimodal, some also processing auditory and/or somatosensory inputs. The 32 areas together cover over one-half the surface of the brain [109,139].

A very rich subcortical network interconnects the cortical visual areas [152]. For example, each visual area in the owl monkey (*Aotis trivirgatus*) projects to approximately five to 15 subcortical structures and nuclei, many closely related to motor performance [48]. Similar conditions also apparently apply to the brains of tree shrews (*Tapaia glis*), bush babies (*Galago senegalensis*), and the domestic cat (*Felis domesticus*). In the cat, 40% of the neurons in the primary visual cortices are sensitive to both visual and auditory stimuli [25].

Further indication of the overwhelming sensory dominance of visual systems comes from the requirement of over 2/3 of the 5000–7000 vital (lethally mutable) genes of the fruit fly (*Drosophila*), for normal assembly of optic ganglia and compound eyes, and of about 50% of all neurons to serve visual functions [132]. And the regulatory homeobox variant *Pax-6* at the top of the cascade for eye development, which is a master control gene in both vertebrates and *Drosophila*, is interchangeable between them [102].

Sensory Information Processing Interferes with Dynamic Stabilization

There is an intrinsic basis (the "fundamental dogma" [105]) for potential incompatibilities between the brain's endogenously initiated nonutilitarian DS of circuitry and the simultaneous occurrence of exogenously-initiated processing of ongoing sensory input (primarily firing at 14–30 Hz; the beta band); learning and memory involve many of the same cortical regions that process sensory information and control motor output [137]. Therefore, for example, neuronal activity circulating in cortical and thalamic networks is modified by activity engendered by incoming sensory information [141]. A classical example of sensory interference is blocking of the alpha rhythm (see later) of restful waking by alerting stimuli [87].

Information processing and firing in the gamma band. Since processing of visual information interferes with refreshment of

infrequently used circuitry, any characteristic electrical activity in the visual cortex during visual processing that supplements firing in the beta band also would be a candidate for the source of interference. Such a candidate has come to the forefront in recent years in the form of synchronous, relatively fast, rhythmic spike bursts in the gamma band (30–80 Hz) that begin to fire in many cells of the striate and prestriate cortex of cats and monkeys upon receipt of effective visual stimuli.

Synchrony of this firing is thought to play a crucial role in combining different visual features of objects [27,33,122], and it may be the neural correlate of awareness [23,66]. This firing appears to have its origin in rhythmic, intrinsic bursting of pyramidal excitatory cells ("chattering cells") in cortical surface layers [34].

The assignations become even more likely with the knowledge that fast, synchronous, gamma-band firing is a general property of brain networks during information processing, including sleep, particularly REM dreaming [66]. For example, gamma-band firing (of intracortical origin) occurs in the primary and secondary auditory cortices during audition, coordinated and modulated by the acoustic thalamus [2].

Although it is suggested that high-frequency beta-band and gamma-band firing induced exogenously in the processing of sensory information interfere with the low-frequency spontaneous firing of nonutilitarian DS, conflict between firing in these different frequency ranges is not intrinsic. When firing in both ranges is induced endogenously during sleep, it occurs cooperatively.

NON-SLEEPING VERTEBRATES

Sightless Cave-Dwellers

One group of nonsleeping vertebrates consists of genetically sightless cave-dwellers, known as "troglobionts" (also called "troglobites"). Numerous studies, including lengthy breeding, have yielded no evidence of the existence of sleep [5,96,111].

The vagal lobes and forebrain of some piscine troglobionts are enlarged, associated with the importance of chemoreceptive communication in dark caves [96,101,138]. The superficial neuromasts on parts of the head of the Mexican blind cave fish (the tetra, *Astyanax mexicanus*, i.e., cave-dwelling populations of *A. fasciatus*) are increased in number [148]. There is a dense, well organized somatosensory representation in the optic tectum, although there is no tectal response to auditory or lateral line stimuli [142]. The latter elaborations could contribute to hypersensitivity to water movements (self-induced in piscine troglobionts) and enhanced localization, avoidance, and discrimination of objects.

Some vertebrate troglobionts alternate periods of activity and rest, but exhibit no locomotor periodicity [96,138]. Troglobiontic salamanders, which also possess a lateral-line organ, appear to be resting at all times or moving very slowly [28]. Some piscine troglobionts have periods of inactivity, described only as "rest." In more than 1 year of study, 30 blind catfish (*Typhlobagrus kronei*) were "actively swimming in the aquarium at all times . . . and accepted food at any time" [97].

In detailed studies by Gertychowa [31], "[t]he observations of other authors that the Mexican blind cave fish is a continually active fish, which has no periods of rest, were confirmed." Breder [5] describes its movements as "aimless wandering." It can be concluded that some vertebrate troglobionts swim continuously, others rest lengthily, but none sleeps. Lengthy rest by some species is not surprising in nutrient impoverished cave environments.

Sharks

The fossil record of sharks, the oldest jawed fishes, extends back at least 450 million years. "Modern" lineages arose in the Jurassic, including three streamlined lines adapted largely for preying on teleosts. Shark evolution was essentially complete by the end of Cretaceous period, by which time most living families had appeared. The remaining living genera evolved in the Tertiary during the Cenozoic rebound from the wide-ranging extinctions at the end of the Cretaceous. The morphology, ecology, and behavior of living marine elasmobranchs (i.e., sharks, skates, and rays) are the most diverse of any marine-vertebrate group except teleosts [9,67].

The body form of many sharks is well-adapted for efficient cruising. Some species in the families Carcharhinidae, Triakidae, Sphyrnidae, Hexanchidae, and Lamnidae apparently swim continuously, although many others sleep [13,20,21,62]. Most carcharhinids (requiem sharks) range far into the great ocean basins, singly or in small to large schools; many are migratory—often induced by seasonal changes in water temperature. Carcharinoid schooling—conspicuous in all fishes in pelagic (open water) habitats [149]—rarely is as cohesive as that of teleosts [99]. Although many carcharinoid species swim continuously, some rest "motionless" on the bottom for extended periods [20,21,67].

Some Triakids (e.g., houndsharks, smooth-hounds, topes) are very active, swift swimmers, such as the tope or soupfin shark (*Galeorhinus galeus*), a species also believed to swim continuously. The dusky smooth-hound (*Mustelus canis*) patrols constantly on the bottom while seeking food, but congeners (members of the same genus) of both species that also patrol, sometimes rest on the bottom [20]. Sphyrnids (e.g., bonnethead, hammerhead, and scoophead sharks) also are very active swimmers, at times forming large migratory schools. Scalloped hammerheads (*Sphyrna lewini*) often are seen in large semistationary schools (schooling at a more or less fixed location) [20,21,62,104]. The Pacific sevengill hexanchid (*Notorynchus maculatus*) ". . . swims constantly and rarely rests on the bottom" [41].

The family Lamnidae includes large to gigantic mackerel, porbeagle, great white, and mako sharks. Five lamnoid and two alopioid (thresher sharks) species, and 13 species of tunas (tribe Thuninni) are "partially warm-blooded"—able to maintain a body temperature significantly above external ambient values. This is achieved by a high level of muscular activity, and by energy conservation via extremely efficient heat-exchanging retia mirabilia—systems of parallel arterioles and venules in close contact, which act as physiological barriers to loss of metabolic heat. Partial warm-bloodedness is facilitated by extraordinarily high oxygen carrying capacities of the blood.

Body temperatures higher than ambient support greater speed, faster and more efficient digestion, and niche expansion (i.e., an ability to range into colder waters). Because of the great energetic costs involved in maintenance of a high-speed lifestyle, the ability to swim rapidly must be presumed to be critical to the success of partially warm-blooded fishes [3,26,37,80,118].

Because the lamnids also are superbly streamlined, fast-swimming, active, pelagic, and epibenthic (bottom to 200 m above), one might expect them, also, to swim continuously. Indeed, "[i]t is probable that all of these fast-moving sharks swim constantly and do not rest on the bottom at any time" [40]. Sandtiger sharks (*Odontaspis taurus*) "spend their life continually swimming" [70]. It can be concluded from the previously mentioned review that many sharks swim continuously.

Sharks, several tuna species, the eastern Pacific bonito (*Sarda chiliensis*), and the Atlantic mackerel (*Scomber scombrus*) lack a gas bladder, usually comprising 4–6% of body volume in marine teleosts [61]. Many of them are obligate continuous swimmers, aerating their blood by "ram gill ventilation." Without also gaining lift by swimming continuously, they would sink [22]. The advan-

tage of giving up the gas bladder appears to be increased vertical mobility, particularly near the sea surface [72].

Teleosts

Earliest teleosts (bony fishes) appeared in the Middle Triassic, about 235 million years ago. The main line of evolutionary progression was through a series of generalized carnivores with increasing improvements in basic feeding mechanisms, more powerful swimming, greater agility, and greater potentials for adaptive radiations. All major phyletic lines were established by Cretaceous times, occupying both marine and fresh-water environments.

Teleosts weathered the extinctions at the end of the Cretaceous comparatively unscathed, prefacing a very marked increase in their diversity and abundance. The teleost "explosion" of the early Eocene (about 55 million years ago) was the most dramatic evolutionary radiation in vertebrate history, numerically eclipsing that of both mammals and birds. Teleosts not only are the dominant vertebrate group in oceans and continental waters, they have the most diverse morphology, ecology, and behavior [44,49,61,67,74, 136].

Daytime-schooling, reef-dwelling teleosts. Nocturnally feeding teleosts that inhabit coral reefs include another nonsleeping group. These engage in a widespread practice of schooling relatively stationarily during the daylight hours. The schools break up at nightfall, as individuals scatter to feed on small invertebrates. Smallest juveniles may feed on plankton in the water column in "feeding clouds;" when threatened, they descend to the reef. The pattern of diurnal schooling and solitary nocturnal feeding occurs in many perciforms and is highly characteristic of silversides (*Pranesus insularum*). It may be universal among inshore clupeids (herrings), the pelagic members of which also form highly polarized schools [42–44,59,76].

Scombroid teleosts. Other continuously swimming teleosts belong to the family Scombridae—including tunas, mackerels, bonitos, and albacores. Scombrids range the seas of the world, often over water so deep that contact with the bottom is lost [40]. Continuous scombroid swimming has coevolved with extremes of adaptations for reduced drag, efficient, fast cruising, and high levels of energy utilization [72,73,80]. "The tuna . . . swim continually, never stopping to rest;" ". . . all life's activities . . . are done on the move . . . [p]ersistence of sustained swimming is impressive . . . [t]ime of day, temperature, dissolved oxygen, and food deprivation have little influence on sustained swimming" [71–73].

Tunas are basically warm-water species [84], capable of highly efficient, long-distance travel in open waters. Some cross the great oceans [78]. Having very efficient peripheral or cutaneous heat exchangers, and great weight and thermal inertia, the highly migratory bluefin tuna group (*Thunnus*) penetrates far into much cooler waters [115,123]. The bigeye tuna (*Thunnus obesus*) usually inhabits still deeper and colder water [18,19]. It can vary whole-body conductivity by a factor of 100 by disengaging its heat exchangers during ascent from cold to warm surface waters, and reengaging them to conserve heat when returning to the depths [37].

Many mackerels (including the Atlantic mackerel), lacking heat exchangers, tend to stay in the warm oceanic surface layer. The very slender, fusiform-bodied wahoos (*Acanthocybium solandri*) are migratory, epipelagic (surface to 200 m deep) and oceanic, found around the world in tropical and subtropical waters [40,60, 130].

Schooling by scombrids. Migrating and hunting scombrids generally form large, highly-polarized schools [120], which tend to be of mixed species, of 100–5000 individuals. There is a strong tendency to assort by size, with larger fishes travelling in smaller

schools. Schooling may begin as early as postlarval stages [19, 116]. It depends largely, but not exclusively, on vision, as schools usually disperse in the dark [73,95]. The pronouncedly schooling mackerel may disband and reform dense schools with daylight variations [116], a strong indication that the urge to school is influenced strongly by "seeing conditions" and the amount of visual input.

Obtaining the Essential Benefits of Sleep by Schooling

Schooling has been regarded primarily as a social grouping based on mutual attraction [119]. But individuals continually reappraise the costs and benefits of being social, as reflected in decisions to join, stay with, or leave aggregations [99]; for example, in mixed schools of two species of juvenile parrotfishes (Scaridae), one species continued to school while the other sought shelter when threatened with predator models [38].

Roughly 2000 marine and 2000 freshwater piscine species engage in fully developed schooling [119]. The habit is strong and rigid, with departures from it being associated with special circumstances [6]. Some teleosts school from the beginning of independent locomotion until death, including periods of breeding (except courtship). Others school only as newborn or fry [59]. Among continuously swimming fishes, schooling is an even more characteristic phenomenon than partial warm-bloodedness.

Nonscombroid schools usually are composed of conspecifics, of similar age and size, engaged in the same activities at a given time, with a high degree of synchrony and polarized swimming [72,88,99]. Schoolers act in concert, moving forward simultaneously, keeping equal distances apart, and changing direction at apparently the same moment, even during complicated evasive maneuvers. There may be little change of position in a well-knit school, but in a looser one individuals constantly shift as they change speed [119]. During internal "churning," one member after another becomes exposed peripherally [6].

School members usually are equipotential, and schools, just as pods (aggregations in contact) and shoals (unpolarized, unsynchronized aggregations), usually are leaderless. For example, all the saithe (*Pollachius virens*) in a still, unpolarized ball follow the first fish to move out, all polarized on parallel courses [146], and in pods of young catfishes (*Ameiurus melas*), "[l]eadership always falls to the fish which happens to be in the van . . . or to the individual farthest in that direction [of turning] [4]."

Schooling may optimize foraging benefits (as, also, in shoals)—being quite prevalent among plankton feeders—may confer hydrodynamic benefits, and the visual contacts may facilitate juvenile growth (social facilitation). Although it can play a large role in protecting small fishes from predation, through synchronized cooperation (confusing predators) and increased vigilance, predation is facilitated in some circumstances. Illustrating that schooling under threat of predation generally is adaptive, is the reaction of many group-living fishes to an approaching predator: they clump more closely and swim away in a polarized school [6,7,59,63,99,116,119,149].

But protection hardly could apply for large sharks, perhaps not even for largest tunas, which lose their otherwise strong propensity to form tightly organized schools and may occur solitarily [6,40]. Just as some reef-dwelling fishes school inactively during the day, so do some large sharks. For example, many hammerheads school semistationarily during the day and disperse and move into deep water or close to the bottom at night to feed [20,21,62,104]. Not only is protection unlikely to be needed during this heretofore puzzling, semistationary schooling, hammerheads school even when no possible predator is present [20].

A basic function of schooling. The key consideration pointing

to a basic function of schooling, of previously overlooked significance, relates to brain activities facilitated by the lesser requirements for sensory processing in school members (see later). The great majority of fishes, at inner positions of schools, need not exercise the full range of their sensory capabilities—they have no need to "listen," "smell," "taste," or process complex visual information. They need only maintain awareness of their position with respect to nearest neighbors, to which the lateral line contributes (see later) and which sometimes is achieved directly through contacts.

On average, the amount of sensory processing carried out in the brains of schooling fishes is greatly reduced compared to the amount in alert, solitary swimmers. In effect, the burden of sensory processing is shifted from individuals to the entire school collectively. In functional terms, the act of daytime schooling (sometimes even referred to as "resting" schooling [76]) provides the benefits for these fishes that sleep and restful waking provide for other fishes. Consistent with this interpretation, when dense vegetation becomes available, schooling bluegills (*Lepomis macrochirus*) disperse and seek cover in it [38]—a site at which there would be less sensory input than in schools, and at which even less sensory processing would be required.

One might have suspected that schooling, sleep, and restful waking are analogous phases of inactivity from the knowledge that schooling can be even more cyclically stereotyped than restful waking and sleep, and that it often is temporally coincident with them. Thus, fishes in large daytime resting schools stream off their patchreefs to their feeding grassbeds at very predictable times after sunset; they return along the same routes just before sunrise, at the precise times that other fishes are terminating and initiating rest or sleep [38,77]. Also suggestive of analogy, behavior in schools would apply as well to fishes resting or sleeping in aggregates. Usually there is no apparent behavioral differentiation, no leader or dominance, no persistent tie or pair bond, and no overt aggression. Additionally, schooling only as newborn or fry in some species parallels the need for greater amounts of sleep in fetuses, newborn, and young of mammals and birds than in adults [55,56].

The contact schools (pods or "tightly packed masses") of striped mullet (*Mugil cephalus*) and rockfishes (*Sebastodes paucispinis*) [59], and of the young of siluroid fishes, the catfishes and bullfishes (e.g., *A. melas*) [4], remind one of Weber's [147] description of sleeping bichirs (*Polypterus*) packed together like sardines in a box (". . . wie in einer Ölsardinenbüchse dicht zusammengepackt . . . ").

Reduced needs for complex visual processing probably also underlie the attraction between two individual conspecifics, and even between noncongeners of commensurate size, leading to their tendency to swim close together. Thus, for several species, a mirror image is not as conducive to close-knit swimming as a conspecific. With conspecifics, including mackerel (*Pneumatophorus grex*) and oceanic bonito or kawawawa (*Euthynnus affinis*), even when separated by transparent partitions, close, parallel swimming may continue for days, or as long as parallel orientation can be maintained [39,119].

That schooling functions sometimes transcend reduction of visual processing is shown by findings with temporarily blinded individual saithe, although not with Pacific (chub) mackerel (*Scomber japonicus*) or jewel fish (*Hemichromis bimaculatus*). Blinded individuals joined, and maintained indefinitely, their position in actively swimming schools of normal saithe. Their schooling, however, was not normal, as reaction times were slower. Schooling was not possible, however, if the lateral line also was sectioned. Lateral line section, alone, led to more accurate side-by-side orientation of neighbors (with eyes more closely in apposition) [95]. This more accurate orientation is consistent with

vision having come to bear the entire sensory burden of maintaining synchrony, polarization, and orientation.

The lateral line enables a fish to perceive water currents and turbulence directly around its body [113] and appears to be involved in monitoring speed and direction of travel of nearest neighbors, functions that overlap partially with those of vision [95] (in fact, there is a visuo-acousticolateral interaction in the torus semicircularis [113]). As a station-keeping device, for example, the lateral line of sprats (*Clupea sprattus*), which, "hardly ever collide," apparently senses earliest changes in a neighbor's movements by monitoring the neighbor's tail [24].

Consonant with these findings, schooling of tunas can occur in the absence of both moonlight and bioluminescence [134]. In most species, visual input apparently is essential; for example, for the young catfish (*A. melas*), "[n]either blinded fishes nor normal fishes in the dark ever aggregate . . . " [4]. Nor does any piscine troglobiont school.

RESTFUL WAKING AS THE EVOLUTIONARY PRECURSOR OF SLEEP

That restful waking, which typically is an antecedent to sleep, probably also was the evolutionary precursor of sleep, is indicated by the continuity of electroencephalographic (EEG) changes from wakefulness to restful waking to sleep. These phenomena also are suggestive of the close reciprocal relationship between reception of visual information and sleep.

In humans, the beta rhythm (14–30 Hz) of waking gives way to the alpha rhythm (8–13 Hz) on either closing the eyelids or merely being deprived of patterned visual stimuli. It ceases on opening the eyelids and conscious analysis of the visual environment. As one lapses into NREM sleep, the alpha rhythm slows, fragments, and disappears, as it is replaced by slower waves in the sequence: spindles, delta waves, and the slow sleep oscillation [65,68,87,114,150]. This close association of the alpha rhythm with cessation of the reception of patterned visual information and eyelid closure suggests that one of its principal functions is the initiation of consolidation of recently acquired visual memories, the refreshment of which in mammals and birds, after an initial consolidation, apparently occurs primarily during REM sleep [58].

Brain waves closely related to the alpha rhythm occur in other mammals and in birds. During restful waking, with the eyelids open or partly closed, there also are increases in synchronous, slow-wave EEG activity; further increases occur on eyelid closure [92,112,135] or in darkness [93]. Contrariwise, slow-wave EEG activity decreases on alerting a restful waking bird [121].

The comparable EEG activity in reptiles (and some teleosts and amphibians) is a superimposed high-voltage, arrhythmic spiking that emerges during quiescence and sleep. This is related, and similar in waveform, to mammalian ventral hippocampal spikes, which are rare or absent in active waking, augmented in restful waking, and increase still further during NREM sleep. For example, in crocodilians and iguanas, such spiking increases on eyelid closure. Conversely, spiking is reduced or eliminated on eyelid opening by sleeping iguanas, or arousal of sleeping tortoises and chameleons [12,30,36,129].

Concerning the background frequency in reptiles, it generally declines by approximately 50% on initiation of the sleep state; for turtles, the decline is from 11–13 Hz to 6–8 Hz [45]. In the catfish (*Ictalurus nebulosus*), low frequency (8–12 Hz) oscillations in the optic tectum during waking give way to lower frequencies (8–10 Hz) during sleep [53].

Because the alpha rhythm arises in posterior temporal and primary visual regions of the neocortex [114,150], and ectothermic vertebrates have only a primordium of neocortex, they are not

expected to have an alpha rhythm. Nor is it unexpected that the brain waves that begin when they close their eyelids are similar to mammalian hippocampal spikes, for even the most primitive vertebrates have a hippocampus, sometimes called the "oldest" cortex.

IMPLICATIONS OF THE ECOBEHAVIOR OF TROGLOBIONTS

A major clue to the basic function of sleep comes from the ecobehavior of nonsleeping, genetically blind troglobionts. The crucial factor relieving troglobionts of a need for sleep appears to be the total absence of visual input. This translates to the total absence of the brain's need to process complex visual information. The increment in neural processing needed to accommodate increased somatosensory representation in the optic tectum [142] and the increased numbers of superficial cephalic neuromasts [148] would be insignificant compared to the decrement accompanying absence of vision.

Because the low level of processing of sensory input to troglobionts probably interferes to a relatively minor degree with refreshment of memories, there is no need to engage in sleep to bring about reduction or elimination of sensory processing. Furthermore, in the more or less featureless, monotonous, cave-pool habitat, the accumulation of memories gained through experience would be minimal, with lesser needs for refreshment.

The suggested implications are that: (1) the spontaneous refreshment of memory circuits by the brain during sleep is not fully compatible with the processing of complex visual information during active waking; and (2) the basic function of sleep is to reduce or eliminate the reception and processing of sensory information, chiefly visual, so that the spontaneous refreshments can be carried out with minimal interference.

BASES FOR ABSENCE OF REST OR SLEEP IN CONTINUOUSLY SWIMMING FISHES

Four major influences are proposed for the absence of a need for rest or sleep in continuously swimming fishes: (1) most inherited memory circuits need no refreshment, as they are maintained by functional DS during continuous day and night swimming; (2) by reducing needs for sensory information processing, schooling provides the essential benefits of sleep and restful waking; (3) life in the largely featureless pelagic environment is comparatively routine, with a need to store relatively few experiential memories; and (4) input and processing of visual information are at a low level or nil during a large fraction of nighttime activity.

Influences of Continuous Swimming

These four influences not only have eliminated the need for rest or sleep, in many cases they have led to the coevolution of adaptations that preclude rest or sleep. Continuously swimming sharks and many scombrids, as mentioned earlier, are obligate "ram gill ventilators." They would suffocate if they were to cease swimming more than momentarily [18,71–73,146]. Some marine mammals also must swim continuously to maintain their orientation and to emerge at the surface at short intervals to breathe, but while doing so, they are able to sleep alternately with only one brain hemisphere at a time (see later) [81–83,91].

In a striking example of this need, placing surface-trolled skipjack tuna, *Katsuwonus pelamis* (41–61 cm long), in a small livewell (81 × 109 × 170 cm) invariably is fatal; in their "frantic" attempts to swim rapidly enough to gain sufficient gill ventilation, they suffer fatal, blunt-force injuries through repeated head-on collisions with the livewell walls [131].

Most inherited memories of continuously-swimming fishes probably are maintained by functional DS, that is, through frequent, around-the-clock use. Inherited memories include, at least, motor circuits, circuits for autonomic functions, and circuits for instinctive (not involving learned components) responses, including those associated with reproduction. Concerning motor mechanisms, a high proportion of piscine bodies are comprised of the muscles used in forward propulsion [80], but probably not a day goes by without all muscles being in frequent use. Any inherited or experiential memories not adequately maintained through use might be refreshed during schooling or nighttime swimming (see later).

Influences of Schooling

With the brain's need to process sensory input during schooling greatly reduced, in some circumstances possibly dispensed with almost entirely, conditions during schooling would be more or less equivalent to those during restful waking or sleep—favorable for refreshing memories, with minimal interference from sensory processing. The nonpelagic fishes that are most likely to have their schooling provide these benefits would be the reef-dwellers that school throughout the day and disperse at night to feed.

With daytime schooling providing the essential benefits of sleep, some schooling fishes probably lead no less challenged an existence during their nighttime feeding than is led during the activity periods of fishes that rest or sleep. Challenges of nightly experiences would be met through learning and memory, with the memory circuits refreshed during schooling.

It will be evident that benefits similar to those obtained by schooling fishes also probably would apply for migrating members of avian flocks. The reduced need for sensory processing when flying continuously in formation, or merely as a cohesive group, in an essentially featureless environment and at night (even for solitary birds), could account for the ability to sustain such continuous activity, without a need for rest or sleep. Similar considerations may apply to varying degrees to individuals in other nonpiscine aggregates, even those of sighted invertebrates, such as squids and cuttlefishes.

Influences of a Comparatively Routine, Pelagic Existence

Many continuously swimming fishes are exposed repeatedly to essentially the same topographically featureless, largely epipelagic, and mesopelagic (200–1000 m deep), environments that their ancestors encountered over a span of many millions of years. Lengthy existence in these unchanged or little changed environments may be reflected in the very little outward change seen in such continuously swimming, pelagic fishes over millions of years [67].

While pelagic fishes do not encounter identical circumstances every day, differing circumstances probably are encountered sufficiently frequently to have memories of them maintained by functional DS. Memories of less frequent events might be refreshed by nonutilitarian DS during schooling and nighttime swimming. It is not implied that scombrids are incapable of learning and storing memories of learned responses. Indeed, learning is believed to occur in all teleosts under natural conditions [119]. Just as for scombrids, large, continuously swimming sharks may be capable of learning simple associations and storing memories for future use, but their mode of life is such that these capabilities may be called upon rarely.

Patterns of escape, hunting, prey capture, and reproduction by continuously swimming, pelagic fishes are included among inherited memories. Except for very large fishes, predator avoidance and prey capture behaviors usually would be in use on a more or

less daily basis. This mode of existence deviates significantly from that of nonpelagic fishes having daily cycles of activity and inactivity. Learning plays an important, rather than minor, role in nonpelagic teleosts, in modifying feeding, foraging strategies, and responding to environmental variability, particularly seasonal [119]. Only epipelagic and mesopelagic marine environments (the "Oceanic Province") are sufficiently unvarying to allow a completely stereotypically behaving predator to survive.

Even reproductive systems (and behavior) of continuously swimming teleosts receive more continuous use and occur much less competitively than is typical for terrestrial vertebrates. In this connection, many teleosts apparently mate indiscriminately, gonadal sex reversal occurs in some during development, some are self-fertilizing, others are simultaneous hermaphrodites, in still others males do not exist (unisexual gynogenetic species) [136].

Temperature permitting, reproduction throughout the year is characteristic for scombrids [19,117,144]. Similar circumstances prevail for small pelagic fishes. For example, among the Clupeoids, the anchoveta (*Engraulis ringens*) in Peruvian waters spawns at low intensity throughout the year, with peaks in August–October; the sardine (*Sardinella anchovia*) in Venezuelan waters also spawns throughout the year, most intensely in December–April. It is no coincidence that continuously swimming, daytime-schooling, tropical reef fishes, such as carangids (jacks or pompanos), lutjanids (snapper-like fishes), and pomadasyids (grunts) also spawn the year around, with a peak in the coldest months [69].

A similar fairly clear-cut case cannot be made for sharks. All those of interest in the present connection are viviparous, with relatively long gestation periods. Their young are born as efficient, active predators. No period of learning or indoctrination is needed. This is an essential attribute for a predatory, pelagic, viviparous species, as the newborn face immediate intense selection for rapid growth and aggressiveness [151]. Although little is known about the reproductive biology of most sharks, it appears likely that of all the inherited memories for bodily functions, those for reproductive activities are the ones most likely to be used infrequently. These memories, then, probably are refreshed during schooling or, in the large pelagic predators that sometimes do not school, during swimming at night.

In their many millions of years of existence in the relatively constant epipelagic and mesopelagic conditions (including interactions with prey and predators), continuously swimming fishes very likely encountered all potential contingencies, and incorporated responses to all of them into their repertory of inherited memories (excepting possible interactions with humans and conditions of human origin). It would follow that, of all sighted vertebrates, the large, continuously swimming, pelagic fishes probably give the most purely instinctive (inherited) behavioral responses. We may be seeing a reflection of this in the assessment of Philippe Cousteau [22] that, ". . . the shark is the most mechanical animal I know . . ." An example is failure of many captive carcharhinoid sharks to use their opaque, nictitating lower eyelids to shield their eyes from artificially introduced bright light, though they struggle violently to avoid the light. On the other hand, the eyelids are employed promptly against naturally occurring hazards [32].

In the same vein, and reminiscent of circumstances in many invertebrates, some complex piscine behaviors are performed precisely the first time, developing with remarkable stability despite environmental perturbations [47]. Numerous examples could be given of behaviors that develop, not as a result of experience (i.e., learning) but as a consequence of maturational changes. For example, swimming and feeding modes of Pacific mackerel, develop in three stages, with the successive development of the caudal fin,

jaws, and pharyngeal teeth [127] (i.e., purely inherited memories are involved).

Influences of Nighttime Swimming

A consideration of this topic highlights a crucial difference between terrestrial and aquatic (and aerial) vertebrates, as regards to limitations on activity that usually must be imposed during refreshment of memories. It is essential that terrestrial vertebrates remain in a nonlocomotory state (resting or sleeping) during periods of reduced visual input and processing, because vision almost always is essential to guide locomotion. Many fishes (and birds), on the other hand, can be fully active under conditions of greatly reduced or excluded visual information.

The great reduction in sensory information processing, particularly visual, in those continuously swimming fishes that have no need to spend the entire night hunting, makes available lengthy periods for refreshment of memory circuits. Such benefits of nighttime swimming would accrue particularly to those continuously swimming fishes that may have the greatest need for them, namely, the very large fishes that sometimes do not school. Sharks would benefit less than teleosts, as their visual acuity is relatively poor [32], with lesser processing of complex visual information, even in bright light.

NO EVIDENCE OF UNIHEMISPHERIC SLEEP IN FISHES

Dolphins engage only in NREM sleep, and with only one brain hemisphere at a time, as determined by EEGs. They accomplish this by closing the lids of only one eye at a time, usually the one on the opposite side of the sleeping hemisphere. Only the lids of the "sentinel" eye, usually on the same side, remain open [81]. This is feasible for dolphins because their optic nerves cross over virtually completely in the optic chiasma [17].

Of all endothermic vertebrates, some marine mammals come closest to confirming the thesis that the basic function of "sleep is of the brain, by the brain, and for the brain" [45]. Thus, some dolphins and porpoises show the least dependence on ancillary benefits of sleep. Certain of them, such as the sea porpoise (*Phocoena phocoena*) and the Indus (*Platinista indi*), and Amazonian (*Inia geoffrensis*) dolphins are on the move continuously (with, at most, momentary immobility) while engaged in unihemispheric NREM sleep (the Indus dolphin, which is blind, is a possible exception, but there is no reason to doubt that like other dolphins, it also sleeps unihemispherically). The bottlenose dolphin (*Tursiops truncatus*), on the other hand, requires some respite from continuous swimming—in the form of quiet "hanging" behavior (25% of recorded time when studied in an aquarium), during which movements of its flippers maintain an orientation that allows periodic breathing [81–83,91].

The optic nerves of birds also cross over virtually completely [133], and many birds also sleep with only one brain hemisphere at a time. As soon as the lids of one eye are closed, the half of the brain on the opposite side falls asleep. Avian sleep and eyelid closure are so closely associated that it is asserted that the eyelids close only in sleep, and that eyelid closure is the equivalent and most reliable behavioral index of sleep [1,52,128].

Despite possessing this ability, there is no evidence that birds sleep with only one brain hemisphere at a time while flying thousands of miles for many days. In the conditions encountered in flight, there is little need to exclude visual input, as there is little or no detail to be seen, and almost half of the time is spent in dim light or darkness. Any employed terrestrial or celestial cues would not require detailed visual analysis. On lengthy flights, then, the

avian brain also might get the essential benefits of sleep with both eyes open.

In view of the existence of unihemispheric sleep in birds and some marine mammals, and the fact that there also is complete optic nerve decussation in many fishes [107], one must consider the possibility that some continuously swimming fishes sleep unihemispherically. Concerning this possibility in sharks, candidate members of the Lamnidae, lacking nictitating lower eyelids (NLEs), would have to occlude a pupil with the upper and lower lids, rotate the eyeball to occlude it, or severely constrict the iris. For the other families all having NLEs, sleeping unihemispherically, with unilateral occluding of a pupil by the opaque nictitating membrane would be possible.

However, the failure of sharks to employ NLEs or eyeball rotation for purposes other than corneal protection, a generally reduced contribution of vision to their activities, except at comparatively close quarters, and the absence of any observation of eyeball rotation, or closure of eyelids or a nictitating membrane during continuous swimming (except during prey consumption or close approach to inanimate objects), renders it very unlikely that they engage in unihemispheric sleep during sustained activity [20,32,35,64,145].

Much the same situation applies to teleosts, except that with rare exceptions, no teleost has opaque ocular structures that could be used to occlude the pupil, only a few can materially alter the size of the (generally round) pupils, and the changes are small and rather sluggish. To occlude their pupils almost all teleosts must rotate their eyeballs [145,147].

The most weighty evidence against the occurrence of unihemispheric sleep in continuously swimming teleosts is that neither in captivity nor in free-living conditions has a continuously swimming teleost ever been seen with a pupil occluded by rotation of its eyeball—despite the prominence and conspicuousness of piscine eyes and untold numbers of observations of scombrids over many years in various captive conditions. For example, a catch of skipjack tuna (1–3 kg) was observed in captivity in a large pool for 5-1/2 months. The fishes remained healthy and schooling, and never were seen to rest or occlude their pupils [85].

ANOTHER PERSPECTIVE ON SCHOOLING FAILURES IN THE ABSENCE OF VISION

It is proposed that the breakup of schools of some teleosts in the dark, and the failure of piscine troglobionts and blinded teleosts to form schools, are not because the fishes lack the necessary nonvisual sensory means to form and maintain schools. Rather, these phenomena may result because there is no reception and processing of visual information in the brain in these circumstances, thereby eliminating a need for a principal function of schooling. In other words, the failure to school results from lack of "instructions to do so from the brain," which cease "being given" when visual processing no longer interferes with refreshment of memory circuits. In those blinded fishes that school (e.g., saithe), and sighted fishes that school in the dark, other advantages of schooling must become determinate.

PISCENE FLEXIBILITY REGARDING ACTIVITY AND SLEEP

Within the framework of the paradigm presented for the absence of a need for sleep in continuously swimming fishes, it can be suggested that periods of inactivity might be acquired and dispensed with in response to relatively minor alterations of behavior and ecology. Indeed, this is a common occurrence: nocturnal or diurnal fishes that otherwise have periods of inactivity, become active continuously when engaged in parental care of eggs

or brood members (predominantly male care with territorial defense) [38].

Although many fishes in aquaria exhibit diurnal cycles of activity, the uniform conditions encountered, inasmuch as they lead to a virtually routine existence, might favor continuous swimming in some fishes. Such an influence occurs with flounders (*Pleuronectes flesus*). Provided with a sand substrate, they buried themselves by day, swimming only in the dark of the night. When no sand was available at dawn, a flounder did not sleep, but continued to swim throughout the day and following night. With sand made available the next morning, it resumed its previous daytime inactivity [8].

In another example, minnows (*Phoxinus laevis*) were diurnal in an open aquarium, but became nocturnal when provided with a shelter [63]. Unable, at first, to sleep in a shelter and refresh memory circuits during the daytime, as they normally do, the minnows found it necessary to reverse phase, with memory circuit refreshment being carried out largely at night.

DID THE FIRST LAND VERTEBRATES SLEEP?

Since continuous swimming without sleep by some fishes is a highly derived condition, and many living fishes sleep [89,106, 147], the first land vertebrates also might have slept. From the present perspectives, this would depend largely on the extent of complex visual processing centrally in the brain. But no structure in the brain of a Carboniferous, osteolepiform, rhipidistian fish (e.g., *Ecosteorhachis nitidus*)—ancestral to amphibians (an ancestral relationship that remains in dispute [17,153])—appears to have been unusually expanded, with no evidence of optic lobe specialization. This is unlike the modern looking brains of the contemporary early ray-finned fishes, the paleoniscids, which had expanded optic lobes [50].

Data are not available on the brains of candidate panderichthyid fishes, which share many unique characters with, and are strikingly similar to, the earliest known tetrapods [49,74]. Nor are data available for the earliest known tetrapods, themselves, such as the Late Devonian *Ichthyostega* (often regarded as the most generalized, or primitive, tetrapod), *Acanthostega*, or *Tulerpeton*, the axial skeletons of which closely resemble those of osteolepiforms [49, 74,143].

Accordingly, based on available data, central, complex visual processing probably was not extensive, with complex retinal processing playing a relatively great role, as it continues to do in nonmammalian vertebrates and some mammals [57,58]. One can speculate that the first land vertebrates had progressed no further toward sleep than a state of restful waking. Some Carboniferous fishes (e.g., paleoniscids), however, probably slept.

SUMMARY—SCHOOLING, CONTINUOUS SWIMMING, REFRESHMENT OF MEMORY CIRCUITS

As noted earlier, continuous swimming without a need for rest or sleep is a highly derived condition, dependent on many specializations of morphology, physiology, and modes of life. At one extreme are the large fishes that sometimes do not school as adults, occupy essentially featureless, pelagic habitats, and lead a comparatively routine existence. Their memory circuits, of which those in the experiential category would be minimal, are maintained and refreshed by functional and nonutilitarian DS during schooling and swimming at night, with greatly reduced or nil visual information processing.

At the other extreme are the reef-dwelling fishes that school during the entire day and disperse at night to feed. In most regards, their daily experiences during feeding are no different from those of comparable fishes that rest or sleep. In entailing greatly reduced

needs for sensory processing, schooling provides them with the essential benefits of restful waking and sleep, that is, it provides favorable conditions for the refreshment of memory circuits that are not in frequent use.

Between these extremes lie the medium to large fishes that characteristically school, lead a comparatively routine existence, and occupy chiefly pelagic habitats. Their significant needs to refresh memory circuits, of which those in the experiential category also would be minimal, are met chiefly during daytime schooling and at night.

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