

EVOLUTION OF SLEEP

Niels C. Rattenborg, PhD & Dolores Martinez-Gonzalez, MD, PhD

Max Planck Institute for Ornithology - Seewiesen

Summary

By tracing the evolution of sleep we may gain insight into the functions of sleep in humans. Although all animals studied sleep, sleep-related brain activity differs across taxonomic groups. Such differences in brain activity may reflect either different mechanisms for performing similar functions or different sleep-related functions in different types of animals. Other than mammals, birds are the only group to exhibit both non-REM and REM sleep. The convergent evolution of mammal-like sleep states in birds may be related to the fact that mammals and birds also independently evolved relatively large brains capable of performing complex cognitive processes. Although sleep in mammals and birds is largely similar, rhythms implicated in processing hippocampal memories in mammals seem to be missing in birds. Consequently, these rhythms may be involved in mammal-specific functions, whereas activity patterns shared by mammals and birds (homeostatically regulated non-REM sleep slow waves and REM sleep activation) may be involved in more fundamental sleep functions.

Introduction

Why we sleep is a seemingly simple, yet unanswered, question. Despite extensive research and multiple ideas, no single theory accounts for all aspects of sleep. This suggests that either current theories need revision, or that sleep serves multiple functions. Indeed, once the need for sleep evolved, additional functions that could be performed more efficiently during sleep may have been relegated to occur during this

state (Mignot 2008). The relative importance of such primarily and secondarily evolved functions likely depends on the biology of a given taxonomic group. Consequently, one approach to identifying the function, or functions, of sleep is to trace its evolution through characterizing sleep in a variety of animals. If sleep itself, or certain sleep traits evolved in conjunction with certain biological traits (Rattenborg et al. 2009), or vary in conjunction with variation in such traits (*reviewed in* Lesku et al. 2009; *see also* Rattenborg et al. 2008), then there is a good chance that they are functionally interrelated. Perhaps the most straightforward example of this approach would be to compare animals that sleep with those that do not. However, no truly sleepless animals have been identified (Cirelli and Tononi 2008). Consequently, we focus on the insights gleaned from comparing the nature of sleep across the animal kingdom. In so doing, we hope to demonstrate how this comparative approach informs our understanding of human sleep.

Mammals

The Class Mammalia is comprised of three subclasses, eutherians (placentals), marsupials, and monotremes. In virtually all eutherian and marsupial mammals examined, sleep is composed of two states, rapid-eye movement (REM) and non-REM sleep. The general features of each state are largely similar across species. The electroencephalogram (EEG) during non-REM sleep (often simply referred to as slow wave sleep in non-human animals) is characterized by high-amplitude slow waves and thalamocortical spindles. Slow waves in the EEG reflect the synchronized slow oscillation of neuronal membrane potentials between a depolarized up-state with action potentials and a hyperpolarized down-state without action potentials (Steriade 2006). The amount of slow wave activity (SWA; 0.5-4.5 Hz spectral power density) during non-REM sleep increases and decreases as a function of time spent awake and asleep respectively, suggesting that SWA reflects a homeostatically regulated process linked to a restorative function (Borbély 2001). In contrast to non-REM sleep, REM sleep is characterized by low-amplitude, high-frequency EEG activity similar to that observed

during wakefulness. Given the presence of an activated brain occurring in a sleeping animal, REM sleep has also been referred to as paradoxical sleep.

Although sleep is usually viewed as a whole brain state, several marine mammals (cetaceans, fur seals, and manatees) are able to engage in non-REM sleep unihemispherically (Figure 1), an adaptation presumably linked to the need to surface to breathe during sleep (*reviewed in* Lyamin et al. 2008). Given that the eye contralateral to the awake hemisphere is usually open, this form of sleep may also enable marine mammals to monitor their environment for predators and conspecifics, such as their mothers, in the case of newborn dolphins (Lyamin et al. 2007). Because cetaceans, fur seals, and manatees do not share a common aquatic ancestor, this form of sleep evolved independently in each group. The evolution of unihemispheric non-REM sleep demonstrates unequivocally that sleep serves an essential function for the brain itself, rather than the body. Importantly, the exploratory study that first discovered unihemispheric non-REM sleep (Mukhametov et al. 1977) and a subsequent study showing that non-REM sleep is homeostatically regulated independently in each hemisphere (Oleksenko et al. 1992), were instrumental in forming current theories for the function of non-REM sleep in mammals, including humans (Krueger et al. 2008; Tononi and Cirelli 2006; Lima and Rattenborg 2007). Indeed, recent studies have found that even in humans, non-REM sleep is regulated locally in the neocortex (Huber et al. 2004). Interestingly, as with non-REM sleep, REM sleep may have also undergone modification in at least some marine mammals. Despite extensive effort, researchers have been unable to obtain unequivocal evidence for REM sleep in cetaceans, suggesting that it either occurs in a modified form that evades detection using standard criteria, or was lost entirely during the evolution of cetaceans. If the latter is correct, then as the only mammals known to have lost REM sleep, cetaceans provide a unique opportunity to examine the function of this poorly understood sleep state. Moreover, that REM sleep has been retained in all other mammals, despite the inherent risk of predation associated with this state (Lima et al. 2005; Lesku et al. 2009), underscores its, albeit poorly understood, biological importance.

Birds

Birds last shared a common ancestor with mammals approximately 300 million years ago (Figure 2). Because it remains unclear whether this as yet unidentified ancestor was even a reptile, modern taxonomists refer to it as the 'stem amniote', rather than the 'stem reptile'. The stem amniote gave rise to two main lineages, the Synapsida which gave rise to mammals, and the Sauropsida which gave rise to reptiles, including birds. Birds evolved from theropod dinosaurs (Xu and Norell 2004), members of the archosaurs. Other than birds, the only living archosaurs are the crocodylians. Despite being a derived type of reptile, avian sleep more closely resembles that of their distant mammalian relatives, than that of their closest crocodylian, or other reptilian, relatives (Rattenborg 2007). Other than mammals, only birds exhibit unequivocal non-REM sleep characterized by high-amplitude slow waves in the EEG, and REM sleep characterized by EEG activation similar to that occurring during wakefulness (Figure 2). The similarities between the mammalian and avian EEG are particularly interesting given that in contrast to the laminar arrangement of pallial neurons in the mammalian neocortex, developmentally homologous neurons are arranged in a largely nuclear manner in birds (Jarvis et al. 2005). In addition to the similar changes in pallial activity, as in mammals, REM sleep is associated with rapid eye movements, reduced muscle tone, and impaired thermoregulatory responses (Heller et al. 1983). In contrast to earlier studies (Tobler and Borbély 1988), recent studies have shown that non-REM sleep SWA is homeostatically regulated in birds in a manner similar to mammals (Martinez-Gonzalez et al. 2008; Rattenborg et al. 2009). Notably, as in mammals (Huber et al. 2004; Huber et al. 2006), non-REM sleep-related SWA increases and decreases locally in the avian brain in response to local increases and decreases in waking brain use, respectively (Lesku et al. 2011a). As such, functional hypotheses based on non-REM sleep homeostasis (e.g., Tononi and Cirelli 2006) may apply to both mammals and birds. As in mammals, the time spent in REM sleep is also homeostatically regulated in birds (Tobler and Borbély 1988, Martinez-Gonzalez et al. 2008). Finally, like marine mammals, birds can also engage in non-REM sleep with one eye open, a behavior associated with reduced SWA in the contralateral hemisphere (Rattenborg et al. 2000; Rattenborg and Amlaner 2010) that enables birds to visually

detect predators during sleep (Rattenborg et al. 1999). Birds that fly non-stop for days, weeks, or perhaps much longer, such as the European swift, might also engage in this form of sleep during flight, although this remains to be confirmed with EEG recordings (Rattenborg 2006).

Hippocampal differences

Despite the marked similarities between mammalian and avian sleep, there are also some potentially informative differences related to the hippocampus (*reviewed in* Rattenborg et al. 2011). Neurophysiological changes in hippocampal activity occurring across wakefulness, non-REM sleep, and REM sleep have been implicated in the encoding, consolidation, and retrieval of memories in mammals (Dieckelmann and Born 2010). In rats, the hippocampus generates a distinct theta rhythm during waking translational movement and REM sleep. The hippocampal theta rhythm occurring during wakefulness is thought to be involved in the encoding and retrieval of information as the animal moves through the environment (Buzsáki 2002). The role of the theta rhythm occurring during REM sleep is less clear, but may involve the offline processing of memories (Poe et al. 2000; Popa et al. 2010). When not in the theta mode, the hippocampus generates intermitted high-amplitude sharp waves and associated high-frequency ripples (Buzsáki 2002). Sharp wave/ripples (SWRs) occur during pauses in behavior, consummatory behaviors, quiet wakefulness, and to a greater extent during non-REM sleep. During non-REM sleep-related SWRs, hippocampal place cells - neurons that fire when an animal is in a specific place - are reactivated in a sequence similar to that which occurred during prior behavior. SWR-related reactivation (or replay) during non-REM sleep, occurs in conjunction with similar reactivation in the neocortex (Ji and Wilson 2007), giving support to the hypothesis that SWRs are involved in a systems-level memory consolidation process that results in the recall of certain types of memory becoming less dependent on the hippocampus and more dependent on the neocortex over time (i.e., the "memory transfer hypothesis"; Dieckelmann and Born 2010). Interestingly, the neocortical slow oscillation is thought to influence the timing of SWR-related reactivation in the hippocampus such that it occurs

during the up-state of the neocortical slow oscillation, and thereby in conjunction with thalamocortical spindling. The co-occurrence of reactivation and spindling is thought to create conditions conducive to the strengthening of the memory representation in the neocortex. Although aspects of this memory consolidation model remain debated, it is featured prominently here because, as discussed below, a comparative perspective may have bearing on this issue.

Neither of the reciprocal modes of hippocampal activity observed in mammals (i.e., theta and SWRs) has been detected in birds during wakefulness, non-REM sleep, or REM sleep (*reviewed in* Rattenborg et al. 2011). Although it is conceivable that differences in cytoarchitecture may obscure detection of mammal-like neuronal activity in EEG and local field potential recordings of the avian hippocampus, other lines of evidence suggest that theta and SWRs are in fact missing in birds. In mammals, theta and SWRs are thought to be the mechanisms through which the hippocampus communicates with high-order association regions, such as the prefrontal cortex (PFC) and entorhinal cortex, during wakefulness and sleep. In birds, the hippocampus shares few connections with comparable high-order regions in the forebrain, including the nidopallium caudolateral, the analogue of the mammalian PFC. Given this difference in hippocampal connectivity, it is perhaps not surprising that the avian hippocampus lacks neurophysiological rhythms comparable to those implicated in communicating with association areas in the mammalian neocortex. Interestingly, thalamocortical spindles, rhythms also implicated in this process, also seem to be missing in birds. Finally, the neurophysiological and neuroanatomical evidence is consistent with the absence of evidence for the "transfer" of memories from the hippocampus to extrahippocampal regions in the avian brain.

Collectively, this suggests that there is a fundamental difference between mammals and birds in brain organization and function related to the hippocampus (Rattenborg et al. 2011). Interestingly, this has direct bearing on our understanding of the function of sleep in mammals. The findings in birds lend support to the hypothesis that non-REM sleep is involved in transferring memories from temporary stores in the hippocampus to the neocortex for long-term storage in mammals; i.e., lacking

connections with most high-order association regions, the avian hippocampus has no need for rhythms implicated in this process in mammals. However, this also suggests that hippocampal memory transfer may be a mammal-specific function of non-REM sleep, whereas the feature of non-REM sleep shared by mammals and birds, homeostatically regulated slow waves, may be involved in a more fundamental sleep function (Figure 3). A similar line of reasoning also applies to REM sleep; hippocampal theta may be involved in a mammal-specific function, whereas neocortical (or pallial) activation in general, may reflect a more fundamental function.

Evolution of non-REM and REM sleep

The sleep traits shared by mammals and birds (i.e., non-REM sleep slow waves and REM sleep activation) were either inherited from a common ancestor with similar sleep traits, or evolved independently in each group in conjunction with other functionally interrelated traits. Studies from the most basal (or ancient) living mammals and birds, as well as studies from non-avian reptiles, amphibians, and fish suggest that several aspects of non-REM and REM sleep evolved independently in mammals and birds via a process of convergent evolution. Studies of the egg-laying monotremes, the most ancient group of living mammals, have greatly informed our understanding of REM sleep evolution. As in other more derived mammals, sleep in the echidna and platypus is characterized at the cortical level by high-amplitude slow waves typical of non-REM sleep (Allison and van Twyver 1972; Siegel et al. 1996; Siegel et al. 1999). In contrast to other mammals, however, cortical signs of REM sleep (i.e., EEG activation) do not appear to be present in monotremes (Allison and van Twyver 1972; Siegel et al. 1996; Siegel et al. 1999; *but see* Nicol et al. 2000). Nonetheless, signs of REM sleep occur in the brainstem concurrent with slow waves in the neocortex. In the echidna, brainstem units fire in an irregular pattern characteristic of REM sleep in eutherian mammals (Siegel et al. 1996), and the platypus shows behavioral correlates of such brainstem activity, including rapid-eye movements, and twitching of the neck and bill, while the neocortex exhibits slow waves (Siegel et al. 1999). Collectively, this work suggests that neocortical non-REM sleep was present in the ancestor to all extant mammals, but REM

sleep was only present at the level of the brainstem. Cortical activation during REM sleep apparently evolved later in the lineage leading to marsupial and eutherian mammals after it diverged from the lineage giving rise to monotremes.

A limitation of this evolutionary scenario is that it is based on only a few species of monotremes. Moreover, it is conceivable that the unusual features of monotreme sleep reflect a derived trait (e.g., as in cetaceans), rather than an ancestral trait. A recent study in the ostrich, a member of the most basal group of living birds, however, lends support to the notion that monotremes exhibit an ancestral sleep state (Lesku et al. 2011b). In all other, more derived birds examined, REM sleep is characterized by EEG activation, and therefore resembles REM sleep in marsupial and eutherian mammals. However, in the ostrich, REM sleep often resembles that of the platypus. Brainstem correlates of REM sleep include rapid-eye movements, and reduced muscle tone, which manifests as a dropping of the head from the upright posture held during preceding non-REM sleep. As in the platypus, this activity often occurs concurrently with high-amplitude, slow waves in the EEG characteristic of preceding non-REM sleep. The presence of this platypus-like, mixed REM/non-REM sleep state in a basal bird suggests that this state reflects a common step in a sequence leading to REM sleep as seen in more derived mammals and birds. Interestingly, in addition to the platypus-like sleep state, ostriches also exhibited periods of REM sleep with EEG activation. In this respect, ostriches may be further along this evolutionary sequence than monotremes. Combined, the work on basal mammals and birds, suggest that cortical activation is an evolutionary new feature of REM sleep, presumably involved in functions not found in more basal members of each group.

The similarities between sleep in basal mammals and birds seemingly suggest that non-avian reptiles and perhaps amphibians would exhibit a similar sleep state characterized by EEG slow waves and REM sleep-like brain stem activity. Although conflicting evidence exists in some cases, most of the available evidence suggests that this is not the case (*reviewed in* Hartse 1994; Rattenborg 2007). In non-avian reptiles, including the closest living crocodylian relatives of birds, the EEG typically shows a general reduction in background power during sleep, and the appearance of

intermittent, high-amplitude sharp waves. Although such sharp waves can occur during quiet wakefulness, they are usually associated with behavioral signs of sleep, including elevated arousal thresholds. Sharp waves also increase during recovery sleep following sleep deprivation. However, such sharp waves should not be confused with homeostatically regulated non-REM sleep-related slow waves in mammals and birds. Instead, several lines of evidence indicate that these sharp waves resemble hippocampal sharp waves observed most prominently during non-REM sleep in mammals. Both sharp waves increase during non-REM sleep following sleep deprivation and respond similarly to various pharmacological agents. Moreover, recent studies have confirmed that the sharp waves recorded in the dorsal cortex of sleeping reptiles originate in the adjacent medial cortex (i.e., reptilian hippocampus) and propagate to the dorsal cortex (Lorenzo et al. 1999). Consequently, although non-avian reptiles do not exhibit high-amplitude slow waves characteristic of non-REM sleep in mammals and birds, they do show signs of mammal-like non-REM sleep-related activity in the hippocampus. If this activity is in fact homologous with mammalian hippocampal sharp waves, then birds apparently lost this trait, as sharp waves have not been recorded in the avian hippocampus using methods that readily detect them in mammals and reptiles.

Reports of REM sleep in non-avian reptiles and fish are based largely on the occasional appearance of limb or eye movements during sleep (Hartse 1994). However, these behaviors have not been observed in all studies, and such movements may reflect brief arousals from sleep instead. REM sleep-related EEG activity, such as a cessation of sharp waves and the onset of a theta rhythm, have not been reported during these behaviors. A single study examined whether brainstem correlates of REM sleep are present in reptiles, as suggested by the work on basal mammals and birds. However, the turtles examined did not exhibit REM-like behaviors during sleep, and unlike the echidna, REM sleep-like brainstem activity was not observed (Eiland et al. 2001). Instead, the EEG showed sharp waves during sleep (as in other studies), and brainstem units fired at a rate reduced from wakefulness. Consequently, although additional studies are needed, the available data suggests that non-avian reptiles do not exhibit REM sleep at the level of the brainstem or cortex. Finally, although it is clear

that amphibians and fish sleep (Tobler 2011; Yokogawa et al. 2007), the electrophysiological correlates of their sleep behavior remain poorly studied and contradictory (Hartse 1994).

Why did non-REM and REM sleep evolve independently in mammals and birds? As for non-REM sleep, if we assume that reptilian sharp waves are indicative of non-REM sleep, then the question becomes, Why do only mammals and birds exhibit high-amplitude slow waves during non-REM sleep? From a mechanistic standpoint, this may be related to the fact that the manifestation of slow waves in the EEG is dependent upon a certain degree of corticocortical connectivity to synchronize the neocortical slow oscillations of neuronal membrane potentials (Amzica and Steriade 1995; Timofeev et al. 2000). In contrast to the heavily interconnected six-layer mammalian neocortex, the reptilian dorsal cortex consists of three layers. A dedicated thalamorecipient layer comparable to layer IV, and supragranular layers II-III involved in corticocortical communication in mammals are absent in reptiles (Medina and Reiner 2000). The comparatively limited connectivity in the dorsal cortex might thus contribute to the absence of sleep-related EEG slow waves (Rattenborg 2007). Alternatively, the slow oscillation may be missing altogether in the reptilian dorsal cortex; however, this remains to be determined. Interestingly, although most of the avian pallium is not organized in a laminar manner like the neocortex, dedicated thalamorecipient regions comparable to layer IV in the neocortex and extensive palliopallial connectivity evolved independently in birds (Medina and Reiner 2000). This connectivity presumably synchronizes pallial slow oscillations (Reiner et al. 2001) resulting in slow waves in the avian EEG. This mechanistic explanation raises the question of whether the slow wave is simply a functionless epiphenomenon of heavily interconnected sleeping brains, or is the slow wave involved in performing functions not found in animals lacking this phenomenon? Several lines of evidence from mammals, including humans, suggest that slow waves, or more precisely, the underlying slow oscillations, are a key component of the mechanisms responsible for sleep's role in memory consolidation (Huber et al. 2004; Marshall et al. 2006). The slow oscillation is also thought to be essential for synaptic downscaling, a process (intimately related to non-REM sleep homeostasis) that decreases synaptic weight (strength and number) accumulated

during wakefulness, which left unchecked would saturate the brain with synapses, leading to increased energy demands and an inability to acquire additional information (Tononi and Cirelli 2006). The presence of synchronized slow oscillations and associated non-REM sleep homeostasis in birds, suggests that processes tied to these aspects of sleep in mammals (e.g., synaptic downscaling) may also occur in birds (Lesku et al. 2011a). Finally, although avian sleep may not be involved in the systems level consolidation of hippocampal memories (see above), emerging evidence suggests that it may nonetheless play a role in other types of memory consolidation (Derégnaucourt et al. 2005; Jackson et al. 2008; Shank and Margoliash 2009, Brawn et al. 2010).

Sleep has been characterized in a variety of invertebrates, including nematodes (Raizen et al. 2008), mollusks (snails; Stephenson and Lewis 2011, and octopuses; Brown et al. 2006), and several arthropods (moths, cockroaches, bees, fruit flies, scorpions, and crayfish) (*reviewed in* Tobler 2011). Given the technical challenges, however, the neurophysiology of sleep in this group has been examined in only a few species. In the first study to show sleep-related changes in central nervous system activity in an invertebrate, Kaiser demonstrated that optomotor interneurons in the optic lobe of bees show reduced sensitivity to visual stimuli at night when bees exhibit a characteristic sleeping posture (Kaiser and Steiner-Kaiser 1983). In crayfish, the frequency of brain local field potential oscillations decreases during sleep when compared to wakefulness (Mendoza-Angeles et al. 2007), although the sleeping frequencies (15-20 Hz) remain markedly faster than those that characterize non-REM sleep in mammals and birds. In the fruit fly, behavioral sleep is characterized by a general decrease in local field potential activity across all frequencies (Nitz et al. 2002). Perhaps surprisingly, given the apparent absence of mammal/bird-like large-scale, synchronous slow oscillations in the brain of sleeping fruit flies, recent studies suggest that sleep may nonetheless play a role in memory consolidation and synaptic downscaling (Bushey et al. 2011; Donlea et al. 2011), processes thought to be mediated by slow oscillations in mammals and birds. Assuming that slow oscillations have not simply evaded detection in flies (and other animals), this suggests that sleep may perform similar functions via different mechanisms in different taxonomic groups. If

correct, this raises the question, Why do only mammals and birds require slow oscillations to perform conserved functions? Although this question awaits a definitive answer, given that large, complex brains capable of performing complex cognitive processes (e.g., tool manufacture and use, vocal learning, and episodic-like memory; Jarvis et al. 2005), and non-REM sleep (as well as REM sleep) coevolved independently in mammals and birds, it seems likely that these traits are functionally interrelated (Rattenborg et al. 2009; Lesku et al. 2011a). Perhaps such brains and cognitive capacities require different mechanisms to achieve similar functions. Alternatively, neurophysiological sleep traits unique to mammals and birds may also perform novel functions. In this respect, unraveling the functional significance of the apparent differences and similarities between sleep across the animal kingdom remains a powerful tool for revealing the functions of sleep as it manifests in the human brain.

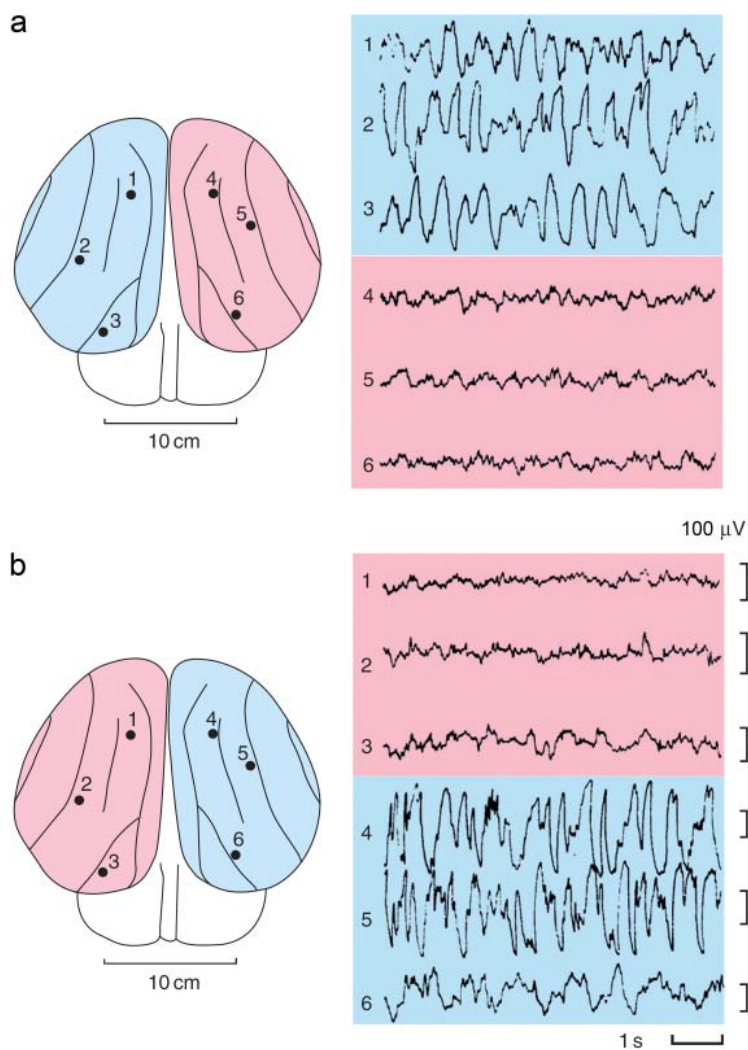


Figure 1:

Unihemispheric sleep in the bottlenose dolphin. Monopolar EEG recordings obtained from the anterior (1, 4), medial (2, 5) and posterior (3, 6) neocortex of each hemisphere. Note the high-voltage, low-frequency activity indicative of non-REM sleep (blue) in only the left (a) or right (b) hemisphere concurrent with low-voltage, high-frequency activity indicative of wakefulness (red) in the other hemisphere. Modified with permission from Mukhameotv et al. (1977).

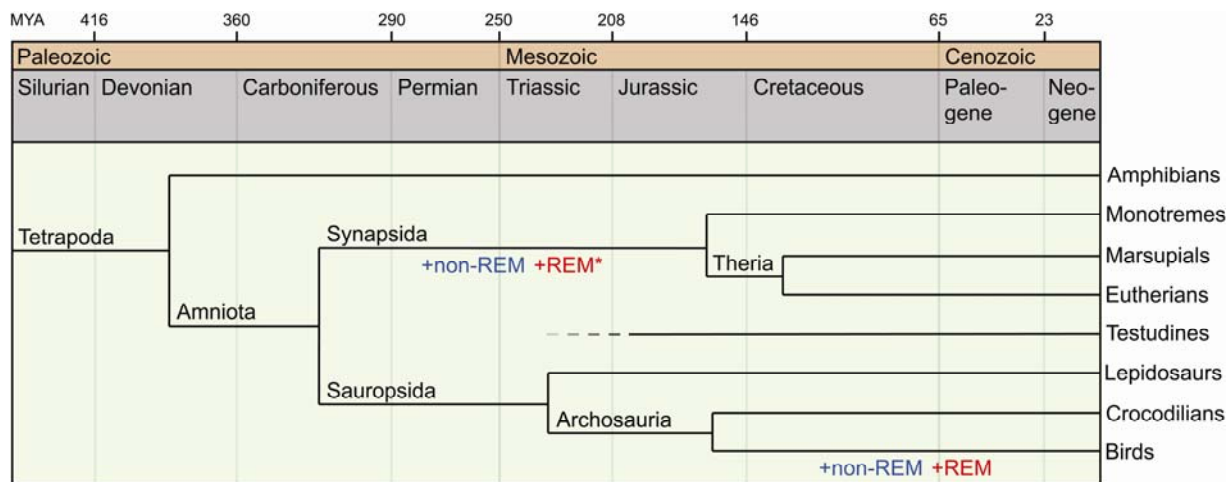


Figure 2

An evolutionary tree for tetrapods showing the convergent evolution of rapid-eye movement (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 neocortical 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 (grey). 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.

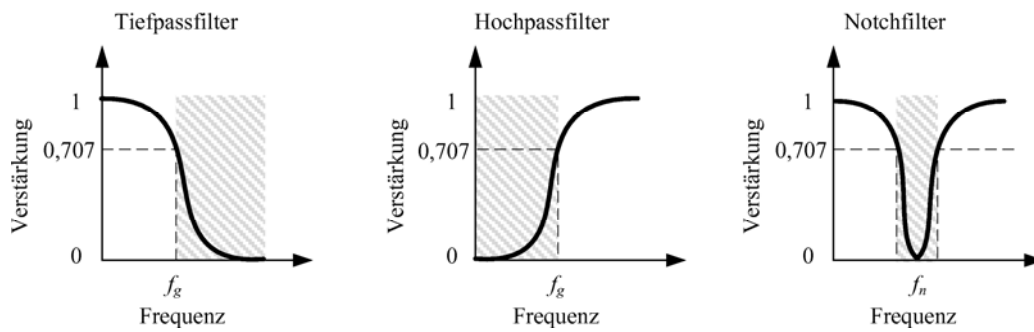


Figure 3

Functional implications of the similarities and differences between mammalian and avian sleep-related brain rhythms. REM: rapid eye movement. Rhythms shared by mammals and birds (grey overlap between circles) are likely to be involved in a fundamental function of each sleep state, whereas rhythms occurring only in mammals are most likely involved in mammal-specific functions. Figure reproduced from Rattenborg et al. (2011). Images: pigeon (Niels Rattenborg), rat reprinted from Macmillan Publishers Ltd: Nature Neuroscience, Mehta (2007).

Literature

- Allison T, van Twyver H, Goff WR: Electrophysiological studies of the echidna, *Tachyglossus aculeatus*. I. Waking and sleep. *Arch Ital Biol* 110: 145–84, 1972
- Amzica F, Steriade M: Disconnection of intracortical synaptic linkages disrupts synchronization of a slow oscillation. *J Neurosci* 15: 4658–77, 1995
- Borbély AA: From slow waves to sleep homeostasis: new perspectives. *Arch Ital Biol* 139: 53–61, 2001
- Brawn TP, Nusbaum HC, Margoliash, D: Sleep-dependent consolidation of auditory discrimination learning in adult starlings. *J Neurosci* 30: 609–13, 2010
- Brown ER, Piscopo S, De Stefano R, Giuditta A: Brain and behavioural evidence for rest-activity cycles in *Octopus vulgaris*. *Behav Brain Res* 172: 355–9, 2006
- Bushey D, Tononi G, Cirelli C: Sleep and synaptic homeostasis: structural evidence in *Drosophila*. *Science* 332: 1576–81, 2011
- Buzsáki G: Theta oscillations in the hippocampus. *Neuron* 33: 325–40, 2002
- Cirelli C, Tononi G: Is sleep essential? *PLoS Biol* 6: e216, 2008
- Derégnaucourt S, Mitra PP, Fehér O, Pytte C, Tchernichovski O: How sleep affects the developmental learning of bird song. *Nature* 433: 710–6, 2005
- Diekelmann S, Born, J: The memory function of sleep. *Nat Rev Neurosci* 11: 114–26, 2010
- Donlea JM, Thimgan MS, Suzuki Y, Gottschalk L, Shaw PJ: Inducing sleep by remote control facilitates memory consolidation in *Drosophila*. *Science* 332: 1571–6, 2011
- Eiland MM, Lyamin OI, Siegel JM: State-related discharge of neurons in the brainstem of freely moving box turtles, *Terrapene carolina major*. *Arch Ital Biol* 139: 23–36, 2001

- Hartse KM: Sleep in insects and nonmammalian vertebrates. In MH Kryger, T Roth, WC Dement (Eds.): Principles and Practice of Sleep Medicine, 2nd ed. Philadelphia: WB Saunders Co. 1994: 95-104
- Heller HC, Graf R, Rutenberg W: Circadian and arousal state influences on thermoregulation in the pigeon. *Am J Physiol* 245: R321–8, 1983
- Huber R, Ghilardi MF, Massimini M, Ferrarelli F, Riedner BA, Peterson MJ, Tononi G: Arm immobilization causes cortical plastic changes and locally decreases sleep slow wave activity. *Nat Neurosci* 9: 1169–76, 2006
- Huber R, Ghilardi MF, Massimini M, Tononi G: Local sleep and learning. *Nature* 430: 78–81, 2004
- Jackson C, McCabe BJ, Nicol AU, Grout AS, Brown MW, Horn G: Dynamics of a memory trace: effects of sleep on consolidation. *Curr Biol* 18: 393–400, 2008
- Jarvis ED, Gunturkun O, Bruce L, et al. Avian brains and a new understanding of vertebrate brain evolution. *Nat Rev Neurosci* 6: 151–9, 2005
- Ji D, Wilson MA: Coordinated memory replay in the visual cortex and hippocampus during sleep. *Nat Neurosci* 10: 100–7, 2007
- Kaiser W, Steiner-Kaiser J: Neuronal correlates of sleep, wakefulness and arousal in a diurnal insect. *Nature* 301: 707–9, 1983
- Krueger JM, Rector DM, Roy S, Van Dongen HP, Belenky G, Panksepp J: Sleep as a fundamental property of neuronal assemblies. *Nat Rev Neurosci* 9: 910–9, 2008
- Lesku JA, Meyer LCR, Fuller A, Maloney SK, Dell’Omo G, Vyssotski AL, Rattenborg NC: Ostriches sleep like platypuses. *PLoS One* in press, 2011b
- Lesku JA, Roth TC, Rattenborg NC, Amlaner CJ, Lima SL: History and future of comparative analyses in sleep research. *Neurosci Biobehav Rev* 33: 1024–36, 2009

- Lesku JA, Vyssotski AL, Martinez-Gonzalez D, Wilzeck C, Rattenborg NC: Local sleep homeostasis in the avian brain: convergence of sleep function in mammals and birds? *Proc Roy Soc B* in press, 2011a
- Lima SL, Rattenborg NC: A behavioural shutdown can make sleeping safer: a strategic perspective on the function of sleep. *Anim Behav* 74: 189–97, 2007
- Lima SL, Rattenborg NC, Lesku JA, Amlaner CJ: Sleeping under the risk of predation. *Anim Behav* 70: 723–36, 2005
- Lorenzo D, Macadar O, Velluti JC: Origin and propagation of spontaneous electrographic sharp waves in the in vitro turtle brain: a model of neuronal synchronization. *Clin Neurophysiol* 110: 1535–44, 1999
- Lyamin OI, Manger PR, Ridgway SH, Mukhametov LM, Siegel JM: Cetacean sleep: an unusual form of mammalian sleep. *Neurosci Biobehav Rev* 32: 1451–84, 2008
- Lyamin O, Pryaslova J, Kosenko P, Siegel J: Behavioral aspects of sleep in bottlenose dolphin mothers and their calves. *Physiol Behav* 92: 725–33, 2007
- Marshall L, Helgadottir H, Mölle M, Born J: Boosting slow oscillations during sleep potentiates memory. *Nature* 444: 610–3, 2006
- Martinez-Gonzalez D, Lesku JA, Rattenborg NC: Increased EEG spectral power density during sleep following short-term sleep deprivation in pigeons (*Columba livia*): evidence for avian sleep homeostasis. *J Sleep Res* 17: 140–153, 2008
- Medina L, Reiner A: Do birds possess homologues of mammalian primary visual, somatosensory and motor cortices? *Trends Neurosci* 23: 1–12, 2000
- Mehta MR: Cortico-hippocampal interaction during up-down states and memory consolidation. *Nat Neurosci* 10, 13–5, 2007
- Mendoza-Angeles K, Cabrera A, Hernandez-Falcon J, Ramón F: Slow waves during sleep in crayfish: a time-frequency analysis. *J Neurosci Meth* 162: 264–71, 2007

- Mignot E: Why we sleep: the temporal organization of recovery. *PLoS Biol* 6: e106, 2008
- Mukhametov LM, Supin AY, Polyakova IG: Interhemispheric asymmetry of electroencephalographic sleep patterns in dolphins. *Brain Res* 134: 581–4, 1977
- Nicol SC, Andersen NA, Phillips NH, Berger RJ: The echidna manifests typical characteristics of rapid eye movement sleep. *Neurosci Lett* 283: 49–52, 2000
- Nitz DA, van Swinderen B, Tononi G, Greenspan RJ: Electrophysiological correlates of rest and activity in *Drosophila melanogaster*. *Curr Biol* 12: 1934–40, 2002
- Oleksenko AI, Mukhametov LM, Polyakova IG, Supin AY, Kovalzon VM: Unihemispheric sleep deprivation in bottlenose dolphins. *J Sleep Res* 1: 40–4, 1992
- Poe GR, Nitz DA, McNaughton BL, Barnes CA: Experience-dependent phase-reversal of hippocampal neuron firing during REM sleep. *Brain Res* 855: 176–80, 2000
- Popa D, Duvarci S, Popescu AT, Léna C, Paré D: Coherent amygdalocortical theta promotes fear memory consolidation during paradoxical sleep. *Proc Nat Acad Sci USA* 107: 6516–9, 2010
- Raizen DM, Zimmerman JE, Maycock MH, Ta UD, You YJ, Sundaram MV, Pack AI: Lethargus is a *Caenorhabditis elegans* sleep-like state. *Nature* 451: 569–72, 2008
- Rattenborg NC: Do birds sleep in flight? *Naturwissenschaften* 93: 413–25, 2006
- Rattenborg NC: Response to commentary on evolution of slow wave sleep and palliopallial connectivity in mammals and birds: a hypothesis. *Brain Res Bull* 72: 187–93, 2007
- Rattenborg NC, Amlaner CJ: A bird's-eye view on the function of sleep. In P McNamara, RA Barton, CL Nunn (Eds.): *Evolution of Sleep: Phylogenetic and Functional Perspectives*. Cambridge: Cambridge University Press 2010: 145–71

- Rattenborg NC, Amlaner CJ, Lima SL: Behavioral, neurophysiological and evolutionary perspectives on unihemispheric sleep. *Neurosci Biobehav Rev* 24: 817–42, 2000
- Rattenborg NC, Lima SL, Amlaner CJ: Half-awake to the risk of predation. *Nature* 397: 397–8, 1999
- Rattenborg NC, Martinez-Gonzalez D, Lesku JA: Avian sleep homeostasis: convergent evolution of complex brains, cognition and sleep functions in mammals and birds. *Neurosci Biobehav Rev* 33: 253–70, 2009
- Rattenborg NC, Martinez-Gonzalez D, Roth TC, Pravosudov VV: Hippocampal memory consolidation during sleep: a comparison of mammals and birds. *Biol Rev Camb Philos Soc*, in press, 2011
- Rattenborg NC, Voirin B, Vyssotski AL, Kays RW, Spoelstra K, Kuemmeth F, Heidrich W, Wikelski M: Sleeping outside the box: electroencephalographic measures of sleep in sloths inhabiting a rainforest. *Biol Lett* 4: 402–5, 2008
- Reiner A, Stern EA, Wilson CJ: Physiology and morphology of intratelencephalically projecting corticostriatal-type neurons in pigeons as revealed by intracellular recording and cell filling. *Brain Behav Evol* 58: 101–14, 2001
- Shank SS, Margoliash D: Sleep and sensorimotor integration during early vocal learning in a songbird. *Nature* 458: 73–77, 2009
- Siegel JM, Manger PR, Nienhuis R, Fahringer HM, Pettigrew JD: The echidna *Tachyglossus aculeatus* combines REM and non-REM aspects in a single sleep state: implications for the evolution of sleep. *J Neurosci* 16: 3500–6, 1996
- Siegel JM, Manger PR, Nienhuis R, Fahringer HM, Shalita T, Pettigrew JD: Sleep in the platypus. *Neurosci* 91: 391–400, 1999
- Stephenson R, Lewis V: Behavioural evidence for a sleep-like quiescent state in a pulmonate mollusc, *Lymnaea stagnalis* (Linnaeus). *J Exp Biol* 214: 747–56, 2011

- Steriade M: Grouping of brain rhythms in corticothalamic systems. *Neurosci* 137: 1087–106, 2006
- Timofeev I, Grenier F, Bazhenov M, Sejnowski TJ, Steriade M: Origin of slow cortical oscillations in deafferented cortical slabs. *Cereb Cort* 10: 1185–1199, 2000
- Tobler I: Phylogeny of sleep regulation. In MH Kryger, T Roth, WC Dement (Eds.): *Principles and practice of sleep medicine*, 5th ed. Philadelphia, PA: Saunders 2011: 112–25
- Tobler I, Borbély AA: Sleep and EEG spectra in the pigeon (*Columba livia*) under baseline conditions and after sleep-deprivation. *J Comp Physiol A* 163: 729–38, 1988
- Tononi G, Cirelli C: Sleep function and synaptic homeostasis. *Sleep Med Rev* 10: 49–62, 2006
- Xu X, Norell MA: A new troodontid dinosaur from China with avian-like sleeping posture. *Nature* 431: 838–41, 2004
- Yokogawa T, Marin W, Faraco J, Pézeron G, Appelbaum L, Zhang J, Rosa F, Mourrain P, Mignot E: Characterization of sleep in zebrafish and insomnia in hypocretin receptor mutants. *PLoS Biol* 5: e277, 2007