Behavioral, neurophysiological and evolutionary perspectives on unihemispheric sleep

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Abstract

Several animals mitigate the fundamental conflict between sleep and wakefulness by engaging in unihemispheric sleep, a unique state during which one cerebral hemisphere sleeps while the other remains awake. Among mammals, unihemispheric sleep is restricted to aquatic species (Cetaceans, eared seals and manatees). In contrast to mammals, unihemispheric sleep is widespread in birds, and may even occur in reptiles. Unihemispheric sleep allows surfacing to breathe in aquatic mammals and predator detection in birds. Despite the apparent utility in being able to sleep unihemispherically, very few mammals sleep in this manner. This is particularly interesting since the reptilian ancestors to mammals may have slept unihemispherically. The relative absence of unihemispheric sleep in mammals suggests that a trade off exists between unihemispheric sleep and other adaptive brain functions occurring during sleep or wakefulness. Presumably, the benefits of sleeping unihemispherically only outweigh the costs under extreme circumstances such as sleeping at sea. Ultimately, a greater understanding of the reasons for little unihemispheric sleep in mammals promises to provide insight into the functions of sleep, in general. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Unihemispheric; Slow-wave sleep; Sleep function; Sleep mechanisms; Sleep regulation; Functional lateralization; Predator detection; Aquatic mammals; Birds; Reptiles

1. Introduction

Animals spend their lives in two apparently mutually exclusive states, wakefulness and sleep. Wakefulness enables animals to adaptively interact with their environment, while sleep serves a vital [1], yet unknown function [2]. Sleep necessarily occurs at the expense of wakefulness, yet adaptive waking performance is contingent upon sleep [3]. Thus, animals face a situation in which sleep and wakefulness are inevitably in conflict. However, several animals have essentially side-stepped this problem by simultaneously engaging in both wakefulness and sleep; one cerebral hemisphere sleeps while the other remains awake, a unique state known as unihemispheric sleep.

The following review is intended to serve as a comprehensive synopsis on unihemispheric sleep. While significant reviews exist on unihemispheric sleep in aquatic mammals [4–6], no single source has incorporated the diverse and often obscure literature on unihemispheric sleep in other animals. Moreover, in the past few years a renewed interest in unihemispheric sleep has resulted in several significant findings that warrant discussion within the context of previous work on unihemispheric sleep. In the interest of providing the reader with an exhaustive review of the subject, we have incorporated virtually every study on unihemispheric sleep, including descriptive studies based on small sample sizes. Although conclusions based on such studies are necessarily tentative, their inclusion simultaneously highlights the breadth and limits of our understanding of unihemispheric sleep. Finally, throughout the review we present several speculative perspectives on unihemispheric sleep. In doing so, we hope to provide the impetus for developing further research and insight into unihemispheric sleep, and sleep in general.

We will discuss unihemispheric sleep at various levels throughout this review. The background, behavioral ecology and evolutionary history of unihemispheric sleep will be discussed for each taxonomic group in which sleep occurs unihemispherically; aquatic mammals (i.e. Cetaceans, Pinnipedia and Sirenia), birds, and possibly reptiles. When appropriate, significant parallels and differences between groups will be highlighted. For organizational
and historic reasons, much of the review will follow the chronological sequence in which discoveries were made. Following a discussion of each group, we will review the potential neurophysiological mechanisms involved in unihemispheric sleep, including a discussion regarding why only one type of sleep (i.e. slow-wave sleep, SWS) occurs unihemispherically. Although humans do not sleep unihemispherically, several related findings that hint at a tendency for unihemispheric sleep in humans will also be included. Throughout the review, promising areas for future research will be identified, especially those which may yield clues to the function of sleep. Finally, having demonstrated the adaptive advantages of being able to sleep unihemispherically, we will attempt to answer the more difficult, and rarely asked question: Why do most mammals sleep bihemispherically?

2. What is unihemispheric sleep?

A definition of unihemispheric sleep is necessarily contingent upon a definition of sleep itself. Sleep can be distinguished from wakefulness using both behavioral and physiological criteria. Behaviorally, sleep is characterized as a period of sustained quiescence in a species-specific posture or site, with reduced responsiveness to external stimulation. However, with sufficient stimulation sleeping animals rapidly return to wakefulness [7,8]. In mammals and birds, behavioral sleep is usually associated with two distinct cyclically alternating physiological sleep states: slow-wave sleep (SWS, also called non-rapid-eye-movement sleep, or quiet sleep) and rapid-eye-movement (REM) sleep (also called paradoxical or active sleep). Although changes in several physiological parameters distinguish SWS and REM sleep from each other and wakefulness (e.g. muscle tone, eye movements, autonomic function, etc.), changes in electroencephalographic (EEG) activity have received the most attention. During wakefulness, the EEG exhibits low-amplitude, high-frequency activity reflecting the activated (or desynchronized) state of the brain. In contrast to wakefulness, SWS is characterized by high-amplitude, low-frequency (or synchronized) EEG activity, often referred to as delta (<4 Hz) or theta (4–8 Hz) activity. (Note: In humans, SWS only refers to stages 3 and 4 of non-REM sleep, whereas in other animals SWS usually refers to all stages of non-REM sleep). EEG spectral power in the delta band is often defined as slow-wave activity. The amount of slow-wave activity is thought to reflect the intensity or depth of SWS [9–12] (but see discussions in Refs. [13–17]). In mammals, but not birds, sleep-spindles, brief bursts of high-frequency activity (e.g. 12–16 Hz in primates) also occur during SWS [18,19]. EEG activity during REM sleep is similar to that observed during wakefulness. However, REM sleep can be distinguished from wakefulness, in part, by a loss of muscle tone (intermittently interrupted by brief skeletal muscle twitching), rapid-eye-movements, suspended thermoregulation, penile erections and autonomic instability, including irregular heart and respiratory rate.

Although two types of sleep exist, only SWS is known to occur unihemispherically. The definition of unihemispheric SWS (USWS) is usually based almost exclusively on EEG activity. Unequivocal USWS occurs when one hemisphere shows unambiguous waking EEG activity, while the other shows unambiguous SWS activity. However, alert wakefulness and SWS are states that fall at the extreme ends of a continuum, characterized by a progression from a low-amplitude, high-frequency EEG during alert wakefulness to a high-amplitude, low-frequency EEG during SWS. Consequently, as discussed below, animals that show unequivocal USWS also display intermediate states (e.g. SWS in one hemisphere and a state intermediate between alert wakefulness and SWS in the other). Such states are often classified as an interhemispheric asymmetry in SWS, rather than outright USWS. While such a distinction might have merit, interhemispheric asymmetries in SWS and USWS appear to simply reflect different degrees of the same phenomenon. Along these lines, pending a functional reason for distinguishing between these states, Mukhametov [5] chose to refer to both states as USWS. Similarly, in this review, we will define USWS as an alternating interhemispheric asymmetry in SWS, associated with behavioral signs of wakefulness, such as unilateral eye closure (i.e. closure of one eye) and/or swimming. By referring to an interhemispheric asymmetry in SWS as USWS we do not intend to indicate that all waking functions remain intact and all sleep functions suspended in the “awake” hemisphere. Certainly, it is conceivable that the intermediate level of low-frequency activity in the “awake” hemisphere represents a further compromise between sleep and wakefulness; the hemisphere remains awake enough to meet the ecological demands for wakefulness, while still obtaining some of the benefits of sleep.

The phenomenon of unihemispheric sleep necessarily challenges the traditional definitions of sleep. For example, aquatic mammals that swim during USWS are clearly not quiescent. Such violations of the traditional definitions have led some to question whether USWS should be categorized as sleep, e.g. [20]. However, this apparent problem lies in the definition of sleep imposed, rather than the phenomenon of USWS itself. In the case of dolphins, which almost never sleep bihemispherically, to discount the presence of USWS on the basis of definitional problems is equivalent to saying dolphins do not sleep. Given the ubiquity of sleep in the animal kingdom [21,22], and the fatal consequences of not sleeping [1], such a conclusion seems unfounded. Consequently, as with any biological definition, the definition of sleep needs to evolve to encompass new discoveries, such as USWS.
3. Unihemispheric sleep in aquatic mammals

3.1. Cetaceans: dolphins, porpoises and whales

The order Cetacea is comprised of two suborders of exclusively aquatic mammals, Odontoceti (dolphins, porpoises and toothed whales) and Mysticeti (filter-feeding baleen whales) [23] (but see Ref. [24]). Based on fossil [25,26] and molecular [24,27] evidence, the closest living relatives to Cetaceans are the even-toed ungulates (Artiodactyla). Interestingly, within Artiodactyla, Cetaceans appear most closely related to the semi-aquatic hippopotamuses [28]. To date, USWS has been identified in four species from the Cetacean suborder Odontoceti (Table 1), however, the EEG has not yet been recorded from the suborder Mysticeti (see Lyamin et al. [29] for behavioral observations of sleep in a baleen whale).

3.2. Background of Cetacean unihemispheric sleep

Lilly [30] was the first to suggest that dolphins (Tursiops truncatus) could sleep unihemispherically:

In regard to laterализation of the sleep pattern, these animals sleep with one eye closed at a time. The eye closures are 180 degrees out of phase; it is rare to have both eyes closed at once … Alternate sides are rested alternatively.

Subsequently, Lilly [31] suggested that dolphins sleep with one eye open to “assure that the animal is always scanning his environment with at least half of his afferent inputs”. Although Lilly did not record unihemispheric sleep EEG activity, his behavioral results clearly anticipated future observations of such sleep in dolphins.

Recordings from the pilot whale (Globicephala macrocephalus; actually a type of dolphin) provided the first electrophysiological evidence for USWS in a Cetacean [32,33]. EEG activity was recorded from the parieto-occipital region of each hemisphere in a single whale. Interhemispheric asymmetry in the EEG, characterized by high-amplitude, low-frequency activity in one hemisphere concurrent with low-amplitude, high-frequency activity in the other hemisphere was observed during periods classified as “relaxed wakefulness”. This asymmetry tended to alternate between hemispheres. Although such sleep was classified as relaxed wakefulness rather than some form of USWS per se, these results provide the earliest EEG evidence for USWS in a Cetacean.

The recognition and comprehensive characterization of USWS in Cetaceans began in earnest in the early 1970s with research from Lev Mukhametov’s laboratory at the Severtsov Institute of Evolutionary Morphology and Ecology of Animals, USSR (now Russian) Academy of Sciences. Mukhametov, Supin and Polyakova [34] were the first to recognize the interhemispheric asymmetry during sleep in Cetaceans as USWS. To date, Mukhametov’s group have identified USWS in all three of the Cetacean species investigated (Table 1); the bottlenose dolphin (Tursiops truncatus) [34,35] (see also Ref. [36]), the common porpoise (Phocoena phocoena) [6], and the Amazonian dolphin (Inia geoffrensis) [37]. Mukhametov and colleagues provide several English summaries of their research on sleep in Cetaceans and other aquatic mammals [4–6].

In all three species studied, three stages of EEG activity were identified: (1) wakefulness, characterized by low-amplitude, high-frequency activity; (2) an intermediate stage between wakefulness and “deep” SWS, characterized by sleep-spindles, theta and delta waves; and (3) “deep” SWS characterized by delta waves of maximal amplitude. Wakefulness and the intermediate stage both occurred bihemispherically and unihemispherically. However, deep SWS only occurred unihemispherically. In bottlenose dolphins, bihemispheric wakefulness occupied approximately two thirds of the time, with the remaining third being comprised mainly of USWS (i.e. wakefulness in one hemisphere and the intermediate stage in the other, or wakefulness in one hemisphere and deep SWS in the other) [6]. Episodes of USWS lasted on average 42.5 min (range 3.5–131.5) and tended to alternate between hemispheres [35]. Similar patterns were observed in porpoises [6] and in Amazonian dolphins [37]. In bottlenose dolphins, all types of sleep were most likely to occur at night and during the second half of the day; sleep time was markedly reduced during the first half of the day and at dusk [35]. Interestingly, REM sleep occurs infrequently and/or in a modified manner in Cetaceans. While electrophysiological studies either report little [33] or no [4,38] signs of REM sleep, several researchers have observed behavioral signs of REM sleep, including muscle twitching, REMs and penile erections [29,39–44] (but see Ref. [45]).

In Cetaceans, each hemisphere functions as an independent unit with respect to sleep. Simultaneous recordings from the frontal, parietal and occipital cortex revealed that while deep SWS may start or end asynchronously within different regions of a single hemisphere, during stable deep SWS, all regions of the hemisphere show similar delta activity (Fig. 1) [5,34]. Furthermore, low-frequency activity recorded from thalamic nuclei occurs concurrently with USWS in the ipsilateral cortex [46]. Thus, USWS is a characteristic of both cortical and subcortical structures. USWS in bottlenose dolphins and porpoises is also reflected in hemispheric cortical temperature. Brain temperature recordings from the left and right parietal cortex during USWS revealed interhemispheric asymmetries in temperature that paralleled hemispheric EEG activity; temperature was higher in the awake hemisphere, and lower in the sleeping hemisphere [47,48]. This relationship is consistent with other studies that found a reduction in brain temperature and metabolism during SWS (reviewed in Ref. [49]).

Given that each hemisphere can sleep independently, an obvious question arises as to whether one hemisphere sleeps more than the other. In early reports, it appeared that within individual dolphins sleep was more likely to occur in one
Table 1  
All studies containing EEG or behavioral signs of unihemispheric sleep. In a few cases, studies which either explicitly report the absence of unihemispheric sleep, or which serve to demonstrate a point regarding unihemispheric sleep (e.g. true seals) are also included (USWS, unihemispheric slow-wave sleep; BSWS, bihemispheric slow-wave sleep; REM, rapid-eye-movement sleep; UEC, unilateral eye closure) (Key: Blank, no data provided; +, present; −, absent; ?, data reported insufficient to determine presence or absence; 1, REM not detected, but may be present in small amounts or in a modified form; 2, UEC present during sleep, but not necessarily associated with USWS in opposite hemisphere; 3, BSWS only recorded following sleep deprivation; 4, EEG recorded from only one hemisphere, or EEG from both hemispheres combined; 5, absence may be due to short observation period; 6, EEG spikes and sharp waves, rather than slow-wave activity during SWS (observed only in reptiles))  

<table>
<thead>
<tr>
<th>Taxon</th>
<th>USWS</th>
<th>BSWS</th>
<th>REM</th>
<th>UEC</th>
<th>Note</th>
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<tr>
<td>Amazonian dolphin (<strong>Inia geoffrensis</strong>)</td>
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<td>+</td>
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<td>−</td>
<td>−</td>
<td>+</td>
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<td>+</td>
<td>−</td>
<td>−</td>
<td>+</td>
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<td>Gray whale (<strong>Eschrichtius robustus</strong>)</td>
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<td>+</td>
<td>+</td>
<td>+</td>
<td>6,76]</td>
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<td>+</td>
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<td>95,96</td>
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<td>Herons, ibises, storks and allies</td>
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<td>Canada goose (<strong>Branta canadensis</strong>)</td>
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<td>+</td>
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<td>113,118,119</td>
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<td>Chloe wigeon (<strong>Anas sibilatrix</strong>)</td>
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<tr>
<td><strong>Galliformes:</strong></td>
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<tr>
<td>Chickenlike birds</td>
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<td>[104,107]</td>
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<tr>
<td>Common turkey (<strong>Meleagris gallopavo</strong>)</td>
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<td>[104,107]</td>
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</table>
hemisphere; certain dolphins slept more with the left hemisphere, while others slept more with the right [4,34,37]. However, recordings performed over several non-consecutive 24-hour sessions revealed that hemispheric sleep time was equivalent when averaged across sessions within individuals [35]. Thus, during any given session one hemisphere may sleep more than the other, but when viewed over a longer time scale both hemispheres sleep equal amounts.

As in Lilly’s early behavioral study of bottlenose dolphins, unilateral eye closure was observed in Mukhamedov’s dolphins. However, a relationship between eye state and the state of the contralateral hemisphere was not observed: the hemisphere contralateral to the open eye was either awake or asleep [4]. Nevertheless, visual stimuli presented to the open eye during USWS elicited behavioral and EEG arousal, even when the contralateral hemisphere was asleep ([50], cited in [4]; see also [44] for behavioral arousal in Amazonian dolphins). This is surprising since neuroanatomical and neurophysiological findings suggest that the hemisphere contralateral to the open eye should be awake. As a result of complete decussation of the optic nerves in dolphins [51,52], only the contralateral visual cortex exhibits evoked potentials in response to flashes of light presented to an eye during wakefulness ([50], cited in [36]). Thus, the findings from awake dolphins are difficult to reconcile with those observed during USWS.

Table 1 (continued)

<table>
<thead>
<tr>
<th>Taxon</th>
<th>USWS</th>
<th>BSWS</th>
<th>REM</th>
<th>UEC</th>
<th>Note</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Domestic chicken (Gallus gallus domesticus)</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<td>+</td>
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<td>Northern bobwhite (Colinus virginianus)</td>
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<td>+</td>
<td>+</td>
<td>+</td>
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<td>[106]</td>
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<tr>
<td>Japanese quail (Coturnix japonica)</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<td>[103]</td>
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<tr>
<td>Gruiformes: Cranes, rails and allies</td>
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<tr>
<td>Stanley crane (Anthropoides paradisea)</td>
<td>+</td>
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<td>[104,105]</td>
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<td>Charadriiformes: Shorebirds, gulls, auks and allies</td>
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<td>Glaucous-winged gull (Larus glaucescens)</td>
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<td>Ring-billed gull (Larus delawarensis)</td>
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<td>Columbiformes: Pigeons and doves</td>
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<tr>
<td>Nicobar pigeon (Caloenas nicobarica)</td>
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<td>[104,107]</td>
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<td>Orange-fronted conure (Aratinga canicularis)</td>
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<tr>
<td>Barn owl (Tyto alba)</td>
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<tr>
<td>Snowy owl (Nyctea scandiaca)</td>
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<td>[104,107]</td>
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<tr>
<td>Burrowing owl (Athena cunicularia)</td>
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<td>Apodiformes: Swifts and hummingbirds</td>
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<td>Passeriformes: Perching birds</td>
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<td>Blue jay (Cyanocitta cristata)</td>
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<td>Brewer’s blackbird (Euphagus cyanocephalus)</td>
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<td>Chelonia: Turtles and tortoises</td>
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<tr>
<td>Box turtle (Terrapene carolina)</td>
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<td>-</td>
<td>+</td>
<td>4, 6</td>
<td>[148]</td>
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<td>Red-footed tortoise (Geochelone carbonaria)</td>
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<td>[149]</td>
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<td>[141]</td>
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<tr>
<td>Caiman (Caiman latirostris)</td>
<td>?</td>
<td>?</td>
<td>+?</td>
<td>+</td>
<td>4, 6</td>
<td>[145]</td>
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<td>Squamata: Lizards and snakes</td>
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<tr>
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<td>?</td>
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<td>-</td>
<td>+</td>
<td>4, 6</td>
<td>[143]</td>
</tr>
<tr>
<td>Chameleon (Chameleo melleri)</td>
<td>?</td>
<td>?</td>
<td>-</td>
<td>+</td>
<td>4, 6</td>
<td>[143]</td>
</tr>
<tr>
<td>Black iguana (Ctenosaura pectinata)</td>
<td>?</td>
<td>?</td>
<td>-</td>
<td>+</td>
<td>4, 6</td>
<td>[144]</td>
</tr>
<tr>
<td>Green iguana (Iguana iguana)</td>
<td>?</td>
<td>?</td>
<td>-</td>
<td>+</td>
<td>4, 6</td>
<td>[146]</td>
</tr>
<tr>
<td>Western fence lizard (Sceloporus occidentalis)</td>
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(continued)
In the three dolphin species studied, USWS was behaviorally indistinguishable from periods of quiet wakefulness, a waking state during which the animal is not actively interacting with its surroundings. During both quiet wakefulness and USWS, bottlenose and Amazonian dolphins swim slowly or hover at the water’s surface [5,37]. When hovering at the surface, only fin movements required to maintain a stable posture were observed. During periods of USWS with constant slow swimming, dolphins may take a breath of air at the surface without awakening the sleeping hemisphere. In a behavioral study, Flanigan also observed slow swimming and hovering at the surface during apparent sleep in bottlenose [39] and Pacific white-sided (Lagenorhynchus obliquidens) [53] dolphins. However, in addition to hovering at the surface, McCormick [54] observed periods of resting on the tank bottom with one or both eyes open in bottlenose dolphins. Periods of resting on the bottom were periodically interrupted by surfacing to breathe (see also [30]). Porpoises (Phocoena phocoena) differ from dolphins in that they swim continuously without ever hovering at the surface [6,45]. Constant swimming during apparent sleep has also been reported in the Dall porpoise (Phocoenoides dalli) (see [54]), Indus dolphin (Platanista indi) [55], and Beluga whale (Delphinapterus leucas) [56,57]. In addition to slow swimming, Lyamin et al. [41] observed lying on the bottom in Beluga whales. Interestingly, lying on the bottom was only observed in the whale that was well adapted to captivity. Finally, having observed slow swimming during sleep in the Pacific white-sided dolphin, bottlenose dolphin and Beluga whale, but not in their predator, the killer whale (Orcinus orca) [40], Flanigan [53] suggested that swimming during sleep facilitates a rapid transition from sleep to escape behavior if a threat arises.

3.3. Function of unihemispheric sleep in Cetaceans

The presence of swimming during USWS in Cetaceans suggests that USWS functions primarily to maintain the motor activity required for surfacing to breathe [6]. Indeed, as mentioned above, surfacing to breathe occurs during USWS. Consistent with this idea, respiration ceases during pentobarbitol-induced bihemispheric slow-wave sleep (BSWS), and breathing during diazepam-induced BSWS only occurs during brief returns to USWS [6,58] (see also Ref. [54]). Apparently, the complex movements and reflexes required for Cetacean respiration are incompatible with BSWS. Mukhametov suggests that this may also explain the absence or modified nature of REM sleep in Cetaceans, since the loss of muscle tone typical of mammalian REM sleep may interfere with the motions required for breathing in Cetaceans [4,38,42]. However, it remains unclear as to why dolphins do not simply hold their breath during brief periods of BSWS, as observed in some seals (see below). One possibility is that by sleeping unihemispherically Cetaceans are able to sleep (albeit with one hemisphere at a time) for extended periods without frequent interruptions to breathe [5]. Finally, USWS might allow sleep, surfacing to breathe and migration to occur concurrently in Cetaceans [59].

USWS in Cetaceans may also serve additional functions unrelated to swimming and breathing. The fact that dolphins frequently keep one eye open and responsive during USWS suggests that dolphins use USWS to visually monitor their environment, as suggested by Lilly [31]. Indeed, in a recent behavioral study of a group of four captive Pacific white-sided dolphins, Goley [60] found that dolphins use unilateral eye closure in a functional manner. At night the dolphins ceased vocalizing, formed a tight group, and swam slowly in a counterclockwise direction (see also Ref. [61]). Goley predicted that the dolphins at either edge of the group would keep the open eye directed away from the group, as if watching for approaching predators. However, in direct contrast to this prediction, the dolphins actually kept the open eye directed towards the center of the group, while the eye facing away from the group remained closed.
Furthermore, when the dolphins changed their position within the group, eye state changed accordingly. For example, when a dolphin switched from the right side to the left side of the group, it switched from having only the right eye closed to having only the left eye closed. Since eye state switches occurred approximately on an hourly basis, a duration similar to that observed for bouts of hemispheric sleep [35], Goley concluded that position and eye state changes may allow each hemisphere a turn to sleep. Given these findings, the lack of a correlation between which eye is open and which hemisphere is asleep reported by Mukhometov [4] remains enigmatic (see above). Finally, although these findings suggest that dolphins use unilateral eye closure to maintain visual contact with their group, unilateral eye closure may also serve a predator detection function. Since the group was vertically staggered as it swam, Goley notes that dolphins may be able to visually monitor their surroundings by scanning past their schoolmates. Certainly, as with many biological processes, unilateral eye closure and USWS are likely to serve several non-mutually exclusive functions in Cetaceans.

3.4. Regulation of unihemispheric sleep in Cetaceans

The discovery of USWS in Cetaceans provided a unique opportunity to address several key issues regarding the regulation of SWS in mammals. Previous studies from various terrestrial species have shown an increase in SWS time and/or intensity (reflected in increased slow-wave activity) following sleep deprivation (reviewed in Refs. [62–64]; but see discussions in Refs. [13–17]) suggesting that the brain homeostatically compensates for lost sleep. However, prior to the discovery of USWS it was unclear whether SWS was regulated as a whole brain phenomenon or locally within different regions of the brain. Following the discovery of USWS in Cetaceans, it became apparent that SWS might be homeostatically regulated independently within each hemisphere.

Unihemispheric sleep deprivation in bottlenose dolphins revealed SWS was in fact regulated unihemispherically [4,65]. Unihemispheric sleep deprivation was achieved by awakening the dolphin whenever the targeted hemisphere fell asleep; the non-deprived hemisphere was allowed to sleep as long as the deprived hemisphere remained awake. The first sign of independent hemispheric sleep regulation was an increase in the frequency of attempts to fall asleep made by the deprived hemisphere as the deprivation procedure progressed. Moreover, following unihemispheric sleep deprivation, SWS time (SWS intensity was not reported) increased primarily in the deprived hemisphere; the non-deprived hemisphere did not compensate for sleep lost in the deprived hemisphere. The unihemispheric sleep rebound was greatest immediately following deprivation, a feature typical of SWS rebounds in mammals (reviewed in Refs. [62–64]), and the normal tendency for sleep to alternate between hemispheres was accentuated during recovery. The results from unihemispheric sleep deprivation in dolphins have several implications for understanding the regulation of SWS. First, these results convincingly demonstrate that the rebounds in SWS observed following sleep deprivation in previous studies are the result of lost sleep, rather than a non-specific variable (e.g. stress, enforced activity, etc.) associated with the deprivation procedure. If the rebound in SWS had resulted from stress induced by the deprivation procedure, then both hemispheres should have shown an increase in SWS in response to unihemispheric sleep deprivation. Second, the presence of unihemispheric sleep regulation appears to contradict theories of sleep regulation based on diffuse sleep factors circulating in the blood or cerebrospinal fluid ([5,65]; reviewed in Refs. [66,67]; see also Ref. [68]). If SWS were primarily regulated by diffuse sleep factors, then deprivation of one hemisphere should have caused an increase in SWS in the non-deprived hemisphere during deprivation, as well as an increase in SWS in both hemispheres following deprivation. Instead, the results suggest that sleep factors accumulate and influence SWS independently within each hemisphere. Although the need for sleep may accumulate independently within each hemisphere, the acquisition of such sleep must involve the reciprocal coordination of both hemispheres since SWS almost never occurs simultaneously in both hemispheres, even following bihemispheric sleep deprivation [34,65].

In addition to enhancing our understanding of SWS regulation, the results from unihemispheric sleep deprivation also provide significant clues to the function of sleep. At the most fundamental level, the results clearly indicate that sleep serves a primary function for the brain, rather than the body. Indeed swimming during USWS in Cetaceans shows that the body does not necessarily rest during sleep. By no means does this indicate that sleep serves no function for the body; certainly sleep may be necessary for the brain (or hemisphere) to effectively regulate several bodily functions such as thermoregulation, immune system integrity and tissue restoration (see [2,69]). The presence of unihemispheric SWS regulation, and USWS itself, also raises the question as to what is the smallest component of the central nervous system that requires sleep. Indeed, the discovery of USWS regulation has influenced current functional sleep theories which propose that sleep may be regulated locally within small portions of each hemisphere ([70–72]; for evidence of local sleep see [73,74]).

3.5. Pinnipedia: eared and true seals

The apparent link between USWS and an aquatic lifestyle led to the exploration of sleep in another group of aquatic mammals, the pinnipeds. The order pinnipedia is comprised of three families: Otariidae (eared seals: sea lions and fur seals), Phocidae (true seals) and Odobenidae (walrus; Odobenus rosmarus). Pinnipeds are particularly interesting since, unlike Cetaceans, they sleep in the water and on land. Electrophysiological sleep states have been investigated in several species of eared and true seals (Table 1), but the
walrus has not been studied. In brief, USWS allows eared seals to sleep and breathe regularly at the water’s surface, whereas true seals hold their breath under water while both hemispheres sleep simultaneously.

### 3.6. Unihemispheric sleep in eared seals

USWS has been observed in all four species of eared seals investigated (Table 1). However, unlike Cetaceans, eared seals also exhibit BSWS and unequivocal REM sleep (Fig. 2). USWS in eared seals consists primarily of an interhemispheric asymmetry in SWS; one hemisphere displays deep SWS, while the other exhibits an intermediate stage [75,76]. As in Cetaceans, USWS is a feature of the entire hemisphere [6,76], although the interhemispheric asymmetry in SWS is most pronounced in the occipital and parietal regions (O.I. Lyamin, personal communication). Episodes of SWS usually start with several minutes of USWS, followed by a transition to BSWS [5]. The amount of SWS composed of USWS increases with age, but even fur seals as young as two weeks old display small amounts of USWS ([78, cited in [77], [6]). A decrease in REM sleep, similar to that observed in terrestrial mammals (reviewed in Ref. [18]), also occurs with increasing age.

Eared seals provide a unique opportunity to test the hypothesis that USWS is linked to sleeping and breathing in water, since they sleep in water and on land, and display both USWS and BSWS [6,76]. Consequently, if USWS is linked to sleeping and breathing in water, the proportion of SWS composed of USWS should increase when sleep in water is compared to that on land. This prediction is based on the assumption that USWS is a less efficient means of meeting a daily hemispheric sleep quota, and therefore should only be utilized when BSWS is less feasible (e.g. in the water). In the four fur seals studied, the proportion of SWS composed of USWS did in fact increase from 41.6% on land to 66.9% in water [6,76]. Along these lines, USWS also increases in young seals when they make the transition from sleeping on land to sleeping in water [78].

The link between USWS and breathing in water is also supported by the observation that fur seals assume a unique posture when sleeping unihemispherically in water. Adult and young [78] fur seals lay on their side with three flippers in the air, while the front flipper in the water constantly paddles (Fig. 3). This posture keeps the nostrils above the water’s surface, thus allowing concurrent sleep and breathing. Sleeping with three flippers out of the water may also minimize heat loss through the flippers [6]. While in this posture, the hemisphere contralateral to the moving flipper tends to be more awake (desynchronized) than the other hemisphere. Although tactile sensory input from the moving flipper or vibrissae in the water may keep the contralateral
hemisphere awake, it seems more likely that the waking state permits movement to occur since the flipper does not move during USWS on land [6]. Interestingly, as soon as the fur seal enters REM sleep, flipper movement stops and the head sinks under water [79]. This may account for the lower amount of REM sleep when sleep in water is compared to that on land [6,79]. Cape fur seals (*Arctocephalus pusillus*) also exhibit USWS when sleeping on land (the EEG has not been recorded in water) and assume the same posture as the northern fur seal when sleeping in the water [75].

USWS has also been recorded in the two species of sea lions investigated, the Stellar’s (*Eumetopias jubatus*) ([214, cited in [75]) and southern sea lions (*Otaria flavescens*) [80]. However, sleep in water has been investigated only in the Stellar’s sea lion. Rather than lying on their side at the surface, as in fur seals, Stellar’s sea lions swim continuously during USWS, a pattern similar to dolphins. Thus, USWS in sea lions is not associated with the posture shown in Fig. 3 for fur seals, but does appear to be linked with motor activity required for surfacing to breathe.

USWS may also serve non-respiratory functions, such as predator detection, since it also occurs on land. Consistent with a predator detection function, USWS appears to be associated with unilateral eye closure in fur seals sleeping on land [75]. Unlike the situation in dolphins, but like that in birds (see below), the hemisphere contralateral to the open eye is more awake (desynchronized) than the other hemisphere in both northern and cape fur seals. Furthermore, on land cape fur seals usually sleep with the open eye facing away from the substrate, suggesting that fur seals use USWS to monitor the environment for predators or conspecifics. Assuming that the association between unilateral eye closure and USWS holds when sleeping in water, this state may also allow fur seals to visually detect predators, such as sharks and killer whales, approaching from below.

In summary, as suggested for Cetaceans, USWS may serve multiple, non-mutually exclusive functions in eared seals.

### 3.7. No unihemispheric sleep in true seals

Ironically, the absence of USWS in true seals provided another unique opportunity to investigate the evolution of USWS in aquatic mammals. Sleep has been studied in four species of seals in the family Phocidae (Table 1). However, the EEG was recorded from both hemispheres in only three species; Caspian seals (*Phoca caspia*) [4,81], young harp seals (*Pagophilus groenlandicus*) [77,82,83] and young elephant seals (*Mirounga angustirostris*) [84,85]. During sleep on land and in the water, all three species display BSWS and REM sleep, but not USWS. The seals usually remain motionless during sleep on land and in the water. During sleep on land or at the water’s surface, breathing may occur without arousal from sleep. Elephant seals floating near the surface may also raise their head above the surface to breathe without awakening from SWS [84]. However, when sleeping under water, seals hold their breath and periodically awaken to return to the surface to breathe. Although sleep in grey seals (*Halichoerus grypus*) was recorded from only one hemisphere, this species also remains essentially motionless and shows long respiratory pauses.
during sleep under water [86]. Since true seals tend to inhabit the polar regions [87], breath holding during BSWS may be linked to the need to sleep while submerged under the polar ice fields [75,82]. The presence of long respiratory pauses and the absence of motion during BSWS under water in true seals lend support to the hypothesis that USWS and the accompanying motor activity allows eared seals to sleep and breathe concurrently in water. When the results from both families of seals are compared it becomes clear that each strategy is a solution to the same problem, sleeping and breathing in an aquatic environment; true seals sacrifice breathing to maintain sleep, and eared seals sacrifice sleep in one hemisphere to maintain breathing.

3.8. Evolution of sleep and breathing in pinnipedia

The interpretation of the evolutionary sequence leading to two distinct forms of sleeping and breathing in water is heavily dependent upon our current understanding of pinniped evolution. Although earlier work suggested an independent origin for true seals and eared seals plus walruses, with true seals evolving from musteloidea (weasel- or otter-like) ancestors, and eared seals and walruses evolving from ursoida (bear-like) ancestors, recent fossil [88] and molecular [89–91] evidence indicates that both groups evolved from a common semi-aquatic ancestor, most closely related to musteloidea [90]. This raises the question as to whether sleeping in water evolved before or after the two groups diverged. If sleeping in water evolved after divergence, then breath holding during BSWS in true seals and USWS in eared seals probably evolved as independent solutions to the same problem. However, if sleeping in water evolved prior to divergence, then sleep in one of the families was secondarily modified; depending upon the ancestral form of sleep, USWS was either lost by true seals or acquired by eared seals.

3.9. Sirenia: manatees

The link between USWS and the aquatic environment led to the investigation of sleep in the final group of aquatic mammals, the Sirenia. The order Sirenia includes three species of manatees and one dugong that appear to be closely related to elephants and hyraxes [92–94]. Sirenia are exclusively aquatic, inhabiting shallow waters. Only two studies have investigated sleep in Sirenia (Table 1).

The first recorded sleep in a single Caribbean manatee 
(*Trichechus manatus*), but failed to detect USWS ([215, cited in [95]). However, the authors caution that the short recording period (only two nights) may have limited their ability to detect USWS. The second study investigated sleep in a two-year-old female Amazonian manatee (*Trichechus inunguis*) [95,96]. In addition to the typical features of mammalian REM sleep and SWS, this manatee also displayed USWS. SWS occupied 27% of the recording time (REM sleep only 1%) with approximately 25% of SWS occurring unihemispherically. In contrast to dolphins and eared seals, USWS was not associated with the maintenance of motor activity required for respiration; the manatee remained motionless at the bottom of the pool during all stages of sleep. In both species of manatee, each respiratory act was associated with a brief, bilateral arousal from either SWS or REM sleep, a pattern similar to that recorded in true seals sleeping under water. In this respect, the presence of USWS in manatees is inconsistent with the hypothesis that USWS evolved in aquatic mammals only to facilitate breathing during sleep. USWS in manatees may therefore serve other functions such as predator detection.

4. Unihemispheric sleep in birds

4.1. Background of avian unihemispheric sleep

And smale fowles … sleepen al the night with open ye Chaucer (1386).

In the prologue to Chaucer’s, *The Canterbury Tales*, birds are observed sleeping with an open eye. Nearly 600 years later, scientists revealed that this observation was not just a tale. Spooner [97] was the first to demonstrate an association between unilateral eye closure and USWS in birds. During EEG studies of young chickens (*Gallus gallus domesticus*), Spooner observed periods of unilateral eye closure associated with an interhemispheric EEG asymmetry; the hemisphere contralateral to the open eye showed activity typical of wakefulness, while the other showed activity typical of SWS. Unilateral eye closure and EEG asymmetry occurred in association with periods of bilateral eye closure and BSWS. Visual stimuli presented to the open eye produced rapid behavioral and EEG arousal, indicating that the contralateral hemisphere was functionally awake. Although not explicitly identified as USWS, Spooner’s observations provide the earliest EEG evidence for USWS in birds or any animal.

Subsequent studies also found an association between unilateral eye closure and USWS in chickens and other galliformes. In a developmental EEG study, Peters, Vonderhe and Schmid [98] observed that sleeping three-week-old chickens responded to a mild stimulus (e.g. a faint sound or gentle blow of air) by opening only the eye closest to the stimulus source, a response associated with desynchronization (or awakening) of only the contralateral hemisphere.

Peters et al. were the first to fully recognize the implications of these findings in young chickens, noting that their result “raises a theoretical question as to whether this particular chick is asleep or awake”. Subsequently, Ookawa also observed an association between unilateral eye closure and USWS in young chickens ([199]; see also Ref. [100] for interhemispheric EEG asymmetry in chicken embryos), adult chickens ([101]; see also Ref. [102]) and adult Japanese quail (*Coturnix coturnix japonica*) [103] (Table 1). Furthermore, as in dolphins and fur seals, surface and subcortical recordings from chickens revealed that USWS
was apparently a characteristic of the entire hemisphere [101].

Despite these early studies, avian USWS went largely unnoticed by sleep researchers until its rediscovery in the glaucous-winged gull (Larus glaucescens). Ball et al. [104,105] investigated the physiology of gulls sleeping in the laboratory and their sleep behavior in the wild. As in chickens and quail, USWS in gulls was also associated with unilateral eye closure. Ball et al. [104] also measured the metabolic rate occurring during various behavioral and EEG states. Since metabolic rate is usually lower during SWS when compared to wakefulness [49], the metabolic rate during USWS should be intermediate between BSWS and wakefulness. However, the metabolic rate during USWS was similar to that occurring during BSWS, with both being lower than wakefulness. In this respect, birds in USWS are ‘metabolically asleep’ with one hemisphere awake. Future studies employing recordings of cortical temperature, an indirect measure of brain metabolism [49], may reveal an interhemispheric asymmetry in cortical temperature similar to that observed in dolphins during USWS.

In wild gulls, bouts of unilateral eye closure usually occurred in close temporal proximity with periods of bilateral eye closure [105]. Episodes of unilateral and bilateral eye closure lasted 3–4 s; such short sleep bouts are typical of birds that sleep in the open [106]. Unilateral eye closure, and presumably USWS, comprised 17% of total sleep time based on eye closure. Closure of the right eye was as likely as closure of the left, indicating no population bias for one hemisphere to sleep more than the other. However, the eye that was closed was influenced by environmental conditions such as the direction of the sun or wind. In general, the eye facing adverse conditions remained closed more often than the other. Although this may indicate a protective function for unilateral eye closure independent of USWS, it seems more likely that closure of the eye towards adverse conditions simply reflects an optimal choice for which eye to sleep with under the prevailing conditions.

Given the association between unilateral eye closure and USWS reported in several studies, Ball et al. [104,107] used eye state to determine the prevalence of USWS in birds. A survey of birds sleeping in a zoological park revealed unilateral eye closure, and presumably USWS, in species from diverse taxonomic groups (Table 1). Unilateral eye closure occurred in 29 species from 13 orders, including social and solitary, terrestrial and aquatic, diurnal and nocturnal, and in species with lateral and frontally facing eyes. Unilateral eye closure was not detected in Cuculiformes (cuckoos), Apodiformes (swifts and hummingbirds), and the flightless raptites; Tinamiformes (tinamous), Rheiformes (rheas) and Casuariiformes (cassowaries and emus). However, Ball et al. [104] caution that further observations are needed to confirm the absence of unilateral eye closure in these groups. These behavioral results suggest that USWS is widespread in birds, and raise the question as to whether their theropod dinosaur ancestors [108,109] also slept unihemispherically.

Despite the prevalence of unilateral eye closure and its association with USWS in birds, a few studies have failed to detect this pattern. Ayala-Guerrero et al. [110] reported periods of interhemispheric asymmetry in high-amplitude slow-waves during SWS in parakeets (Aratinga c nica laris), but apparently these periods were not associated with unilateral eye closure. Tobler and Borbely [111] were unable to detect unilateral eye closure in pigeons (Columba livia), due to the difficulty of observing both eyes simultaneously, and no signs of USWS were observed in the EEG. Szymczak et al. [112] recorded episodes of USWS from the ectostriatum (most other studies have recorded the EEG from the hyperstriatum accessorium, or visual Wulst) of the European Blackbird (Turdus merula), but were also unable to observe both eyes simultaneously. Although the eye facing the camera was almost always closed during USWS, the authors did not report whether the hemisphere closest to the camera was almost always awake, as would be expected if the eye facing away from the camera were open.

Several factors may account for the discrepancies in the reporting of avian USWS. Perhaps the simplest explanation is that USWS is genuinely lacking in some species. However, a more probable explanation involves the nature of the avian EEG. When compared to mammals, the magnitude of change in EEG amplitude and frequency from wakefulness to SWS is relatively small in birds (reviewed in Refs. [106,111]). This is true, in part, to low-frequency activity occurring during wakefulness. Given the small differences in EEG activity between wakefulness and SWS, assessments based on visual scoring of the EEG may fail to detect all but the most extreme levels of interhemispheric asymmetry. Furthermore, subtle levels of interhemispheric asymmetry associated with unilateral eye closure may only become apparent when the state of both eyes is monitored closely.

In the first objective assessment of avian USWS, we used digital period amplitude analysis (PAA) of the EEG in mallard ducks (Anas platyrhynchos) to characterize the association between unilateral eye closure and USWS [113]. PAA is a time domain algorithm which uses zero voltage crosses, first derivatives and integrated wave amplitudes to quantify the amplitude, or power (μV²), of different frequencies in the EEG [114]. In this study, episodes of each eye state were paired up with the PAA results from the corresponding EEG. As expected, on average, low-frequency power (1–6 Hz) [106] in the hemisphere contralateral to the closed eye was greater than that in the hemisphere contralateral to the open eye, indicating USWS (Fig. 4). However, low-frequency power in the hemisphere contralateral to the open eye was still greater than that occurring during wakefulness with both eyes open. Since the open eye and contralateral hemisphere were capable of responding rapidly to a threatening visual stimulus, this
intermediate level of power was interpreted as indicating a quiet waking state, intermediate between a fully alert state and SWS. Thus, while these results objectively confirm that unilateral eye closure is associated with USWS in mallards, they also reveal the subtle nature of this effect, a finding that may explain some of the discrepancies in the reporting of USWS mentioned above. Indeed, we recently completed a PAA analysis of sleep in pigeons (Columba livia), which revealed an association between unilateral eye closure and USWS similar to that observed in mallards [115]. Future analyses of the avian EEG using similar objective techniques (e.g., PAA or fast Fourier transform power spectral analysis) (reviewed in Refs. [116,117]) may reveal similar effects in additional species.

4.2. Function of avian unihemispheric sleep

Relatively few studies have addressed the function of USWS in birds. Given that birds keep one eye open during USWS, the most intuitive explanation is that birds use USWS to monitor their environment for predators while still obtaining some of the benefits of sleep. Rattenborg et al. [118,119] explicitly tested the predator detection hypothesis by manipulating the level of risk perceived by sleeping birds. Since the risk of predation varies considerably over time and space [120], it was reasoned that birds should possess an ability to facultatively control whether they sleep unihemispherically or bihemispherically. This expectation is based upon the assumption that USWS is a less efficient means of meeting daily hemispheric sleep require-
ments when compared to sleeping with both hemispheres simultaneously. Consequently, when sleeping under low risk a bird should sleep with both hemispheres simultaneously, thereby maximizing the amount of sleep obtained per hemisphere per unit of time. However, under high risk a bird should increase the proportion of sleep that is unihemispheric, thereby mitigating to some extent the conflict between sleep and vigilance. Finally, since threats often arise from a specific direction, birds should chose to orient the open eye during USWS in the direction of a potential threat.

Birds are in fact capable of facultatively controlling when they sleep unihemispherically in response to changes in predation risk. When compared to mallard ducks sleeping safely in the center of a group, those positioned at the edge of a group (a position which animals perceive as dangerous) [121,122] showed a 150% increase in USWS and a strong preference for directing the open eye away from the center of the group [118,119]. Thus, birds not only have the capacity to facultatively control when they sleep unihemispherically, but they utilize this ability in a manner that reduces the conflict between sleep and predator detection. While birds may also use USWS to visually monitor their surroundings for things other than predators (e.g., conspecifics, food availability, changes in the weather, etc.), predator detection is likely to be the most important given the consequences of failing to detect an approaching predator.

Avian USWS may also serve functions unrelated to monitoring the environment. Circumstantial evidence suggests that some birds may sleep while flying, and it has been suggested that such sleep occurs unihemispherically [59,70,123]; but see [124]. For example, since the European swift (Apus apus) spends the night in flight, they may obtain some sleep while flying (reviewed in Ref. [125]). Similarly, the wideawake tern (Sterna fuscata) spends months at sea and quickly becomes waterlogged if it lands on the water’s surface, leading Ashmole [126] to suggest that they “get their rest on the wing”. Many birds that sleep at night during most of the year abruptly shift to flying long distances at night during migration. Whether such birds forgo sleep during migration, shift to sleeping during the day, or sleep while flying is unknown. The only direct, yet anecdotal, evidence for unihemispheric sleep during flight is our observation of glaucous-winged gulls closing one eye while flying to their roost (C.J.A., personal observation). Given the association between unilateral eye closure and USWS previously demonstrated in this species [104,105], these gulls were probably sleeping unihemispherically while flying.

Sleep during flight may not be as remarkable as it first seems. For instance, birds may simply engage in brief bouts of sleep while gliding. However, sleep during powered flight may also be possible, since stereotypical locomotor movements, such as walking or flapping are controlled by spinal reflexes. In fact, flight can occur in birds with both hemispheres disconnected from the spinal cord [106],

Fig. 4. The relationship between eye state and EEG power for the left (open circles) and right (filled circles) hemispheres in the mallard. The four eye states are both left and right eye open (LO/RO), both left and right eye closed (LC/RC), left eye closed and right eye open (LC/RO), and left eye open and right eye closed (LO/RC). For each individual mallard (N=6) EEG power was standardized as a percent of the average power observed during bihemispheric slow-wave sleep, averaged across all frequency bins for each bird’s hemisphere. Episodes of REM sleep were excluded from the LC/RC data. Reported values are means ±S.E. Greater low-frequency power in the hemisphere contralateral to the closed eye during unilateral eye closure indicates USWS, see Rattenborg et al. [113,119] for further details.
suggested the possibility of bihemispheric sleep during flight. Although flight may be possible during bihemispheric sleep, USWS may well be needed to navigate and manage the finer adjustments necessary for flight. Indeed, birds flying in flocks may utilize USWS to monitor their position relative to the rest of the flock in a manner similar to that observed in Pacific white-sided dolphins sleeping while swimming in a group (see above).

4.3. Unihemispheric sleep and functional lateralization in the avian brain

One area of avian sleep research that promises to yield significant clues to the function of sleep is the potential relationship between USWS and functional lateralization in the avian brain. Several studies from diverse species of birds have revealed that each hemisphere is specialized to perform certain cognitive functions (reviewed in Refs. [127,128]). Given that SWS may be related to some aspect of brain functioning during wakefulness, relationships between hemispheric sleep and functional lateralization may provide insight into the causal factors for sleep. Since young chickens display functional lateralization (reviewed in Refs. [123,129]) and USWS, this species provides a unique opportunity to investigate the potential relationship between waking brain function and sleep.

Two behavioral studies have explored the relationship between functional lateralization and USWS in chickens. In both studies, eye state was used as an indirect measure of brain state. First, Rogers and Chaffey ([130], cited in [123]) recorded eye states in small groups of 1–17 day old male chickens. Time spent in both bilateral and unilateral eye closure showed consistent changes with age. First, due largely to the decline in bilateral eye closure, the proportion of eye closure that was unilateral increased with age. Second, during week two, chickens closed the left eye more frequently than the right. An examination of the pattern of eye state transitions provided a clue to the possible function of this bias. During the second week, transitions from wakefulness to USWS occurred equally with closure of the left or right eye. However, transitions from bilateral eye closure to unilateral eye closure usually involved opening the right eye. Rogers [123] suggests that this preference for opening the right eye, presumably to monitor the environment, is related to the fact that the left hemisphere is sensitive to major changes in the environment, whereas the right hemisphere is sensitive to changes in detail [131]. Thus, chickens may preferentially open the right eye to check for major changes in the environment, such as the approach of a predator or the location of conspecifics. However, whether this eye preference reflects an adaptive behavioral decision or a greater need for sleep in the right hemisphere at this age remains unclear.

Recently, Mascetti et al. [132] demonstrated shifts in eye preferences during USWS associated with changes in the chicken’s rearing conditions. Eye state was recorded from female chickens during the first two weeks of life. Chickens were raised either with an imprinting object (plastic ball) or in isolation. As in the previous study, bilateral eye closure decreased and unilateral eye closure increased with age. Furthermore, a significant bias for closure of the left eye was also observed during the second week under both rearing conditions. However, during the first week, only chickens raised without an imprinting object showed a bias for closure of the left eye; chickens raised with an imprinting object showed no bias for closing one eye more than the other during the first week. Mascetti et al. tentatively suggest that in chickens raised with an imprinting object, the need to consolidate imprinting memories, a process thought to occur in the left hemisphere [133], may lead to more sleep in the left hemisphere and an increase in right eye closure, thereby reducing the bias for left eye closure observed in the absence of an imprinting object (the initial bias for left eye closure remains unexplained). However, following imprinting in chickens, Solodkin et al. [134] observed an increase in REM sleep, but not SWS (USWS was not addressed in this study). Since REM sleep occurs bihemispherically (see below) with both eyes closed, the shift in unilateral eye closure reported by Mascetti et al. does not appear to be related to REM sleep. Nevertheless, since several studies also implicate SWS in memory processing [135–138], Mascetti et al.’s findings may still reflect an increase in left hemisphere SWS due to unihemispheric memory processing.

Young chickens also showed shifts in lateralized eye use during USWS in response to changes in the environment. Mascetti et al. observed an increase in right eye closure following changes in the visual characteristics of the imprinting object. Since fully awake young chickens selectively use the left eye and right hemisphere to view novel objects [131,139], Mascetti et al. suggested that the increase in right eye closure reflects an increase in the use of the left eye in response to novelty in the environment (i.e. changing the characteristics of the imprinting object). In this respect, USWS is not simply an epiphenomenon of each hemisphere requiring different amounts of sleep, but may also reflect adaptive decisions regarding eye use. According to this hypothesis, we would expect that by changing the characteristics of the chicken’s environment it should be possible to elicit use of either the left or right eye during USWS. For example, changing the characteristics of a cue which provides the chicken with meaningful information (impending danger, food availability, etc.) should affect which eye it uses during unilateral eye closure; cues requiring the specializations of the right hemisphere should be viewed with the left eye, whereas those requiring the specializations of the left hemisphere should be viewed with the right eye. However, the extent to which a bird utilizes the preferred hemisphere should be limited by that hemispheres need for sleep. Presumably, the less preferred hemisphere will eventually take over while the preferred hemisphere sleeps. Ultimately, given the presence of functional lateralization
in the avian brain, the eye a bird chooses to use during USWS is likely to influence the manner in which the whole bird responds to its environment [59].

The behavioral results from young chickens demonstrate a unique and largely unexplored opportunity to relate waking brain function to sleep. Future studies may clarify whether the age-related shifts in eye preference during USWS indicate a greater need for sleep in one hemisphere and/or an adaptive utilization of hemispheric specializations during USWS. Presumably, these factors are interrelated since extended use of the preferred hemisphere may lead to a greater sleep debt in that hemisphere.

5. Unihemispheric sleep in other vertebrates?

5.1. Reptiles

Despite displaying unequivocal behavioral signs of sleep, several conflicting electrophysiological correlates of behavioral sleep have been reported in reptiles (reviewed in Ref. [140]). Most studies report an association between behavioral sleep and intermittent high-amplitude, spikes and sharp waves in the EEG. However, a few studies report an association between behavioral sleep and high-amplitude, low-frequency activity, e.g. [141]. Complicating matters further are studies that failed to detect any changes in the EEG during behavioral sleep, e.g. [142]. Although some controversy persists, Hartse [140] argues convincingly that high-amplitude, spikes and sharp waves define a reptilian sleep state homologous with mammalian and presumably avian SWS.

To date, no electrophysiological study has reported unihemispheric sleep in a reptile. However, most of the reptilian sleep studies predate widespread knowledge of this phenomenon, and many only employed a single EEG recording that combined the electrical activity from both hemispheres. Nevertheless, the apparent prevalence of unilateral eye closure during behavioral sleep in reptiles suggests that sleep, in some form, may occur unihemispherically. Unilateral eye closure during behavioral sleep has been reported in species from each of the three orders of reptiles. Unilateral eye closure was observed in another species which reported an association between behavioral sleep and spikes and sharp waves, e.g. [147]. However, a few studies report an association between behavioral sleep and high-amplitude, low-frequency activity (see discussion in Ref. [140]). However, they did not report whether unilateral eye closure had an affect on EEG activity.

Unilateral eye closure was also observed in another species of caiman (C. latirostris), but no EEG evidence for unihemispheric sleep was reported [145].

Unilateral eye closure has been reported in two species of turtles. In the box turtle (Terrapene carolina) unilateral eye closure, particularly of one specific eye, was observed usually at the onset of behavioral sleep [148]. However, after induced arousal, unilateral eye closure was also observed for up to 4–12 h following resumption of behavioral sleep. As in iguanas [144], periodic opening of one or both eyes reduced the occurrence of spikes and sharp waves in the EEG, which recorded the combined activity of both hemispheres. Flanigan [149] also recorded sleep behavior and EEG activity from the red-footed tortoise (Geochelone carbonaria). However, unlike the previous study on turtles, the EEG was recorded from each hemisphere separately. Unilateral eye closure occurred at the onset of behavioral sleep, especially during respiratory acts. Furthermore, as in the box turtle, periodic opening of one specific eye often persisted for several hours after induced arousal. EEG spikes and sharp waves occurred bilaterally and unilaterally, suggesting that sleep, in some form, may occur unihemispherically. However, the brief opening of one eye was associated with a reduction in the incidence of large amplitude spikes and sharp waves in both hemispheres. In this respect, unilateral eye closure appears to be associated with a bihemispheric awakening or lightening of sleep, rather than unihemispheric sleep. However, the actual data upon which these conclusions are based were not reported. Given the significant implications that such findings may have for understanding the evolution of unihemispheric sleep,
further studies utilizing objective methods for quantifying EEG activity (e.g. PAA or fast Fourier transform power spectral analysis) (reviewed in Refs. [116,117]; see also Refs. [150,151]) are clearly needed for reptiles.

Recently, Mathews and Amlaner [152,153] attempted to clarify whether reptilian unilateral eye closure shows greater affinity with wakefulness or sleep. Sleep behavior was studied in the western fence lizard (Sceloporus ocidentalis). Based on the results from earlier sleep studies in reptiles, it was reasoned that if unilateral eye closure reflects a sleeping state, then it should occur primarily while in a prone sleeping posture during the dark phase of the photoperiod and arousal latencies should be longer during unilateral eye closure when compared to both eyes open. On all measures, unilateral eye closure showed greater affinity with wakefulness than sleep. Unilateral eye closure occurred more often during the light phase while the lizards assumed elevated postures, previously ascribed to wakefulness. Furthermore, arousal latencies in response to visual stimuli presented to the open eye during unilateral eye closure were not elevated when compared to both eyes open. While these results argue against unilateral eye closure reflecting a sleep state, the functional basis of unilateral eye closure in reptiles remains unclear. This is particularly problematic since by closing one eye, reptiles reduce their ability to visually detect passing prey or approaching predators.

One possible non-sleep related function for unilateral eye closure is the prevention of evaporative water loss through the eyes. By closing one eye at a time, reptiles may be able to reduce water loss, while still being able to visually monitor a portion of their surroundings. However, Kavanau [70] suggests that if prevention of water loss was the only function for eye closure, then the eyelids should be transparent, as in snakes and some lizards, rather than opaque as observed in most reptiles. Transparent eyelids would allow visual processing to persist while the eye remained moist. Instead of preventing water loss, Kavanau suggests that as the need for sleep evolved, opaque eyelids became necessary to block the stream of visual information that would otherwise interfere with proposed sleep processes involved in maintaining adaptive neural circuitry. Given that eye closure occurs unilaterally, this line of reasoning suggests that sleep, in some form, may occur unihemispherically in reptiles.

To complicate matters, Mathews and Amlaner [152,153] suggest that short arousal latencies may not necessarily indicate an absence of USWS. Certainly, the results from visual tests performed on birds and dolphins during USWS (see above) challenge the assumption that USWS should impair arousal latencies; despite having one hemisphere asleep, birds and dolphins respond rapidly to visual stimuli presented to the open eye. Thus, arousal latencies to visual stimulation may not effectively differentiate wakefulness from USWS. Indeed, elevated arousal latencies would seem to defeat the apparent purpose of keeping one eye open. However, the extent of visual processing during USWS still needs to be determined. It is conceivable that visual processing during USWS is restricted to the detection of gross changes in the environment, while finer levels of processing are in fact impaired.

Another approach to determining whether unilateral eye closure reflects USWS as per avian unilateral eye closure is to compare the circumstances under which reptiles and birds use unilateral eye closure. If reptilian unilateral eye closure is a precursor to avian USWS then reptiles should use unilateral eye closure in a manner similar to that observed in birds. As reviewed above, birds use unilateral eye closure and USWS to monitor their environment for approaching predators. Similarly, Tauber et al. [143] suggested that unilateral eye closure served a ‘sentinel’ function in chameleons. Certainly, the observation that unilateral eye closure persisted after induced arousal in the box turtle [148] and red-footed tortoise [149] is consistent with a predator detection function if the turtles perceived the experimenter to be a threat. Along these lines, it would be interesting to know whether the turtles’ open eye faced the direction from which the experimenter approached. Finally, Mathews and Amlaner’s [153] finding that unilateral eye closure in the western fence lizard occurs primarily in the light phase while in an elevated posture, a pattern similar to that observed in young chickens [132], is also consistent with a predator detection function. Mathews et al. [154] recently tested the predator detection hypothesis directly, and showed that unilateral eye closure increased following exposure to a predator. Furthermore, the lizards showed a preference for directing the open eye toward the last known location of the predator. Both of these responses are very similar to those observed in mallards sleeping under low and high risk [118,119].

Another parallel between reptiles and birds is the potential link between a preference for closing one eye more than the other and functional lateralization in the brain. As mentioned above, an eye preference was observed in black and green iguanas [144], box turtles [148], and red-footed tortoises [149]. This preference is particularly interesting since, as in birds, recent studies have found hemispheric specializations in reptiles (reviewed in Refs. [128,155]). Moreover, a preference for opening one specific eye following a disturbance (i.e. induced arousal), is similar to the response observed in chickens following changes in their imprinting object [132]. However, in the reptile studies, the authors did not report whether it was always the left or the right eye that remained open. Consequently, it is unclear whether an eye closure bias exists in reptiles.

5.2. Amphibians

The prevalence of behavioral signs of unihemispheric sleep in reptiles suggests that their amphibian ancestors slept in a similar manner. Relatively few studies have investigated sleep in amphibians (reviewed in Ref. [140]), and none of these provide adequate information to assess the presence or absence of EEG signs of unihemispheric
sleep. Moreover, as in reptiles some studies report EEG correlates of behavioral sleep, while others failed to detect any sleep-related changes in the EEG. Unilateral eye closure has only been reported in the bull frog (Rana catesbiana) [156]. However, it only occurred briefly during respiratory acts, and did not appear to be associated with behavioral sleep. The other studies in amphibians neither report the presence nor absence of unilateral eye closure. Thus, additional studies aimed at detecting unilateral eye closure, and potential neurophysiological correlates, during behavioral sleep would be informative.

5.3. Fish

The few studies of sleep in fish provide no evidence for unihemispheric sleep. Only two studies have investigated the EEG in fish (reviewed in Ref. [140]). In the tench (Tinca tinca), the EEG remained unchanged during wakefulness and behavioral sleep [157]. Conversely, in the cattfish (Ictalurus nebulosus), the transition from wakefulness to sleep was characterized by an increase in low-frequency activity and spikes [158]. However, since the EEG apparently recorded the combined activity of both hemispheres, no evidence for unihemispheric sleep was provided. Although several studies have reported behavioral sleep in fish (reviewed in Ref. [140]), the absence of eye closure in most fish necessarily precludes behavioral signs of unihemispheric sleep, such as unilateral eye closure. Along these lines, Kavanau [124] argues against the presence of unihemispheric sleep in constantly swimming fish based, in part, on the absence of unilateral eye closure. Despite the absence of unilateral eye closure, sleep in some form may nevertheless occur unihemispherically in fish.

6. Neurophysiological mechanisms of unihemispheric sleep

The neuroanatomical structures and neurophysiological processes responsible for USWS remain largely unknown. An understanding of the potential mechanisms behind USWS is contingent upon an understanding of sleep mechanisms in general. Since only SWS occurs unihemispherically, we will focus on those mechanisms involved in the alternation between SWS and wakefulness. Although virtually all of the research into sleep mechanisms is derived from mammals, several of these mechanisms probably also apply to birds (reviewed in Refs. [106,159,160]).

The alternation between wakefulness and SWS involves the integration of influences from several components of the central nervous system (reviewed in Ref. [161]). Certain components actively promote wakefulness, whereas others actively promote SWS. The components involved in wakefulness include the reticular formation, locus coeruleus, posterior hypothalamus, subthalamus and basal forebrain. The reticular formation consists of a network of neural tissue in the central region of the brainstem that spans from the medulla to the thalamus and hypothalamus. The reticular formation receives collateral input from various ascending sensory pathways, and projects via two main routes, dorsally to the thalamus, and ventrally to the posterior hypothalamus, subthalamus, and basal forebrain. Projections from these regions cause activation throughout the cortex. Although cortical activation is influenced by sensory input indirectly via the reticular formation, and to a lesser extent via sensory pathways, sleep does not simply arise from the absence of sensory input. In addition to being influenced by the reticular formation, the posterior hypothalamus, subthalamus and basal forebrain are capable of activating the cortex without input from the reticular formation. Consequently, wakefulness arises from both sensory input and wakefulness promoting neurons. Conversely, SWS arises from a combination of reduced sensory input via the reticular formation and increased activity in sleep promoting neurons in the medulla, preoptic area, anterior hypothalamus, and basal forebrain.

Sleeping with one hemisphere at a time would appear to require a degree of hemispheric separation. In mammals, the corpus callosum is the main route of interhemispheric communication. Although the corpus callosum is not directly involved in controlling SWS, extensive interhemispheric communication may prevent the development of sleep in only one hemisphere at a time. Accordingly, when compared to other mammals, Cetaceans have an unusually small corpus callosum [162]. For example, despite having cerebral hemispheres five times larger than humans, the corpus callosum of killer whales is the same size as in humans [36]. Similarly, birds lack a corpus callosum, and only have small interhemispheric commissures [163]. While these findings seem to support a role for the corpus callosum in USWS, other lines of evidence argue against such a role. Although the degree of interhemispheric EEG coherence (a measure of synchrony between homologous portions of each hemisphere) may be reduced following sagittal transection of the corpus callosum [164–166], or in humans lacking a corpus callosum [167,168], sleep is invariably binhemispheric under these conditions. Thus, while the corpus callosum seems to be involved in interhemispheric synchronization of EEG activity during sleep, it does not contribute to the genesis of BSWS. Consequently, the small interhemispheric connections observed in animals with USWS do not appear to account for USWS.

Having ruled out interhemispheric connections, USWS must arise from the functional independence of subcortical structures. The results from early lesion studies provide some clues to the potential mechanisms responsible for USWS. In cats, SWS developed asynchronously in each hemisphere only following sagittal transection of the lower brainstem [165,169]. This pattern was observed even when the interhemispheric commissures, including the corpus callosum, were left intact. These findings suggest that USWS may arise from the separation or ‘uncoupling’ of sleep regions in the lower brainstem. However, the functional
independence of such sleep regions alone does not account for the highly coordinated USWS in animals like dolphins. Mukhametov [4] suggests that USWS in dolphins arises from “the functional independence and (authors’ italics) reciprocal interrelation of the two halves of some synchronizing or desynchronizing system in the lower brainstem”. Transition-
ing between USWS and BSWS in eared seals and birds also appears to be a coordinated process, since, as previously mentioned, these animals are apparently capable of controlling when they sleep unihemispherically.

One promising approach to identifying the neuroanatomical structures involved in coordinating USWS would be to compare the brains of animals with USWS to those lacking USWS. Anatomical differences in regions involved in the control of sleep and wakefulness may yield clues to USWS. For instance, when compared to mammals lacking USWS, the posterior commissure of mammals with USWS was larger and showed greater decussation of the ascending fibers from the locus coeruleus in the brainstem (P. Manger, personal commu-nication). This difference was most profound in dolphins, the group of animals in which USWS is most well developed. These findings are promising since the noradrenergic neurons of the locus coeruleus are known to be involved in maintaining vigilance and cortical activation [170] (reviewed in Ref. [161]). Interestingly, elephants also showed this modifi-
cation in the posterior commissure. Given this finding, and recent evidence that suggests that manatees and elephants share a common aquatic ancestor [92], elephants may also sleep unihemispherically.

In birds, the association between unilateral eye closure and USWS has greatly influenced discussions of avian USWS control. In particular, several authors relate USWS to the fact that the optic nerves decussate completely at the optic chiasma in birds [97,98]. For example, Spooner [97] attributed USWS in young chickens to “complete decussa-
tion of the optic tract and almost complete anatomical separation of the anterior reticular formation neurons by the third ventricle (p. 75)”. Accordingly, this has led to the suggestion that avian USWS results from unilateral visual input which activates the contralateral hemisphere (either directly via the visual pathways or indirectly via the reticular formation), rather than the active involvement of sleep and wakefulness promoting regions, as suggested for dolphins [6]. While unilateral visual input may contrib-
ute to USWS, several lines of evidence indicate that USWS arises from the active control of sleep and wakefulness separately in each hemisphere. First, complete decussation at the optic chiasma is only the first step in the avian visual system. The avian visual system includes two main path-
ways, the thalamofugal pathway and the tectofugal path-
way, which are thought to be homologous with the mammalian geniculostriate and colliculothalamocortical pathways, respectively [171]. In birds with laterally posi-
tioned eyes, the thalamofugal pathway conveys visual information primarily to the visual Wulst (i.e. hyperstriatum accessorium) of the contralateral cerebral hemisphere [172–175]. Since most avian sleep studies have recorded the EEG from the Wulst, this projection pathway appears to be consistent with the proposition that avian USWS arises from unilateral visual input. However, USWS is also recorded from the ectostriatum [101,112], a portion of the cerebral hemisphere that receives bilateral visual input from the tectofugal pathway [172]. Consequently, if USWS was simply the result of unilateral visual processing, then only the Wulst contralateral to the closed eye should show SWS, while the ectostriatum of both hemispheres should show waking activity. However, since one entire hemisphere, including the ectostriatum is involved in USWS, visual input alone does not appear to account for avian USWS.

Other lines of evidence also argue against a primary role for unilateral visual input in maintaining USWS. In an attempt to determine whether USWS was strictly a result of unilateral visual input, Ookawa studied sleep in unilater-
ally [176] and bilaterally [177] blinded chickens. If USWS was a result of unilateral visual input, then blinded chickens should no longer exhibit USWS. However, despite the absence of visual input, USWS was still observed in the blinded birds. Similarly, USWS was also observed in gulls during complete darkness [104]. While these studies suggest that USWS is endogenously controlled, Ookawa [177] notes that USWS may also occur in response to unilateral auditory input, as observed in young chickens [98]. Although unilat-
eral sensory input may awaken one hemisphere or keep one hemisphere from falling asleep, the observation that transi-
tions from BSWS to USWS occur in the apparent absence of external stimuli in young chickens [123] and mallard ducks [119], indicates that USWS is endogenously controlled under certain circumstances. Moreover, as shown in mallards, such transitions are performed in a precise and adaptive manner, with the eye facing a threat being more likely to open. From this line of evidence, it is clear that instead of being a passive result of unilateral visual input, avian USWS is an endogenously controlled adaptive state of readiness during which visual processing can occur.

Finally, a discussion of the potential mechanisms involved in avian USWS control would be incomplete without considering the role of melatonin. In birds and mammals, melatonin is released from the pineal gland during the dark phase of the photoperiod. In pigeons, constant light suppresses circadian rhythms in circulating melatonin [178] and sleep [179], whereas infusions of physiolog-ical levels of melatonin restore sleep during constant light [180,181]. Thus, in contrast to mammals in which melatonin appears to induce species-specific noctur-
nal behavior (i.e. sleep in diurnal mammals and wakefulness in nocturnal mammals) [182], melatonin has a direct sleep inducing effect in pigeons (Note: melatonin is probably not the only factor controlling sleep in birds, since many birds are aphasic, engaging in sleep and wakefulness throughout the photoperiod; [106,183]). Despite melatonin’s somno-
ogenic effect in pigeons, we have recently recorded unilateral eye closure and USWS in pigeons during the dark phase of
the photoperiod [115]. Interestingly, Berger’s group did not address the issue of unilateral eye closure or USWS in the studies mentioned above. This apparent discrepancy may be attributable, in part, to the difficulty in viewing both eyes simultaneously and the subtle level of interhemispheric asymmetry in low-frequency activity associated with unilateral eye closure in birds (see discussion above). Nevertheless, our results may be compatible with the sleep inducing effects of melatonin if certain neural mechanisms enable birds to selectively activate one hemisphere during sleep, thereby overriding the effects of melatonin. Interestingly, these results suggest that while diffuse sleep factors (melatonin in this case) can exert global sleep-inducing effects, other mechanisms may competitively regulate wakefulness at a local level within the brain (see Ref. [68]).

7. Unihemispheric REM sleep?

Sleep in mammals and birds is composed of two distinct states, SWS and REM sleep, yet only SWS is known to occur unihemispherically. This raises the question as to why unihemispheric REM sleep has not been observed. Actually, the issue of unihemispheric REM sleep encompasses two questions: (1) why does REM sleep not occur unihemispherically with SWS in the other hemisphere; and (2) why does REM sleep not occur unihemispherically with wakefulness in the other hemisphere. Noting the similarity in EEG activity occurring during wakefulness and REM sleep, a few early studies entertained the idea that the “awake” hemisphere during USWS might actually be in REM sleep, rather than wakefulness. However, given the absence of other signs of REM sleep, it was concluded that the hemisphere was in fact awake [34,47,177]. Indeed, a combination of SWS in one hemisphere and REM sleep in the other would seem to defeat the likely function of unihemispheric sleep: obtaining the simultaneous benefits of wakefulness and sleep.

The reasons for the absence of strictly unihemispheric REM sleep (REM sleep in one hemisphere and wakefulness in the other) are less clear. Two potentially interrelated explanations may account for the absence of unihemispheric REM sleep. REM sleep in one hemisphere may interfere with waking functions, or wakefulness in one hemisphere may interfere with REM sleep functions. Regarding the former, Horne [184] suggests that since some form of mentation (i.e., ‘dreaming’) probably occurs in animals during REM sleep [185], animals may be unable to adaptively reconcile the different forms of mentation occurring in each hemisphere during unihemispheric REM sleep. Moreover, it is interesting to note that while cats with a sagittal transection of the interhemispheric commissures and brainstem were able to simultaneously display REM sleep in one hemisphere and SWS in the other, REM sleep in one hemisphere and wakefulness in the other was never observed [165]. In reference to interfering with REM sleep, it is conceivable that some of the proposed functions for REM sleep, such as memory processing [137,186,187], require that both hemispheres be in a state of REM sleep. Alternatively, the loss of muscle tone associated with REM sleep may simply counteract potential benefits gained from being able to engage in unihemispheric REM sleep. Finally, since long bouts of REM sleep may be incompatible with respiration in aquatic mammals [42] and predator detection in birds, an inability to develop unihemispheric REM sleep may have led to the reduction or modification of REM sleep in both aquatic mammals [42] and birds [106]. As a result, these animals may have developed other means of compensating for less REM sleep [42,188] (see also Ref. [189]).

8. Human unihemispheric sleep?

Humans are not known to sleep unihemispherically. Even following transection of the corpus callosum, or in humans lacking a callosum, sleep is invariably bihemispheric. Yet, certain studies, which have found interhemispheric asymmetries during BSWS in humans, seem to warrant discussion within the context of USWS. First, in a study of interhemispheric EEG asymmetry, Armitage et al. [190] found greater asymmetry in theta and delta activity during SWS (i.e., human stage 4 sleep) when compared to stage 2 or REM sleep (see also Ref. [191]). Moreover, the direction (left > right, or right > left) of this asymmetry tended to alternate between hemispheres, a pattern which Armitage et al. related to the alternation of USWS in aquatic mammals and birds. Interestingly, auditory evoked potentials elicited during sleep also show greater absolute interhemispheric asymmetry during SWS when compared to stage 2 or REM sleep [192]. This later finding is particularly relevant with respect to USWS, since it indicates that at any given time one hemisphere maintains greater auditory contact with the environment. Armitage et al. [190] attributed these EEG asymmetries to an ultradian rhythm in hemispheric synchronicity (see also Ref. [193]) which may be influenced by factors that determine hemispheric sleep debt, such as task performance during prior wakefulness.

Recent findings suggest that waking performance can, in fact, influence subsequent SWS unihemispherically. Kattler et al. [73] addressed several fundamental questions regarding SWS regulation by selectively stimulating one portion of the brain during wakefulness. Previous studies had shown an increase in SWS time and/or intensity (reflected in slow-wave activity) in response to increased time spent awake (reviewed in Ref. [62]), however, it has been unclear whether time awake alone produces this effect, or whether the type of activity occurring during wakefulness also has an affect. Furthermore, recent theoretical models of SWS regulation suggested that SWS might be regulated locally in response to brain use [71,72,194,195]. To test whether waking activity has a local influence on SWS, Kattler et al. [73] increased the amount of waking activity occurring in
one portion of the brain by vibrating one hand. Previous positron emission tomography studies demonstrated that this type of stimulation primarily activates the somatosensory cortex of the contralateral hemisphere [196–198]. As predicted, following stimulation, slow-wave activity during SWS increased only in the contralateral somatosensory cortex. The fact that this effect was restricted to the brain region stimulated during prior wakefulness demonstrates that slow-wave activity during SWS can be influenced by local brain use. Thus, even in animals lacking USWS, the propensity for sleep can be influenced at the hemispheric, or even more local, level.

In addition to being sensitive to prior waking performance, changes in the level of interhemispheric EEG asymmetry are also correlated with mental disorders. Several EEG parameters distinguish patients with major depressive disorders (MDD) from healthy controls [199–201]. Of particular relevance to unihemispheric sleep is the finding that interhemispheric EEG coherence (a measure of independence of EEG activity in the two hemispheres) is relatively low in MDD patients.

Recently, Sinton et al. [202] have also identified a similar phenomenon in rats. When compared to rats sleeping in pairs, rats sleeping alone show lower interhemispheric coherence. Sinton et al. suggest that lower coherence in rats is related to the stress of isolation. Stress may also account for the similar results in humans with MDD [200]. Although stress may mediate lower interhemispheric coherence in isolated rats, this effect may still reflect an adaptive response. As previously mentioned, in healthy humans, one cerebral hemisphere may be more responsive than the other to auditory input during SWS. Along these lines, lower interhemispheric coherence may allow isolated rats to maintain greater auditory contact with the surrounding environment. As a result, rats sleeping alone may be better equipped to detect approaching predators. This hypothesis can be readily tested by comparing auditory arousal thresholds during SWS between isolated and paired rats. Similar analyses of interhemispheric coherence and arousal thresholds in healthy humans sleeping under low and high stress conditions would also be of particular interest, since stress induced insomnia may arise, in part, from hypersensitivity to environmental stimuli.

It is tempting to speculate that the potential link between stress and lower interhemispheric coherence in terrestrial mammals is evolutionarily homologous to USWS in birds and possibly reptiles. However, reduced interhemispheric coherence is not the only change noted in the EEG of isolated rats and MDD patients. Isolated rats and MDD patients also show lower intrahemispheric coherence, a finding not known to occur in animals with USWS. Moreover, MDD patients also show greater beta (16–32 Hz), theta and delta activity in the right hemisphere during REM sleep, greater beta in the right hemisphere during SWS (reviewed in Ref. [201]), as well as stable asymmetries in waking prefrontal alpha (8–13 Hz) activity (reviewed in Refs. [203,204]). Thus MDD appears to be associated with a general dysregulation of brain activity at various levels. Furthermore, unlike rats given a partner, this dysregulation does not disappear during remission in MDD patients [201,204]. Consequently, while stress may mediate both USWS (at least in birds) and lower interhemispheric coherence in terrestrial mammals, it remains unclear whether these effects are homologous. A greater understanding of the mechanisms behind both USWS and EEG dysregulation in MDD may clarify whether these states are in some way related.

9. Why do most mammals sleep bihemispherically?

Given the utility of sleeping unihemispherically, it is surprising that most mammals sleep bihemispherically. Sleep has been investigated in several of the major groups of mammals [18,21,205,206], yet only aquatic mammals are known to sleep unihemispherically. The restricted occurrence of USWS in mammals becomes even more intriguing if the reptilian ancestors to mammals slept unihemispherically. Although the results from modern reptiles clearly remain equivocal with respect to USWS, and there are limitations inherent in drawing conclusions about ancient reptiles from studies on modern reptiles [207], the prevalence of unilateral eye closure in modern reptiles suggests that the reptilian ancestors to mammals and birds may have slept unihemispherically. Assuming that the reptilian ancestors did sleep unihemispherically, or exhibited a precursor state, then why did only mammals lose the capacity to sleep unihemispherically? A clue may lie in the early stages of mammalian evolution. Early mammals were small, nocturnal, shrew-like insectivores [208,209] that presumably slept during the day, hidden safely in their burrows to avoid predation from diurnally active reptiles. Presumably, as a result of being protected in their burrows, there was no need for unihemispheric sleep. In fact, sleeping unihemispherically may have been selected against since it would be a less efficient means of sleeping. By the time the descendants of early mammals radiated back into diurnal niches, they may have lost the capacity to sleep unihemispherically.

Sleeping exclusively bihemispherically may have also been favored if this form of sleep is somehow superior to the bihemispheric sleep exhibited by animals capable of unihemispheric sleep. For example, BSWS in animals capable of USWS may be fundamentally different from BSWS in animals that do not sleep unihemispherically. In the former, the two hemispheres may be viewed as sleeping independently, but at the same time, whereas in the latter, the hemispheres may be sleeping as a coordinated or integrated whole. Along these lines, sleep may play a role in integrating the functions of different brain regions. Thus, BSWS in terrestrial mammals may be superior to the BSWS in animals with USWS because it allows integration within and between hemispheres, rather than just within a
particular hemisphere. Assuming that the proposed or other unspecified benefits of sleeping exclusively bihemispherically are incompatible with an ability to sleep unihemispherically, it may have been beneficial for early mammals to forgo unihemispheric sleep, in particular if they had a lower need for maintaining vigilance during sleep as suggested above.

Regardless of whether mammals lost the ability to sleep unihemispherically, or never had the capacity in the first place, the limited occurrence of USWS in mammals suggests that the evolution of USWS is constrained by costs associated with sleeping unihemispherically. For example, the neuroanatomical reorganization required for USWS may be incompatible with the proposed benefits of sleeping exclusively bihemispherically, or other adaptive functions of the central nervous system occurring during either sleep or wakefulness. Such functions may be related to the significant changes in brain organization that occurred when early mammals invaded nocturnal niches [210]. Consequently, only under certain circumstances, such as sleeping at sea, may the benefits of USWS outweigh the costs. Although the specifics of such a tradeoff remain obscure, this scenario needs to be considered when attempting to explain the limited occurrence of USWS in mammals. Ultimately, a greater understanding of the mechanisms involved in USWS might reveal whether such a tradeoff exists.

Finally, the near absence of USWS in mammals may result from a more simple explanation; sleeping unihemispherically is not the only solution to the conflict between wakefulness and sleep. Indeed, other solutions may be easier to develop. For example, some animals such as ruminants compromise between sleep and wakefulness by engaging in extended periods of drowsiness [211], an intermediate state between SWS and wakefulness. Presumably, by engaging in drowsiness animals maintain some degree of awareness while simultaneously obtaining some of the benefits of sleep. Since all mammals engage in drowsiness during the transition from wakefulness to sleep, the evolution of this strategy would simply involve the elaboration of an existing state, rather than a reorganization of the nervous system. Behavioral adaptations may also mitigate the conflict between sleep and wakefulness. For example, by sleeping in safe locations or in large groups many animals reduce the risk of predation during sleep. In this respect, the need to sleep may have had a profound influence on the evolution of habitat selection and sociality in animals [212,213].

10. Conclusions

(1) A largely unexplored area in behavioral ecology is the inherent conflict between sleep and wakefulness. Wakefulness is clearly an adaptive state that allows animals to interact with their environment, yet its efficacy is contingent upon sleep, a vulnerable state of reduced responsiveness. The evolution of unihemispheric sleep exemplifies this point and serves as a unique solution to the problem. Although mammals and birds exhibit two types of sleep (i.e. SWS and REM sleep), only SWS occurs unihemispherically. Since alert wakefulness and deep SWS fall at the extreme ends of a continuum, animals that display unequivocal USWS also show intermediate states; one hemisphere may sleep deeply, while the other is in a state between full alertness and SWS. Such interhemispheric asymmetries in SWS reflect different degrees of unihemispheric sleep, and appear to have the same functional basis as unequivocal USWS.

(2) Among mammals, USWS has only been observed in three aquatic orders (i.e. Cetacea, Pinnipedia and Sirenia). In Cetaceans, virtually all of their sleep is USWS, whereas eared seals and manatees also display bihemispheric SWS (BSWS) and REM sleep. In Cetaceans and eared seals, USWS allows surfacing to breathe and sleep to occur simultaneously in an aquatic environment. Despite sharing a common aquatic ancestor with eared seals, true seals are not known to sleep unihemispherically. Instead, true seals hold their breath while sleeping bihemispherically under water, a strategy that may have arisen in conjunction with breath holding under the polar ice fields. The function of USWS in Sirenia remains unclear since they do not use USWS for surfacing to breathe. Therefore, USWS in Sirenia is likely to serve other functions such as threat detection. Indeed, USWS may also serve a predator detection function in Cetaceans and eared seals, since they keep one eye open during USWS.

(3) In contrast to mammals, USWS appears to be widespread among birds. Birds also exhibit both BSWS and REM sleep. An association between USWS and unilateral eye closure suggests that USWS serves a predator detection function in birds. Indeed, birds are capable of facultatively controlling when they sleep unihemispherically verses bihemispherically in a manner consistent with such a function. Birds may also use USWS to monitor other aspects of their environment, and circumstantial evidence suggests that birds may actually sleep unihemispherically during extended flights.

(4) The few studies of sleep in fish and amphibians failed to detect either behavioral or electrophysiological evidence for unihemispheric sleep. Several studies have investigated sleep in modern reptiles, however, the results are equivocal with respect to USWS, and sleep in general, since the electrophysiological correlates of mammalian and avian SWS are not consistently present in reptiles. However, the presence of unilateral eye closure during behavioral sleep suggests that sleep, in some form, may occur unihemispherically in reptiles. Moreover, the use of unilateral eye opening for predator detection in both reptiles and birds suggests that avian unilateral eye closure, and possibly USWS, evolved from reptilian unilateral eye closure.

(5) There is a tendency to view USWS as a highly specialized form of sleep which evolved from bihemispheric...
sleep. Certainly, the observation that only highly specialized aquatic mammals display USWS supports this view. However, the apparent prevalence of USWS in birds and the possible existence of USWS in modern reptiles suggest that USWS is in fact the ancestral form of sleep. Even if closure of one eye is not associated with unihemispheric sleep in reptiles, this behavioral state may have served as a precursor for USWS. Ultimately, a final conclusion on the early stages of USWS evolution awaits future studies aimed at identifying potential neurophysiological correlates of unilateral eye closure in reptiles.

(6) The reasons for the relative absence of USWS in mammals remain obscure. The mammalian brain does not appear to be fundamentally constrained in its ability to develop USWS since this state has apparently arisen on at least three separate occasions in mammals (i.e. Cetacea, Pinnipedia and Sirenia). Even terrestrial mammals such as rats and humans exhibit slight interhemispheric asymmetries in EEG activity during BSWS, which may indicate a propensity for unihemispheric sleep. Alternatively, the limited occurrence of USWS suggests that there are costs associated with sleeping unihemispherically. Specifically, the reorganization of the central nervous system required for USWS may interfere with other adaptive brain functions, such as integrating the functions of both hemispheres. Consequently, the benefits of USWS may outweigh the costs only under extreme circumstances, such as sleeping at sea. The relative absence of USWS may also reflect the fact that other solutions to the conflict between sleep and wakefulness are easier to develop. For example, many mammals engage in extended periods of drowsiness, an intermediate state that may serve as a compromise between sleep and wakefulness. Ultimately, a greater understanding of the reasons for little USWS in mammals promises to provide insight into the functions of sleep in general.

(7) Although very little is known about the precise neurophysiological mechanisms involved in USWS, the control of USWS in aquatic mammals and birds appears to involve the coordination of functionally independent sleep and wakefulness regions, possibly located in the brainstem. A greater understanding of the mechanisms responsible for USWS promises to yield further insight into the mechanisms behind SWS in general.

(8) The discovery and investigation of USWS has significantly influenced our overall understanding of sleep. In particular, the finding that SWS is homeostatically regulated independently within each hemisphere in dolphins demonstrates that sleep serves a primary function for the brain. However, the specific aspects of wakefulness that cause and/or are dependent upon sleep remain unclear. The discovery of consistent shifts in hemispheric sleep time associated with functional lateralization in the developing avian brain provides a promising paradigm in which to address these questions. Clearly, the manner in which animals reconcile the fundamental conflict between sleep and wakefulness has and will continue to serve as a powerful tool for unraveling the functional reasons behind sleep.

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