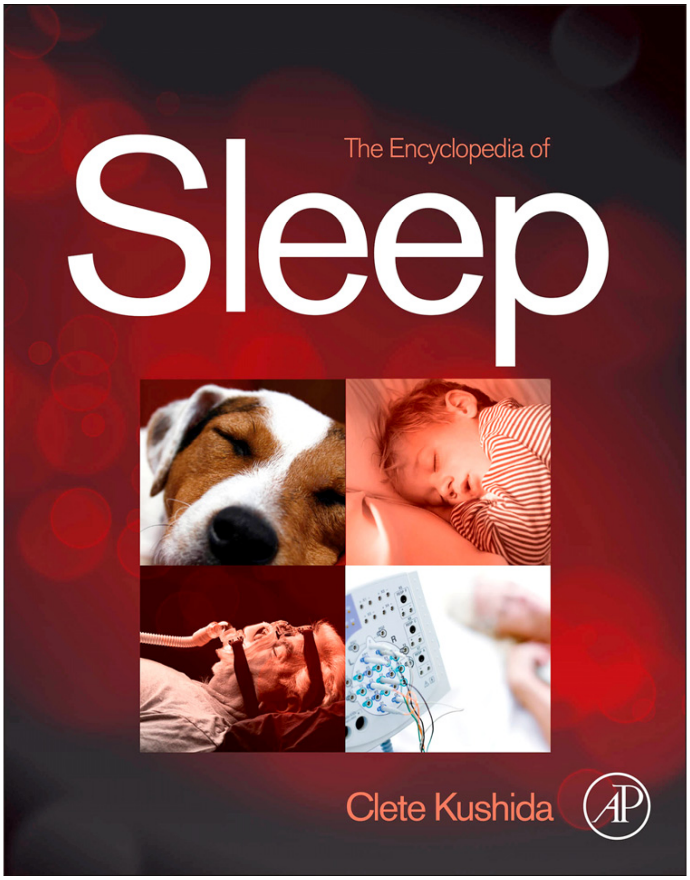

Lesku J.A. and Rattenborg N.C. (2013) Sleep in Birds. In: Kushida C. (ed.) The Encyclopedia of Sleep, vol. 1, pp. 51-56. Waltham, MA: Academic Press.

Sleep in Birds

J A Lesku, The University of Western Australia, Crawley, WA, Australia
N C Rattenborg, Max Planck Institute for Ornithology, Seewiesen, Germany

Glossary

Activation: Low-amplitude, high-frequency electroencephalogram activity, as observed in an alert mammal or bird, or during rapid eye movement (REM) sleep.

Derived: A term in evolutionary biology to qualify a trait(s) present in one animal (or one taxonomic group of animals), but not present in its most recent common ancestor.

Pallium: Part of the developing telencephalon that gives rise to the mammalian neocortex and the avian pallium.

Sharp waves/ripples: Highly synchronous bursts of hippocampal activity thought to reflect the transfer of information from the hippocampus to the prefrontal cortex.

Introduction

The function of the brain activity that defines rapid eye movement (REM) sleep and non-REM sleep in humans and other mammals is an unanswered question in neuroscience. One method for revealing the function of these states is examining natural variation in sleep across species. For instance, there is great variation in the time mammalian species spend in REM and non-REM sleep. If such variation reflects underlying differences in the need for sleep, then identifying the factors responsible for maintaining such variation should provide an insight into what sleep does. A similar 'evolutionary' approach seeks to explain the existence of mammalian-like REM and non-REM sleep outside of mammals. Such an approach is particularly useful for species that have independently evolved REM and non-REM sleep, as species distantly related to mammals will differ from them in more ways than more closely related species, thus reducing the number of candidate traits potentially related to the function of sleep.

Under this paradigm, birds become a particularly important taxonomic group through which to study sleep. Mammals and birds last shared a common ancestor more than 300 Ma (Figure 1). During this long period of genetic independence, brain organization diverged greatly between these groups. Notably, much of the mammalian brain is arranged as a laminar neocortex, whereas the developmentally homologous avian pallium is arranged in a largely nuclear manner. Despite this difference, there are remarkable similarities between mammals and birds, all of which arose through convergent evolution. Like mammals, birds have relatively large brains with a high degree of corticocortical (or palliopallial) connectivity, capable of performing complex cognition, such as tool manufacture and use. Interestingly, although birds are more closely related to crocodiles and other reptiles than to mammals, birds are the only nonmammalian group to engage in unequivocal REM and non-REM sleep. Indeed, these states have been described in all avian species studied, spanning 13 taxonomic orders, including the most evolutionarily basal (or 'ancient') group of living birds, the large flightless ratites (e.g., ostriches), and the weakly volant tinamous, suggesting that both states were present in the most recent common ancestor to living birds (Figure 1).

REM Sleep

As observed in mammals, the electroencephalogram (EEG) during avian REM sleep resembles the high-frequency, low-amplitude activity of an alert animal, but with bilateral eye closure and REMs (Figure 2). Mammalian-like muscle atonia has only rarely been reported in birds, but behavioral signs of reduced tone, such as head drooping, swaying, and sliding of the wings off the side of the body, are common. As in mammals, thermoregulatory responses are reduced during REM sleep compared to those during wakefulness and non-REM sleep. The incidence and duration of REM sleep episodes generally increases across the main sleep period in birds, a pattern also observed in mammals. Like mammals, avian REM sleep increases following sleep deprivation, reflecting REM sleep homeostasis. Unlike mammals, however, in whom episodes of REM sleep can be tens of minutes long, episodes of avian REM sleep are rarely longer than 10 s. Indeed, although songbirds may have more REM sleep than previously recognized, birds generally have less REM sleep overall when compared to mammals. Moreover, in contrast to mammals, REM sleep in birds is not accompanied by a hippocampal theta rhythm. Consequently, this pattern of brain activity is likely unimportant for the common function of REM sleep in mammals and birds. Functional hypotheses that account for the similarities between mammalian and avian REM sleep (e.g., pallial activation) are more likely to explain the fundamental (or core) purpose of this state, rather than aspects of REM sleep specific to only one group.

In mammals, the expression of REM sleep across early ontogeny is highly dependent on the degree of precociality at birth. Altricial species (those that are more dependent on their parents for food, warmth, etc.) show a marked reduction in the percentage of total sleep time allocated to REM sleep through the first postnatal weeks, as well as more exaggerated behavioral correlates of REM sleep, such as twitching and REMs. These observations led (in part) to the hypothesis that REM sleep provides endogenous stimulation necessary for the early development of the central nervous system, including the neocortex. Unfortunately, the ontogenetic development of avian sleep has been studied in too few species for much

http://dx.doi.org/10.1016/B978-0-12-378610-4.00012-7

Encyclopedia of Sleep, (2013), vol. 1, pp. 51-56

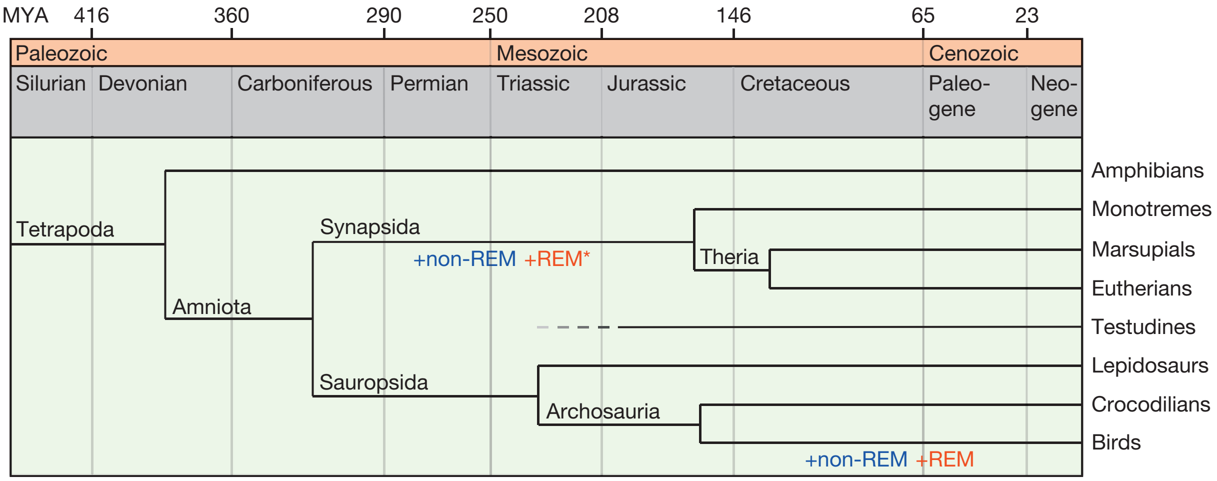

Figure 1 An evolutionary tree for tetrapods showing the convergent evolution of REM and non-REM sleep in mammals and birds. + REM* in the early mammalian lineage indicates the absence of cortical activation during REM sleep in monotremes. However, based on the presence of REM sleep-related brainstem activity in sleeping echidnas, and REMs and twitches of the head and bill in sleeping platypuses, at least some aspects of REM sleep were present in the most recent common ancestor to all mammals. REM sleep with cortical activation is present in marsupial and placental mammals. Time (millions of years ago, mya) is given at the top of the plot above geological era (brown) and period (gray). These evolutionary relationships are well established, except for the relatedness of testudines (turtles) to other reptiles. Hence, the root of testudines is not depicted. Lepidosaurs include lizards, snakes, and tuatara. Adapted from Rattenborg NC, Lesku JA and Martinez-Gonzalez D (2011) Evolutionary perspectives on the function of REM sleep. In: Mallick BN, Pandi-Perumal SR, McCarley RW and Morrison AR (eds.) *Rapid Eye Movement Sleep: Regulation and Function*, pp. 58–70. Cambridge: Cambridge University Press.

generalization. Additional studies on the development of sleep in young birds are needed to determine whether the ontogenetic changes in sleep in altricial and precocial birds parallel those observed in mammals.

Non-REM Sleep

Avian non-REM sleep, like mammalian non-REM sleep, is characterized by high-amplitude, slow (<4 Hz) waves (Figure 2), which reflect the synchronized $\sim$1 Hz oscillation of neuronal membrane potentials between a depolarized upstate with action potentials and a hyperpolarized downstate without. Although mammalian non-REM sleep is associated with thalamocortical spindles (8–14 Hz) and highly synchronous bursts of hippocampal activity – sharp waves/ripples – these brain rhythms are absent during avian non-REM sleep. Non-REM sleep in birds is further characterized by tonic muscle activity without phasic events and an absence of REMs, although brief, fast oscillations of the eyes have been reported in some species (e.g., Figure 2). Birds that consolidate wakefulness into a single block show a decline in slow-wave activity (SWA; $\sim$0.5–4.5 Hz power density) during sleep, suggestive of mammalian-like non-REM sleep homeostasis. Accordingly, short-term (6–8 h) sleep deprivation results in a global (or whole-brain) increase in SWA during subsequent sleep. As in mammals, SWA also increases and decreases locally in the avian brain following local use and disuse, respectively, during prior wakefulness, apparently reflecting underlying changes in synaptic strength. Because the amount of SWA is a function of prior wakefulness, and decreases as SWA-rich non-REM sleep accrues, SWA is thought to reflect homeostatically regulated processes linked to the function of non-REM sleep. Furthermore, because such regulation is shared between mammals and birds, SWA may serve a similar function in both groups.

Birds often keep one eye open during non-REM sleep. This behavior has been observed in many avian orders and may be an ancestral trait as reptiles also engage in unilateral eye closure. Unilateral eye closure in birds is associated with interhemispheric asymmetries in the level of SWA, with the hemisphere receiving projections from the closed eye showing greater SWA (i.e., more intense sleep). Such asymmetries are similar to those observed in sleeping cetaceans and fur seals; however, the magnitude of the asymmetry is generally smaller in birds. Nevertheless, in both birds and some aquatic mammals, interhemispheric asymmetries in SWA may serve as a compromise between competing needs for sleep and monitoring the local environment. Indeed, when compared to mallard ducks (*Anas platyrhynchos*) safely flanked by other birds, those sleeping exposed at the edge of a group engage in more unilateral eye closure and direct the open eye away from the group, as if watching for approaching predators. Sleep also competes with other demands, such as long-distance migration in songbirds. White-crowned sparrows (*Zonotrichia leucophrys gambelii*) in a migratory state reduce sleep by two-thirds when housed in the laboratory. A similar phenomenon has been observed in migratory Swainson's thrushes (*Catharus ustulatus*). The great reduction of sleep in migratory birds does not mean that sleep is unimportant or functionless, but rather that animals might have a mechanism to cope with sleep loss when it is advantageous to forego sleep. Consistent with this idea, migratory birds increase the time spent in a drowsy state (e.g., Figure 2), indicating that the need for sleep persists in these animals. Finally, although it has been suggested that birds engaging in long, nonstop flights sleep on the wing, this has not been confirmed with direct measures of brain activity.

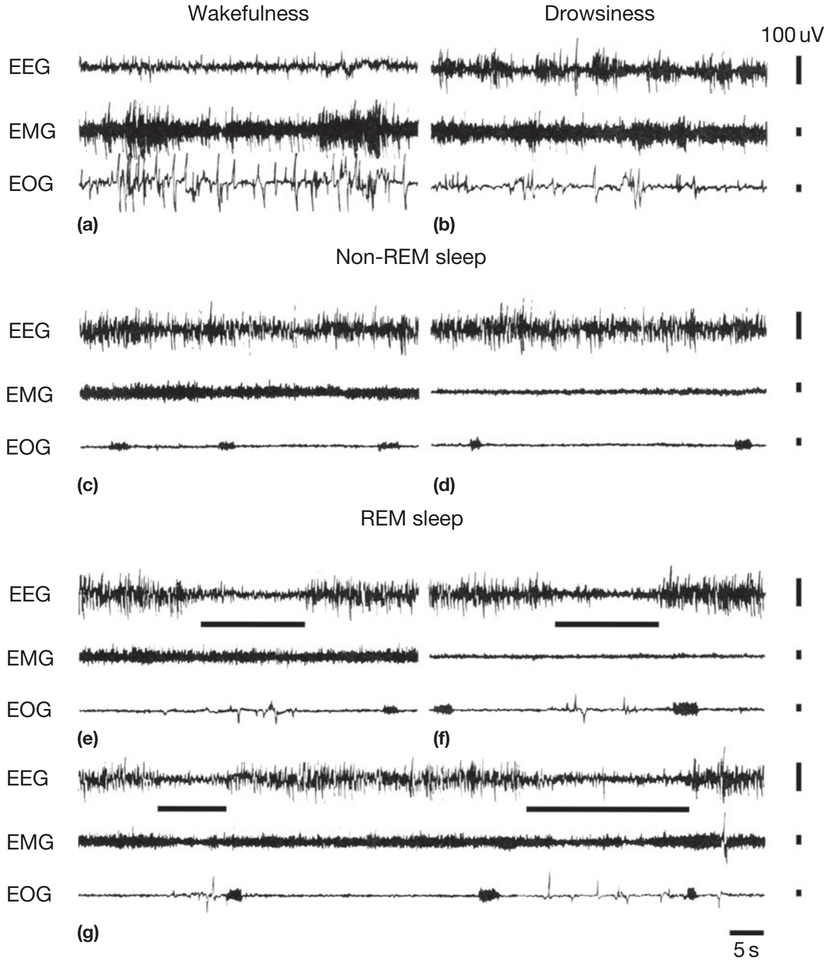

Figure 2 Typical avian electroencephalogram (EEG), electromyogram (EMG), and electrooculogram (EOG) activity, in this case from an emperor penguin (*Aptenodytes forsteri*), during wakefulness (a), drowsiness (b), non-REM sleep (c, d), and REM sleep (e–g). During drowsiness, the EEG alternates between typical patterns of wakefulness and non-REM sleep. Non-REM sleep is characterized by high-amplitude, slow waves with (c) or without (d) tonic EMG activity. The phasic EOG activity during non-REM sleep reflects brief, rapid oscillations of the eye. REM sleep (horizontal bar) can likewise occur with (e) or without (f, g) muscle tone. REMs are common during REM sleep. Modified from Buchet C, Dewasmes G, and Le Maho Y (1986) An electrophysiological and behavioral study of sleep in emperor penguins under natural ambient conditions. *Physiology & Behavior* 38: 331–335.

Non-REM Sleep and Connectivity

Any discussion on sleep in birds must necessarily include a discussion of sleep in reptiles, because birds are a derived type of reptile that evolved from bipedal dinosaurs (Figure 1). In contrast to the low-amplitude, fast waves, and high-amplitude, slow waves that define REM and non-REM sleep, respectively, in mammals and birds, most studies on sleeping reptiles report an EEG with voltages such as those observed during quiet wakefulness, but with intermittent high-voltage spikes originating from the medial cortex – the homologue of the mammalian hippocampus – and propagating to the dorsal cortex. Thus, reptiles lack sleep states comparable to those identified in mammals and birds, particularly the slow waves of non-REM sleep, which occupy the majority of sleep time in all mammals and birds studied. Importantly, in mammals and presumably birds, the slow oscillation underlying non-REM sleep is synchronized by corticocortical (or palliopallial) connectivity, as revealed in vivo, in vitro, and through computer simulations of brain activity, in a manner sufficient to generate EEG slow waves. Moreover, the mammalian brain has extensive connectivity in cortical layers II and III, which play an integral role in synchronizing the slow oscillation; the avian hyperpallium likewise shows extensive interconnectivity (Figure 3). In accordance with the absence of slow waves in sleeping reptiles, the three-layered reptilian dorsal cortex lacks layers II and III, and shows limited corticocortical connectivity (Figure 3). Thus, reptiles either lack the slow oscillation or the connectivity necessary to synchronize neuronal activity in a manner detectable in the EEG. As such, the occurrence of non-REM sleep-related SWA in amniotes seems to be related to the extent of interconnectivity in the neocortex, hyperpallium, and dorsal cortex.

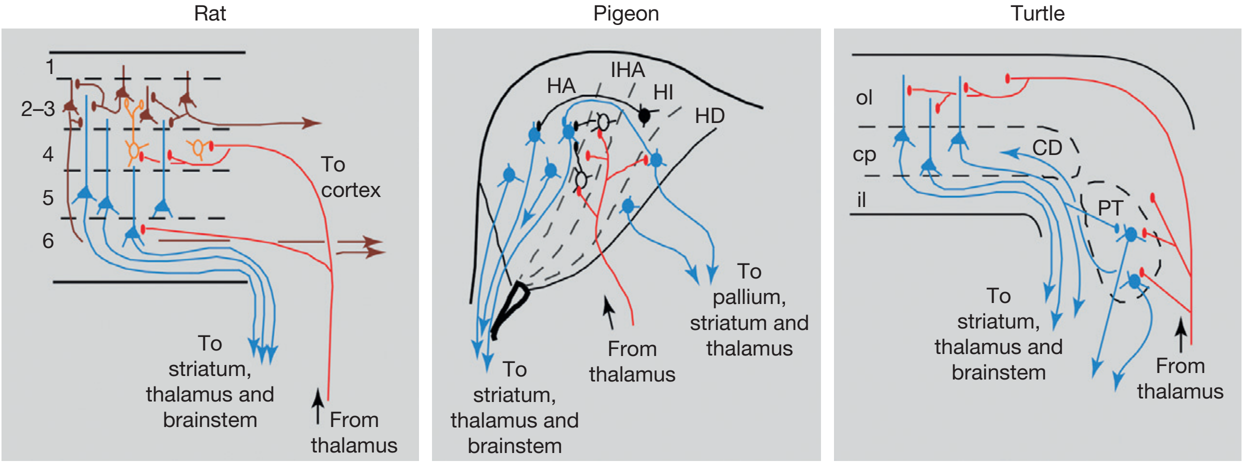

Figure 3 Comparison of the dorsal forebrain in representative mammalian (rat), avian (pigeon), and reptilian (turtle) species. Note the comparatively high degree of interconnectivity in the rat neocortex and the pigeon hyperpallium compared to the dorsal cortex in turtles (HA, hyperpallium apicale; IHA, nucleus interstitialis hyperpallii apicale; HI, hyperpallium intercalatum; HD, hyperpallium densocellulare; ol, outer layer; cp, cell plate; il, inner layer; CD, dorsal cortex; PT, pallial thickening). Modified 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.

The Slow Oscillation as a Shared Feature of Sleep in Mammals and Birds

Next, we provide two examples on how sleeping birds can provide insight into why mammals, including humans, sleep. First note that if a feature of the mammalian brain hypothesized to be functionally important for REM or non-REM sleep is present in birds, then this would provide additional support for its importance in mammals; alternatively, if this feature were absent in birds, despite similar states of sleep, then such a trait could either be functionally irrelevant in mammals or only relevant to certain aspects of mammalian sleep not involved in its core function. Here, we apply this reasoning to the slow oscillation underlying mammalian and avian non-REM sleep. There are two main hypotheses for the function of the slow oscillation in mammals. A prominent model for sleep-dependent memory consolidation proposes that the slow oscillation temporally couples hippocampal sharp waves/ripples with thalamocortical spindles to transfer memories from the hippocampus to the prefrontal cortex for more permanent storage. For this hypothesis to also apply to birds, and thus represent a core function of non-REM sleep, birds must exhibit hippocampal sharp waves/ripples, thalamocortical spindles, and neuroanatomical connections between the hippocampus and the avian equivalent of the prefrontal cortex, namely the nidopallium caudolaterale. However, none of these have been identified in birds. The absence of sharp waves/ripples, spindles, and requisite neuroanatomical connections in birds suggest that hippocampus-to-neocortex memory transfer is not a fundamental function of the slow oscillation.

The synaptic homeostasis hypothesis proposes that the slow oscillation reduces the number and strength of synapses, accumulated during prior wakefulness, to an optimal level. In the absence of such a mechanism, the energy and space demands of the brain would exceed sustainability, and neural circuits would saturate, reducing the ability to acquire new information. The synaptic homeostasis hypothesis is well supported by data from mammals. That is, synapses strengthen in response to brain use during wakefulness. This increase in connectivity results in a more synchronous slow oscillation during subsequent sleep, as reflected in the level of SWA. It is hypothesized that the slow oscillation not only reflects synaptic potentiation, but is also the mechanism by which non-REM sleep reduces the strength of synapses. Accordingly, stimulation at a frequency similar to the slow oscillation induces long-term depression, and genes involved in synaptic downscaling are preferentially expressed during sleep. By reducing synaptic strengths, synaptic homeostasis can account for some of the enhancements in performance observed post-sleep by increasing the signal-to-noise ratio of relevant circuits.

Unlike the model of hippocampus-to-neocortex memory transfer outlined earlier, the synaptic homeostasis hypothesis may well apply to sleeping birds. Like mammals, synapses appear to strengthen during wakefulness in birds, which increases the level of SWA during subsequent sleep, as revealed by local increases in SWA following enhanced local brain use during wakefulness in pigeons (Figure 4). In mammals, such changes are facilitated (in part) by the potentiating and synaptogenic action of neurotrophins, such as brain-derived neurotrophic factor (BDNF) expressed during wakefulness. Whether a similar relationship between BDNF and SWA exists in birds is unclear, but genes involved in long-term potentiation are expressed in the forebrain of awake white-crowned sparrows, and during sleep, genes involved in long-term depression are upregulated. However, whether such downscaling results in improvements on cognitive tests is largely unknown. Although sleep plays a role in song learning in juvenile zebra finches (*Taeniopygia guttata*), counter to expectations under the synaptic homeostasis hypothesis, song quality after a night of sleep is lower than at the end of the preceding day. Interestingly,

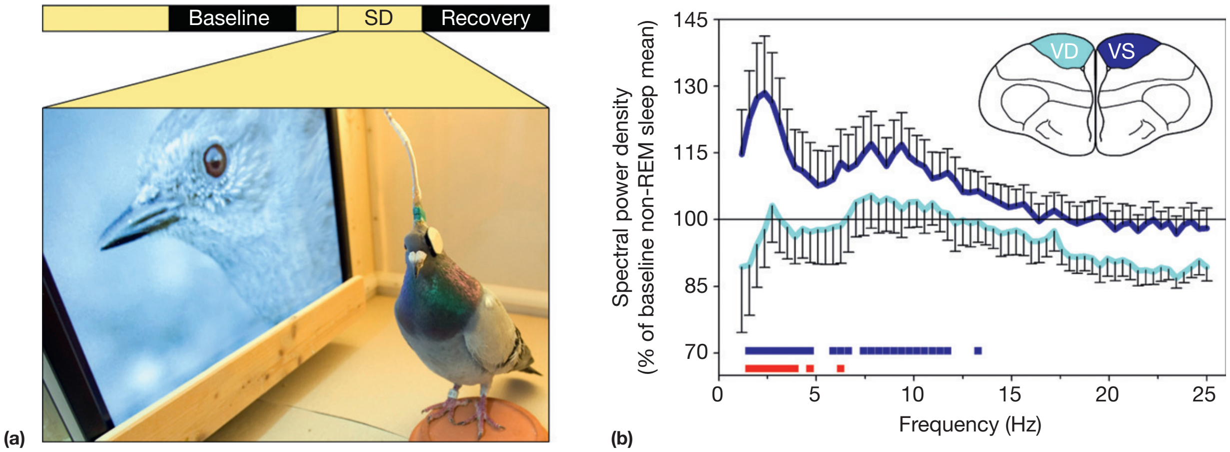

Figure 4 Avian local sleep homeostasis. (a) Experimental design: a 12 h baseline night follows an undisturbed day; 4 h into the next day, pigeons were kept entirely awake while watching David Attenborough's 'The Life of Birds' with only one eye; the birds were then allowed to engage in recovery sleep. (b) Spectral power density of non-REM sleep during the first 3 h of the recovery night for the visually-stimulated hyperpallium (VS, dark blue) and visually-deprived hyperpallium (VD, light blue) expressed as a percent of the baseline night mean (100% line). Coloured squares at the bottom of the plot reflect pairwise comparisons between power density of the VS hyperpallium during the recovery and baseline nights (dark blue), and the VS and VD hyperpallia during the recovery night (red). Note the significant <5 Hz inter-hyperpallial asymmetry in power density with greater power in the VS hyperpallium. Power density of the VD hyperpallium was not significantly different from baseline. Inset: drawing of a frontal view of a transverse section through the cerebrum of a pigeon highlighting the hyperpallium. Modified from Lesku JA, Vyssotski AL, Martinez-Gonzalez D, Wilzeck C, and Rattenborg NC (2011) Local sleep homeostasis in the avian brain: Convergence of sleep function in mammals and birds? *Proceedings of the Royal Society B: Biological Sciences* 278: 2419–2428.

however, over the long term, the degree to which the song deteriorates predicts the quality of the final song. Determining how non-REM sleep-mediated synaptic downscaling influences performance in birds is an important avenue for future research. Nevertheless, the available electrophysiological and molecular data suggest that such downscaling occurs in both mammals and birds, and may therefore represent a core function of non-REM sleep. Although recent evidence suggests that downscaling occurs in sleeping *Drosophila*, fruit flies appear to lack the mammal (or bird)-like slow oscillation during sleep. Consequently, *Drosophila* apparently have a downscaling mechanism unrelated to synchronous low-frequency neuronal activity. Understanding the reason for this difference may provide insight into whether slow oscillation-mediated downscaling serves an additional function not found in flies, or a more efficient means for downscaling in relatively complex brains, such as those found in mammals and birds.

Conclusions

Our understanding of why we sleep has been enhanced by studying sleep in birds. The presence of REM and non-REM sleep in all avian and most mammalian species studied, as well as their 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). The presence of REM sleep-related pallial activation in mammals and birds suggests that activation is the most functionally important feature of REM sleep. Hippocampus-to-neocortex memory transfer is likely a function of the slow oscillation, but only in mammals, whereas synaptic homeostasis may reflect a core function of the slow oscillation present in mammals and birds alike. Indeed, the highly interconnected brains of mammals and birds, capable of performing uniquely complex cognition, may depend on slow oscillation-mediated synaptic downscaling to maintain optimal functioning.

See also: **Background:** Mammalian Sleep; **Features, Factors, and Characteristics of SRBD:** Phylogeny and Animal Models; **Training and Research:** Planning Sleep-Related Animal and Translational Research.

Further Reading

Derégnaucourt S, Mitra PP, Feher O, Pytte C, and Tchernichovski O (2005) How sleep affects the developmental learning of bird song. *Nature* 433: 710–716.

Emery NJ and Clayton NS (2005) Evolution of the avian brain and intelligence. *Current Biology* 15: R946–R950.

Heller HC, Graf R, and Rautenberg W (1983) Circadian and arousal state influences on thermoregulation in the pigeon. *American Journal of Physiology* 245: R321–R328.

Jones S, Pfister-Genskow M, Benca RM, and Cirelli C (2008) Molecular correlates of sleep and wakefulness in the brain of the white-crowned sparrow. *Journal of Neurochemistry* 105: 46–62.

Lesku JA, Roth TC, Rattenborg NC, Amlaner CJ, and Lima SL (2009) History and future of comparative analyses in sleep research. *Neuroscience & Biobehavioral Reviews* 33: 1024–1036.

Lesku JA, Meyer LCR, Fuller A, et al. (2011) Ostriches sleep like platypuses. *PLoS ONE* 6: e23203.

Low PS, Shank SS, Sejnowski TJ, and Margoliash D (2008) Mammalian-like features of sleep structure in zebra finches. *Proceedings of the National Academy of Sciences of the United States of America* 105: 9081–9086.

Margoliash D and Schmidt MF (2009) Sleep, off-line processing, and vocal learning. *Brain Language*. http://dx.doi.org/10.1016/j.bandl.2009.09.005.

Martinez-Gonzalez D, Lesku JA, and Rattenborg NC (2008) Increased EEG spectral power density during sleep following short-term sleep deprivation in pigeons

(*Columba livia*): Evidence for avian sleep homeostasis. *Journal of Sleep Research* 17: 140–153.

Medina L and Abellán A (2009) Development and evolution of the pallium. *Seminars in Cell and Development Biology* 20: 698–711.

Ookawa T and Gotoh J (1964) Electroencephalographic study of chickens: Periodic recurrence of low voltage and fast waves during behavioral sleep. *Poultry Science* 43: 1603–1604.

Rattenborg NC (2007) Response to commentary on evolution of slow-wave sleep and palliopallial connectivity in mammals and birds: A hypothesis. *Brain Research Bulletin* 72: 187–193.

Rattenborg NC, Amlaner CJ, and Lima SL (2000) Behavioral, neurophysiological and evolutionary perspectives on unihemispheric sleep. *Neuroscience & Biobehavioral Reviews* 24: 817–842.

Rattenborg NC, Martinez-Gonzalez D, and Lesku JA (2009) Avian sleep homeostasis: Convergent evolution of complex brains, cognition and sleep functions in mammals and birds. *Neurosci & Biobehavioral Reviews* 33: 253–270.

Rattenborg NC, Martinez-Gonzalez D, Roth TC, and Pravosudov VV (2011) Hippocampal memory consolidation during sleep: A comparison of mammals and birds. *Biological Reviews* 86: 658–691.

Encyclopedia of Sleep, (2013), vol. 1, pp. 51-56