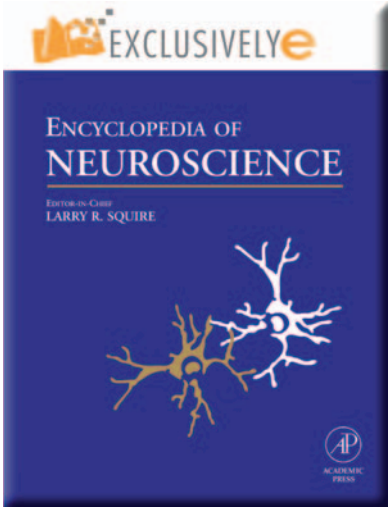

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Sleep and Sleep States: Phylogeny and Ontogeny

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Introduction

Sleep is a prominent yet enigmatic animal behavior. Despite the apparent ubiquity of sleep and associated vulnerability that (in part) defines sleep, the functions of sleep remain elusive. The seemingly simplest approach to determining sleep's functions would be to compare animals that sleep with those that do not and then determine whether a relationship exists between various traits thought to be functionally involved in sleep and the presence or absence of sleep. However all animals adequately studied sleep in one form or another making such comparisons currently impossible. Nevertheless, of the 30 or more animal phyla, detailed sleep information is known for only two: Chordata (includes vertebrates) and Arthropoda (includes insects). Thus, there is an opportunity for truly sleepless animals to be discovered in the future. For example, sponges (phylum: Porifera) are nearest to the base of the Metazoan phylogenetic tree and lack a nervous system. Based on the generally accepted belief that a plastic nervous system is the biological target benefiting from sleep, sponges should not sleep.

Determining whether sleep evolved many independent times or only once early in the evolution of animals is of fundamental importance in contemporary comparative sleep research. With the application of genetic approaches to the study of sleep, it has become important to establish homology between sleep in mammals and sleep in invertebrates, such as the fruit fly (*Drosophila melanogaster*), where genomes generally have less redundancy and are amenable to manipulation. Establishing homology between sleep in fruit flies and sleep in mammals would reinforce the usefulness of invertebrate models for determining the molecular correlates of human sleep. Even without homology at the molecular level, comparative studies can enhance our understanding of sleep. For instance, evolutionary convergence (i.e., distantly related species that independently evolved similar sleep-related traits) can provide insight into sleep by revealing overriding principles otherwise obscured by nonessential traits specific to one lineage.

The lack of a highly resolved cladogram of sleep across Animalia has not impeded comparative analyses of sleep. Indeed, many studies have tried to determine the relationships between the time species spend asleep and various constitutive, physiological, and ecological traits. Historically, this approach has been applied only in mammals, in which the electrophysiological correlates of sleep have been identified and quantified in a large number of species; however, a recent study provides insight into the correlates of sleep in birds as well. Although the strengths of functional hypotheses derived from comparative analyses are necessarily limited given the correlational nature of the data, the evolutionary patterns gleaned from such analyses, especially those that employ modern phylogenetic statistical techniques, provide a framework for the development of experimentally testable hypotheses.

As with comparing sleep among taxonomic groups, changes in sleep occurring during early development can provide insight into the functions of sleep. For example, changes in sleep duration, intensity, or the relative proportion of the two sleep states in mammals and birds over early ontogeny might be functionally linked to the concurrent development of the central nervous system. In this article, we review current knowledge of sleep in various taxonomic groups and over early ontogeny, and we relate important patterns to existing hypotheses for the functions of sleep. By doing so, we demonstrate the contribution that comparative sleep research has made to our greater understanding of why we sleep.

Behavioral Definition of Sleep

Sleep is foremost an animal behavior broadly characterized by quiescence with reduced responsiveness to stimuli. Sleep can be distinguished from other quiescent states (e.g., hibernation) by rapid reversibility to wakefulness with sufficient stimulation and homeostatic regulation; that is, sleep shows a compensatory increase in intensity or time following sleep loss. Sleeping animals often retreat to a species-specific location and assume a characteristic posture. Although the occurrence of concurrent sleep and swimming in some aquatic mammals is an exception to the quiescence criterion, these criteria apply to the vast majority of animals studied, ranging from insects to mammals and birds.

Mammalian Sleep

Behavioral sleep is associated with specific changes in brain activity. Placental and marsupial (or therian) mammals exhibit two basic states of sleep: slow-wave sleep (SWS), also known as non-rapid eye movement

(non-REM) sleep, and REM sleep. In nonhuman animals, the term SWS usually refers to all non-REM sleep, whereas SWS refers only to stages 3 and 4 of non-REM sleep in humans. SWS is characterized by an electroencephalogram (EEG) of low-frequency, high-amplitude activity arising from the large-scale synchronous slow oscillations of neurons in the neocortex. SWS is homeostatically regulated with SWS-related slow-wave activity (SWA) (typically 0.5–4.0 Hz EEG power density) reflecting the intensity of SWS, as arousal thresholds are correlated with the amount of SWA and SWA increases as a function of prior time awake. REM sleep is characterized by an EEG of high-frequency, low-amplitude activity similar to wakefulness, with a hippocampal theta rhythm (between 4 and 9 Hz or higher depending on the species) observed in some mammals, and an atonic electromyogram. Heart and respiratory rate are irregular during REM sleep, and thermoregulatory mechanisms that rely on motor control are diminished. REM sleep does not appear to have an intensity component, although the time spent in REM sleep can increase following sleep loss. In mammals that engage in extended periods of wakefulness, the time spent in SWS is the greatest and SWS-related SWA is the highest early in the subsequent sleep bout, whereas the proportion of time devoted to REM sleep increases toward the end of the sleep bout.

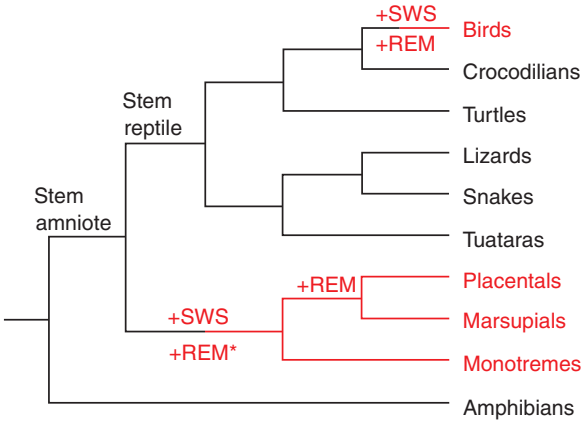

Figure 1 Cladogram for amniotes showing the evolutionary appearance of slow-wave sleep (SWS) and rapid eye movement (REM) sleep. Here, SWS and REM sleep arose independently in the most recent common ancestor to mammals and the most recent common ancestor to birds. However, in mammals, REM sleep first appeared in the common ancestor to all mammals as a heterogeneous state with neuronal activity in the brain stem indicative of REM sleep (+REM*) occurring concurrently with EEG activity indicative of SWS. In the most recent common ancestor to placental and marsupial mammals, REM sleep and SWS became segregated into two distinct states, with EEG activation occurring in conjunction with REM sleep-related brain stem activity. Evidence suggests that reptiles engage in SWS, but without the EEG slow-wave activity similar to that observed in mammals and birds.

Monotremes

The study of sleep in monotremes, an egg-laying order of mammals that are the closest extant relatives to therian mammals (Figure 1), may provide insight into sleep in the most recent common ancestor to therian mammals. An early study of the short-beaked echidna (*Tachyglossus aculeatus*) found only EEG activity indicative of SWS during sleep, thereby suggesting that REM sleep evolved after the appearance of the therian lineage. The electrophysiological correlates of sleep in the echidna were reexamined using a combination of EEG and brain stem neuronal recordings. As in the earlier study, REM sleep with cortical activation was not observed. However, during sleep with cortical slow waves, brain stem reticular neurons fired in an irregular pattern similar to that observed in placental mammals during REM sleep. This suggests that aspects of REM sleep in the brain stem and SWS in the cortex occur concurrently. Moreover, an EEG-based study of the duck-billed platypus (*Ornithorhynchus anatinus*) suggests that this mixed sleep state is typical of monotremes (Figure 1). Although neuronal activity in the brain stem was not recorded, the platypus showed frequent rapid eye movements and twitching of the head and bill, similar to that associated with REM sleep in therian mammals, whereas the cortex exhibited an EEG pattern indicative of SWS. Based on the incidence of twitches, the time spent in REM sleep was estimated at up to 8 h per day, the highest in any animal. A comparison of sleep times with therian mammals is difficult to interpret, however, given the heterogeneous nature of sleep and the absence of cortical correlates of REM sleep in monotremes.

Aquatic Mammals

Sleeping in the water poses a significant challenge for air-breathing mammals. Among Cetaceans, the electrophysiological correlates of sleep have been recorded only in the Odontocetes (dolphins and porpoises). Dolphins and porpoises exhibit unihemispheric SWS (USWS), a mixed state in which one cerebral hemisphere shows EEG activity characteristic of deep SWS while the other shows a pattern indistinguishable from wakefulness (Figure 2). Although the lighter stages of SWS can occur concurrently in both hemispheres, deep SWS occurs only unihemispherically. Evidence suggests that SWS is homeostatically regulated independently in the two hemispheres, which is an example of regional use-dependent SWS homeostasis, a phenomenon discovered only recently in terrestrial mammals including humans. Dolphins and porpoises swim and

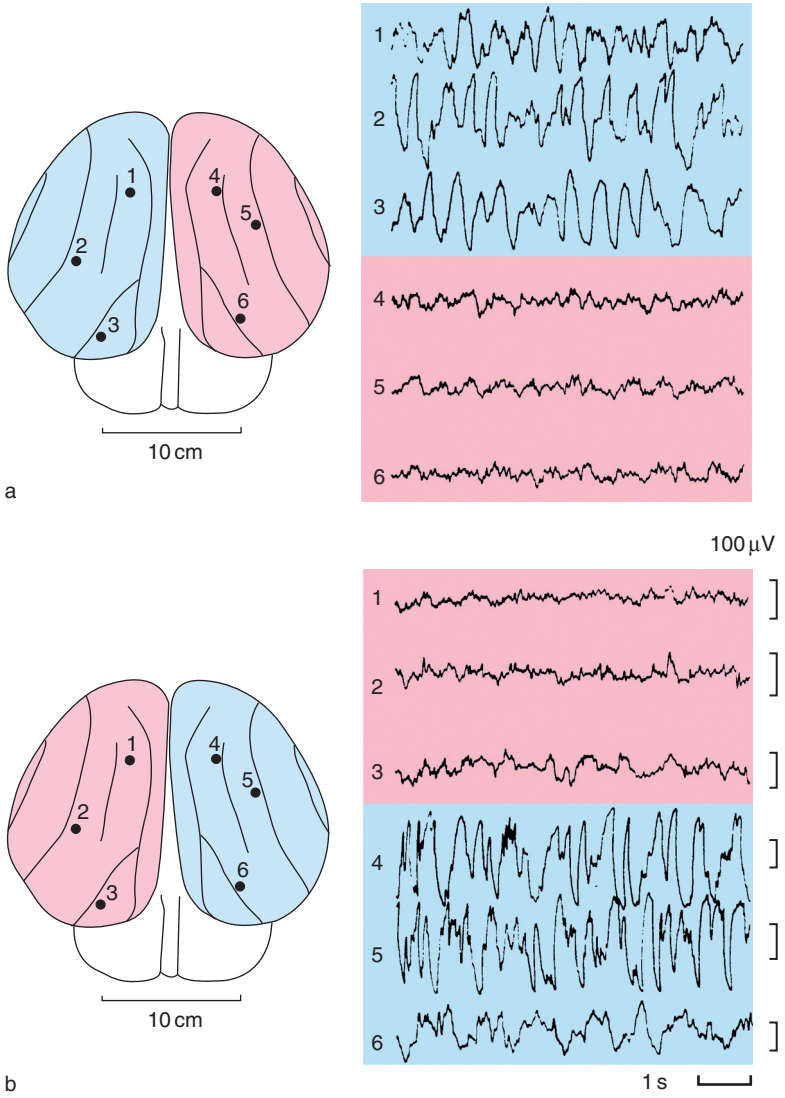

Figure 2 Examples of unihemispheric slow-wave sleep in the bottle-nosed dolphin (*Tursiops truncatus*). The EEG was recorded from the anterior, medial, and posterior neocortex. Note the high-amplitude, low-frequency activity indicative of slow-wave sleep (blue) in only the left (a) or the right (b) hemisphere concurrent with low-amplitude, high-frequency activity indicative of wakefulness (red) in the other hemisphere. Reproduced from Mukhameotv LM, Supin AY, and Polyakova IG (1977) Interhemispheric asymmetry of electroencephalographic sleep patterns in dolphins. *Brain Research* 134: 581–584, with permission from Elsevier.

surface to breath during USWS, but they can also float at the surface or rest motionless underwater. Given that the eye opposite the awake hemisphere remains open, USWS may allow dolphins and porpoises to monitor the environment for conspecifics and predators during sleep. Although behavioral signs of REM sleep (e.g., twitching and rapid eye movements) have been observed infrequently in quiescent Cetaceans, unequivocal REM sleep has not been recorded electrophysiologically, suggesting that Cetaceans have lost REM sleep secondarily. Nevertheless, REM sleep could occur in very small amounts or in a modified form in Cetaceans. Interestingly, manatees (order: Sirenia) also exhibit USWS and small amounts of REM sleep. Unlike Cetaceans and manatees, seals can sleep in the water and on the land. Seals in the family Phocidae hold their breath during periods of bilateral SWS and REM sleep underwater, whereas seals in the family Otariidae show interhemispheric asymmetries in the intensity of SWS while sleeping on the surface of the water.

Early Ontogeny of Mammalian Sleep

The time spent asleep changes greatly over early development. In mammals, newborns generally sleep the longest. This high amount of sleep declines over early ontogeny until it stabilizes at a species-specific level similar to that seen in adults. Sleep homeostasis

has been demonstrated in postnatal day 5 rats, before SWS and REM sleep appear in the EEG as differentiated states. Evidence suggests that SWS and REM sleep actually differentiate before the EEG shows sleep-related changes in cortical activity. The proportion of total sleep time devoted to REM sleep (%REM sleep) and SWS also changes greatly during the first postnatal weeks. Interestingly, the magnitude of these changes appears to be influenced by the degree of precociality at birth (Figure 3). Altricial mammals (those that are relatively more dependent on their parents at birth for food, warmth, and protection; e.g., rats and cats) show a marked reduction in %REM sleep through the first postnatal weeks (Figure 3) and show more exaggerated behavioral characteristics of REM sleep, such as rapid eye movements and twitches. Conversely, newborn precocial mammals (e.g., guinea pigs) are more developed relative to altricial mammals, and they exhibit a %REM sleep comparable with that of adults (Figure 3). These observations led (in part) to the hypothesis that REM sleep provides endogenous stimulation necessary for the early development of the central nervous system, particularly that related to the visual system. Indeed, experimental evidence implicates REM sleep in maturational processes of the visual system during early ontogeny. As discussed later, phylogenetic comparative analyses also support the idea that REM sleep facilitates early brain development.

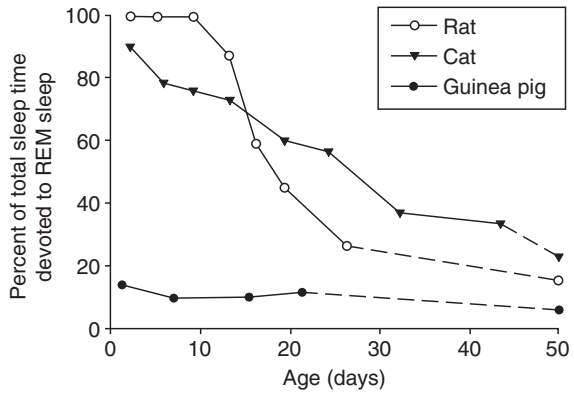

Figure 3 Changes in the percentage of total sleep time devoted to rapid eye movement (%REM) sleep across early development in the rat, cat, and guinea pig. In the altricial rat and cat, REM sleep constitutes most of total sleep time and decreases to levels close to that of adults approximately 1 month after birth. Conversely, %REM sleep in the precocial guinea pig is relatively stable over early ontogeny and into adulthood. Note, however, that even as adults, altricial species have higher %REM sleep than more precocial species. Reprinted Jouvet-Mounier D, Astic L, and Lacote D (1970) Ontogenesis of the states of sleep in rat, cat, and guinea pig during the first postnatal month. *Developmental Psychobiology* 2: 216–239, with permission from John Wiley & Sons, Inc.

Unlike newborn terrestrial mammals, newborn Cetacean calves are continuously active, swimming alongside their mothers during the first few weeks postpartum. Although electrophysiological recordings have not been obtained during this period of activity, the calves close one eye intermittently while swimming underwater and, therefore, might be engaging in USWS. However, calves are unlikely to be engaging in REM sleep if REM sleep is incompatible with swimming. The possible absence of REM sleep in newborn calves during their first weeks of life seemingly challenges theories for a functional role of REM sleep in brain development; however, given that Cetacean calves are extremely precocial, REM sleep could nonetheless play a role in brain development *in utero*.

Avian Sleep

Birds are a particularly interesting taxonomic group in which to study sleep. Birds have brains comparable in relative size to those of mammals and cognitive abilities that include vocal learning and tool making; however, much of the avian forebrain is organized in a manner markedly different from mammals. Although the dorsal two-thirds of the avian forebrain (a region formerly thought to be primarily striatal) is derived from the same embryonic neural tissue (the pallium) that gives rise to the mammalian neocortex, the avian pallium is arranged in a nuclear manner that lacks the true laminar organization of the neocortex (Figure 4). Interestingly, despite this difference in pallial organization, birds are the only nonmammalian taxonomic group to show unequivocal SWS and REM sleep (Figure 1).

Like mammalian SWS, avian SWS is characterized by an EEG of low-frequency, high-amplitude activity. Birds that sleep predominantly at night (e.g., domestic hens, *Gallus domesticus*; European blackbirds, *Turdus merula*; nonmigrating white-crowned sparrows, *Zonotrichia leucophrys gambelii*) show slow-wave activity during SWS that is greatest early in the night and gradually declines thereafter in a manner suggestive of mammalian-like SWS homeostasis. Indeed, we recently demonstrated that pigeons (*Columba livia*) show a compensatory increase in SWS-related low-frequency EEG power density following short-term sleep deprivation, suggesting that mammalian and avian sleep is regulated in a similar manner.

Avian REM sleep also shares several features in common with mammals. REM sleep is associated with closure of both eyes, rapid eye movements, occasional bill movements, and behavioral signs of reduced muscle tone such as dropping of the head. However, muscle atonia has been observed only in

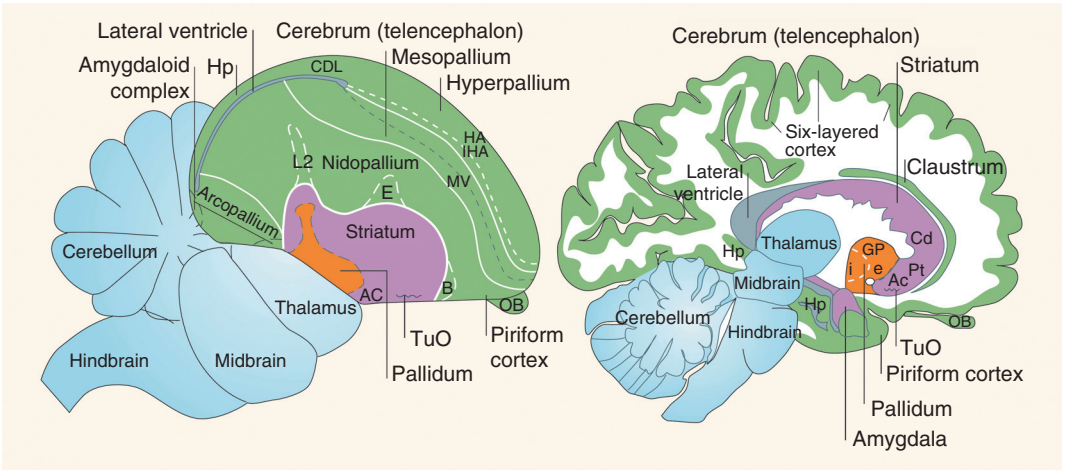

Figure 4 Modern consensus view of avian and mammalian brain relationships. Historically, much of the avian telencephalon was thought to be homologous to the mammalian striatum. However, converging lines of evidence demonstrate that the dorsal two-thirds of the avian telencephalon is actually derived from the pallium (green), the same neural tissue that gives rise to the mammalian neocortex. The new nomenclature reflecting this fundamental change in our understanding of brain evolution is depicted in the sagittal view of a zebra finch (left) and human (right) brain. Ac, accumbens; B, basorostralis; Cd, caudate nucleus; CDL, dorsal lateral corticoid area; E, entopallium; GP, globus pallidus (i, internal segment; e, external segment); HA, hyperpallium apicale; Hp, hippocampus; MV, mesopallium ventrale; IHA, interstitial hyperpallium apicale; L2, field L2; LPO, lobus parolfactorius; OB, olfactory bulb; Pt, putamen; TuO, olfactory tubercle. The several large, white regions are axon pathways (i.e., white matter) in the cerebrum. Lamina (cell-sparse zones separating brain subdivisions) are marked as solid white lines, primary sensory neuron populations are distinguished from neighboring regions by dashed white lines, and regions differing in cell density or size are demarcated by dashed gray lines. Reprinted by permission from Macmillan Publishers Ltd: *Nature Reviews Neuroscience* (Jarvis E, Gunturkun O, Bruce L, et al., 2005, 6: 151–159), Copyright 2005.

birds that can securely rest their head on the back. As in mammals, thermoregulatory responses are diminished during REM sleep. During REM sleep, the EEG reverts to a pattern similar to wakefulness, but often with lower amplitude. Unlike mammalian REM sleep, however, a hippocampal theta rhythm has not been found in birds. Episodes of REM sleep typically last 2–10 s and occur in clusters. The short duration of REM sleep episodes does not appear to be related to a need to maintain balance because REM sleep episodes are equally short when birds are sitting with their heads supported on their backs. In many birds, REM sleep increases throughout the night, in a manner similar to humans. In pigeons, this reflects an increase in the incidence and the duration of REM sleep episodes across the night. The proportion of total sleep time devoted to REM sleep appears to be lower in bird species (mean, 8%) than in mammalian species (mean, 17%). As in mammals, the time spent in REM sleep increases following sleep deprivation. Finally, since REM sleep and SWS have been recorded in every avian species investigated, both states were likely present in the most recent common dinosaur ancestor to birds (Figure 1).

Like aquatic mammals, birds often sleep with one eye open, a behavioral state associated with SWS in the hemisphere opposite the closed eye and EEG activity intermediate between wakefulness and SWS in the hemisphere opposite the open eye. Birds have the ability to switch from sleeping with both eyes closed to sleeping with one eye open in response to a perceived increase in the risk of predation. Here, birds direct the open eye toward the potential threat and are able to respond to threatening stimuli presented to the open eye. In contrast to mammals, where unihemispheric SWS occurs only in aquatic mammals, such interhemispheric asymmetries in slow-wave activity are common in birds and may be an ancestral trait. As in Cetaceans that swim in a coordinated manner during unihemispheric SWS, sleeping with one eye open and half the brain awake may allow birds to sleep during flight. Although there is strong evidence showing that birds, such as common swifts (*Apus apus*) and frigatebirds (*Fregata* sp.), spend periods lasting days to weeks or longer in constant flight, sleep in flight has not been confirmed with electrophysiological recordings.

Early Ontogeny of Avian Sleep

The ontogenetic development of avian sleep has been studied in relatively few species. In precocial chickens (*Gallus gallus*), the EEG correlates of SWS and REM sleep can be distinguished 1 day before hatching, whereas in the altricial pigeon (*Columba livia*) EEG activity is absent at hatching and does not resemble that of adults until 14 days later. Although it is

unclear whether chicken chicks show more or less REM sleep than adults shortly after hatching, the proportion of sleep allocated to REM sleep seems to reach adult levels within the first week post-hatch. Among altricial birds, the ontogeny of SWS and REM sleep has only been examined in magpies (*Pica pica*), in which juveniles sleep longer and have more REM sleep than adults. Additional studies on early sleep ontogenesis in species of greater taxonomic diversity are needed to determine whether the ontogenetic changes in sleep in altricial and precocial birds parallel those observed in mammals. Interestingly, chicken chicks that imprint on a moving object on the day of hatching exhibit more REM sleep during the first 3 h following imprinting than nonimprinted control chicks, suggesting that REM sleep may play a role in this acute form of learning. Sleep also appears to play a role in song learning in juvenile zebra finches (*Taeniopygia guttata*).

Sleep in Reptiles

The presence of SWS and REM sleep in all mammalian and avian species investigated suggests that either these states were present in the most recent common ancestor to extant mammals, birds, and reptiles or they evolved independently in mammals and birds. Several studies have attempted to distinguish between these alternatives by examining the electrophysiological correlates of sleep behavior in reptiles and, to a lesser extent, amphibians and fish. Unlike mammals and birds, however, where largely similar results have been obtained across species and laboratories, the results from reptiles have been less consistent and therefore subject to more diverse interpretations. Although some controversy persists, the EEG during reptilian sleep behavior typically shows intermittent high-voltage spikes arising from a background pattern similar to or slightly reduced in amplitude compared to quiet wakefulness. Because the incidence of spikes is correlated with arousal thresholds and increases following sleep deprivation, spikes appear to reflect sleep intensity. Studies have shown that these spikes originate in the reptilian hippocampus, thereby corroborating earlier pharmacological evidence indicating that reptilian spikes are comparable to similar spikes occurring in the mammalian hippocampus during SWS. Despite this similarity at the level of the hippocampus, however, the reptilian dorsal cortex does not generate concurrent high-amplitude slow waves typical of SWS in mammals and birds.

REM sleep has been reported in reptiles and fish based on the presence of eye, head, and limb movements during sleep. However, it remains unclear whether these behaviors truly reflect REM sleep-related twitching similar to that observed in mammals and birds or partial arousals from sleep. Although the presence of brain stem neural activity suggestive of REM sleep in sleeping echidnas raised the possibility that reptiles also exhibit REM sleep at the level of the brain stem, no sign of REM sleep was detected in the brain stem of sleeping turtles, despite the presence of neural structures involved in generating REM sleep in mammals. The presence of unequivocal SWS and REM sleep in mammals and birds, but not in reptiles, amphibians, or fish, suggests that these sleep states arose independently in the mammalian and avian lineages through convergent evolution (**Figure 1**).

Corticocortical Connectivity and SWS

Historically, the absence of slow waves in the EEG of sleeping reptiles has been attributed to the lack of a thick cortex similar to that which generates slow waves in mammals. However, the presence of slow waves in sleeping birds, despite the absence of a neocortex (**Figure 4**), demonstrates that the neocortex is not essential for the genesis of EEG slow waves. Instead, the extent of connections within the mammalian neocortex, avian hyperpallium, and reptilian dorsal cortex may explain why slow waves are present during sleep in mammals and birds but not reptiles (**Figure 5**). In mammals, corticocortical connections in layers II and III play an integral role in synchronizing the slow oscillation of neurons in a manner sufficient to generate slow waves in the EEG. In accord with the absence of slow waves in sleeping reptiles, the three-layered reptilian dorsal cortex lacks layers II and III, and it shows limited corticocortical connectivity (**Figure 5**). Furthermore, although birds lack a true neocortex, the hyperpallium shows extensive interconnectivity (**Figure 5**). Thus, the occurrence of sleep-related slow-wave activity in amniotes seems to be related to the extent of interconnectivity in the neocortex, hyperpallium, and dorsal cortex, although additional factors may also play a role.

A persistent question in sleep research is whether the EEG correlates of sleep are involved in the functions of sleep or simply reflect an epiphenomenon of the state. For example, the presence of slow waves in the EEG of sleeping mammals and birds may simply be an emergent property of a heavily interconnected neocortex and hyperpallium. Alternatively, as suggested by experimental work in mammals, the corticocortical connections that give rise to slow waves may also depend on slow waves to maintain the level of connectivity at an energetically and functionally adaptive level. Experimental evidence indicates that slow waves may also be involved in sleep-dependent memory processing and plasticity. Additional studies are needed, however, to determine whether slow

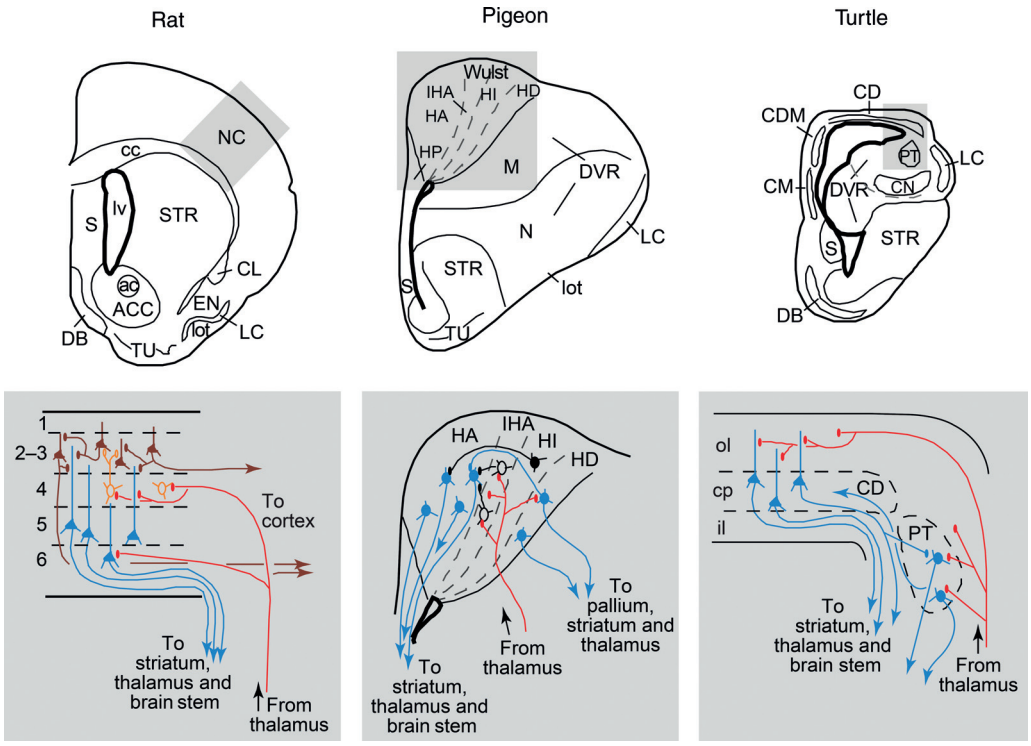

Figure 5 Comparison of the dorsal pallium in representative mammalian, avian, and reptilian species. The top row shows coronal cross sections through the brain. The area shaded in gray is expanded in the bottom row to show network connections. Note the comparatively high degree of interconnectivity in the rat neocortex and the pigeon Wulst (i.e., hyperpallium) compared to the turtle dorsal cortex. ac, anterior commissure; ACC, nucleus accumbens; cc, corpus callosum; CD, dorsal cortex; CDM, dorsomedial cortex; CL, claustrum; CM, medial cortex; CN, core nucleus of the DVR; cp, cell plate; DB, diagonal band of Broca; DVR, dorsal ventricular ridge; EN, endopiriform region; HA, hyperpallium apicale; HD, hyperpallium densocellulare; HI, hyperpallium intercalatum; HP, hippocampus; IHA, nucleus interstitialis hyperpallii apicalis; il, inner layer; LC, lateral cortex; lot, lateral olfactory tract; lv, lateral ventricle; M, mesopallium; N, nidopallium; NC, neocortex; ol, outer layer; PT, pallial thickening; S, septum; STR, striatum; TU, olfactory tubercle. Reproduced from Medina L and Reiner A (2000) Do birds possess homologues of mammalian primary visual, somatosensory and motor cortices? *Trends in Neurosciences* 23: 1–12, with permission from Elsevier.

waves evolved independently in mammals and birds (and not in reptiles) to maintain their heavily interconnected brains and associated cognitive abilities, or whether similar processes occur during reptilian sleep in a manner undetectable in the EEG. As indicated by the presence of hippocampal spikes during sleep, at least some of the neural correlates of SWS seem to be present in reptiles (Figure 1). A comparison of sleep-related gene expression among mammals, birds, and reptiles may clarify the evolutionary history of SWS and REM sleep.

Comparative Perspectives on the Functions of Sleep

More is known about sleep in mammals than in any other group of animals. Electrophysiological sleep data exist for just less than 100 mammalian species. An examination of this comparative data set reveals that the time spent in SWS and REM sleep varies greatly across Mammalia. Many studies have tried to identify the evolutionary determinants responsible for maintaining such interspecific variation in the structure of sleep. The identification of significant predictors of sleep times may help shed light on the functions of SWS and REM sleep. For example, species with a higher mass-specific basal metabolic rate (i.e., basal metabolic rate per gram of body mass) were once thought to engage in more SWS, a relationship that could support an energy conservation role for SWS, because metabolic rates are lower during SWS. Additionally, it was once thought that species with greater encephalization allocated a lower proportion of time spent sleeping to REM sleep, seemingly refuting a neurophysiological role for REM sleep, such as memory processing and plasticity. However, excluding our own analysis, all comparative studies of sleep treated each species (or, in one case, family) as a statistically independent unit. Independence is a basic assumption of all statistical analyses, but species cannot be considered independent because they are related to one another through common

ancestry. Phylogenetic comparative methods (e.g., independent contrasts) were developed by evolutionary biologists to deal with such interspecific relatedness in comparative studies; however, until recently, these procedures had not been used in comparative sleep research.

In our analysis, we controlled for shared evolutionary history among species using independent contrasts and analyzed our phylogenetically controlled data using a multivariate analysis that incorporated hypotheses for the functions of SWS and REM sleep. Many of our results were different from those in previous studies. Unlike all previous studies, we found that species with greater encephalization (i.e., brain mass controlling for body mass using regression) allocate a greater proportion of time asleep to REM sleep, thus providing the first comparative support for a neurophysiological role for REM sleep. Although no relationship was found between encephalization and the time spent in SWS, cumulative slow-wave activity may be the more accurate measure of SWS. Contrary to some comparative studies and expectations under the energy conservation hypothesis, we found that species with a higher residual basal metabolic rate (BMR) engage in less SWS and sleep less altogether. These relationships might reflect increased foraging demands associated with higher residual BMR and thus less time available for sleep. Nevertheless, mammals with higher residual BMRs may obtain functionally comparable amounts of SWS by engaging in more intense SWS, although such intensity data are largely unavailable. Alternatively, the restorative processes occurring during sleep could be achieved more quickly with higher residual BMR and thus take less time to accomplish.

Predation risk should be among the strongest selection pressures influencing how to structure sleep and how long to sleep because sleeping is dangerous. Interestingly, the vulnerability associated with sleep may depend on the sleep state. For example, due to high arousal thresholds, deep SWS and REM sleep may be particularly dangerous sleep states from an antipredator standpoint. Indeed, in the context of our multivariate models, we found that species sleeping at relatively exposed or risky locations in the wild engage in less REM sleep and allocate a lower proportion of sleep time to REM sleep in the laboratory. Although the time spent in SWS was largely independent of predation risk, once again, SWS intensity may respond more strongly to the risk of predation. As per previous studies, we found that species more precocial at birth engage in less REM sleep as adults, a relationship that was not mediated strongly by predation risk because precocial species did not generally sleep in more vulnerable locations than relatively altricial species. The degree of precociality as a predictor of REM sleep time in adults may reflect an extension of the ontogenetic changes in REM sleep shown in **Figure 3**, which supports the idea that REM sleep is particularly important in early brain development. However, why high levels of REM sleep during early ontogeny should persist in adults remains enigmatic.

Correlates of Avian SWS and REM Sleep

As discussed previously, the electrophysiological correlates of avian sleep are remarkably similar to those observed in mammals. In addition to these similarities, there is also great variation in the time avian species spend in SWS and REM sleep. Thus, an obvious question is whether birds share the same evolutionary determinants of SWS and REM sleep as mammals? We addressed this question by conducting the first electrophysiologically based comparative analysis of avian sleep architecture using the same phylogenetically controlled variables as in our mammalian analysis. Overall, we found that birds that sleep at relatively exposed sites in the wild engage in less SWS in the laboratory, but this was the only significant relationship identified. Thus, if relationships identified in mammals reflect functional aspects of sleep architecture, then the same functions may not apply broadly to birds.

Sleep in Invertebrates

More than 97% of all animal life is invertebrates, of which 80% are arthropods, the taxonomic group which includes insects. Surprisingly, however, of the 30 or more animal phyla, sleep has been studied in only 2: Chordata (includes vertebrates) and Arthropoda (includes insects), with much work having been focused on the fruit fly (*Drosophila melanogaster*) and the honeybee (*Apis mellifera*). Sleep in honeybees is characterized as a sustained period of quiescence accompanied by increased arousal thresholds and specific postures (e.g., antennal immobility). Optomotor interneurons in the optic lobes of forager honeybees show lowered sensitivity during the subjective night, when forager bees are often quiescent, than during the subjective day. Sleep in honeybees was shown to be homeostatically regulated as antennal immobility increased following 12 h of sleep deprivation. Sleep has also been demonstrated in scorpions (*Heterometrus* and *Pandinus* spp.), cockroaches (*Blaberus giganteus* and *Leucophaea maderae*), and crayfish (*Procambarus clarkii*). Also, preliminary work suggests that sleep is present in three additional animal phyla: Nematoda (*Caenorhabditis elegans*), cephalopods (*Octopus vulgaris* and *Sepia pharaonis*) in the phylum Mollusca, and box jellyfish (*Chironex fleckeri*) in the phylum Cnidaria.

Conclusions

Our understanding of how and why we sleep has been enhanced by studies examining the evolution and ontogeny of sleep. The presence of SWS and REM sleep in all avian and mammalian species studied, and their apparent absence in reptiles, suggests that these states arose independently twice: once in the ancestor to birds and once in the ancestor to mammals (Figure 1). A comparison of neurocytoarchitecture among homeotherms suggests that the degree of corticocortical (or palliopallial) connectivity is responsible for EEG slow-wave activity in mammals and birds. Interestingly, REM sleep-related cortical activation evolved independently in the ancestor to therian mammals and the ancestor to birds (Figure 1). The similarity in the electrophysiological correlates of behavioral sleep in homeotherms suggests similarities in functions, possibly related to having heavily interconnected brains and associated cognitive abilities. However, in phylogenetically controlled comparative analyses, the evolutionary determinants of sleep times in birds were markedly different from those identified in mammals. Identifying the reasons for these differences is a promising area for future work.

Our understanding of the evolution, ontogeny, and functions of sleep would benefit greatly from studies in species representing broader phylogenetic diversity. Here, the study of species nearest the base of the Metazoan phylogenetic tree would be most revealing. A systematic approach to selecting taxa for study should be employed that takes into consideration neuroanatomy, neurophysiology, and phylogenetic position in the context of current hypotheses for the functions of sleep. Future work should also expand existing genetic work on fruit flies and rats to nonmammalian vertebrate taxa and to nonarthropod invertebrate taxa. The success of these endeavors will depend on the broad collaboration of animal behaviorists, evolutionary biologists, geneticists, and neurophysiologists, but will do much to aid our greater understanding of sleep.

See also: Circadian Function and Therapeutic Potential of Melatonin in Humans; Mammalian Sleep and Circadian Rhythms: Flies; Sleep Architecture; Sleep Oscillations and PGO Waves; Sleep and Sleep States: Hippocampus–Neocortex Dialog; Sleep and Sleep States: Gene Expression; Sleep and Waking in Drosophila.

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