The New Science of Dreaming

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Biological Aspects

EDITED BY DEIRDRE BARRETT
AND PATRICK McNAMARA

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Phylogeny of Sleep and Dreams

Patrick McNamara, Charles Nunn, Robert Barton,
Erica Harris, and Isabella Capellini

Sleep is a need. Whether we like it or not, we eventually succumb to sleep. It is an involuntary physiologic function. Like many other involuntary functions, sleep appears to be maintained around a homeostatic set point. Following sleep deprivation in many animals, there is a compensatory rebound in the amount of sleep engaged in, such that the lost sleep is "made-up," and a relatively constant daily amount of sleep is maintained over the long-term. The manifestations of sleep rebound phenomena vary across amniotes (that is, birds, reptiles, and mammals, the three classes of animals we will be considering in this chapter).

In mammals, the deprivation of NREM sleep leads to a remarkable increase in both the amount and intensity of NREM slow wave activity (SWA; or sleep stage IV in primates). This effect is well-known and has been demonstrated in a diverse array of species including humans, squirrel monkeys, rats, mice, Syrian and djungarian hamsters, cats, and ground squirrels (Tobler, 2005). REM sleep is also homeostatically regulated in mammals (as REM amounts are increased after REM deprivation), but it is unclear whether an intensity dimension exists for REM sleep. Outside of the order mammalia, the manifestations of sleep rebound vary. Some reptiles (crocodiles, for example) exhibit sleep-associated sharp slow waves and then rebound effects in the amount of these waves after rest deprivation. In birds, there is little physiologic evidence for sleep rebound effects after sleep deprivation, but behavioral signs of unihemispheric sleep (for example, increased duration of unilateral eye closures) are increased in some birds after sleep deprivation.

Returning to mammals, the phenomenon of post-deprivation sleep rebound points to a potential homeostatic function of sleep, meaning some physiologic process that is indexed by sleep duration (and intensity) and maintained at an optimal level. This homeostatic component of sleep raises the question of biologically imposed constraints on sleep and even potential adaptive functions of sleep. If sleep serves some primary homeostatic physiologic function, it operates under specific biologic constraints that in turn are likely to have an evolutionary history. Investigation of that history may reveal important information about sleep's functional correlates.

SLEEP-RELATED MENTATION (SRM)

SRM refers to any perceptual or mental state that occurs in temporal relation to some sleep process or state. In humans we call some forms of SRM "dreams," where "dreams" refer to extended experiences of emotion-laden imagery structured into story-like action episodes typically concerning the dreamer and his/her socially significant others. Many SRMs, however, are not dreams. Instead, they may be classified as hypnagogic images or fleeting and isolated thought fragments, ongoing ruminations, verbalizations, or all manner of other types of mentation. Whether or not REM or NREM sleep processes "cause" associated perceptual or mentation experiences is an empirical question that needs to be decided after appropriate investigation. There is little doubt, however, that each of the two major sleep states influences the SRM experience in humans.

REM dreams, for example, tend to be more vivid, story-like, emotional, and action-oriented than their NREM counterparts even after controlling for length of report, time of night, and other variables (Nielsen, 2000). On the assumption that brain activation patterns produce all forms of mentation, the most salient candidate for the production of REM dreams is the characteristic pattern of brain activation known to occur during a REM episode, namely intense amygdalar, limbic, temporal, and occipital activation along with prefrontal deactivation (Hobson, Pace-Schott, & Stickgold, 2000). This pattern of REM-associated brain activation suggests that memorable REM dreams (that is, dreams that are remembered upon awakening) should on average contain a greater number of unpleasant (fear, anger, rage, and so on) than pleasant emotions. Content analyses of hundreds of dreams have generally, though not invariably, supported this supposition (Domhoff, 2003; Revonsuo, 2000).

Clinical evidence also supports the supposition that REM-associated brain activity produces a tendency towards unpleasant emotional content in dreams. One can see clear evidence of negatively toned dream content in the dreams of patients who have lost the ability to inhibit the motor execution of internally experienced dreams (that is, the normal REM-associated inhibition of the spinal motor neurons is destroyed). Patients with so-called REM Behavior Disorder (RBD) may physically react to events transpiring in their dreams (Mahowald & Schenck, 2000). Up to 89 percent of the dreams reported by RBD patients involve the dreamer being attacked by an animal or a violent person. Patients react to the hallucinated attack in myriad and dangerous ways. Some individuals have been observed to jump out of bed and run wildly out of the room. Or individuals may attempt to jump out of windows or fire unloaded guns. In bed, they may punch, kick, or even attempt to strangle their bed partners (Olson, Boeve, & Silber, 2000). EEG measurements verify that patients are typically in REM sleep when these violent behaviors take place. The lack of spinal motor inhibition normally associated with REM is confirmed via similar neurophysiologic measurement. When the patient awakens, he is relatively lucid and has no difficulty providing a detailed verbal report of what was happening in the dream. The report typically involves threats of various kinds to the dreamer and closely matches the dreamer's violent bed behaviors.

Taken together, the hundreds of studies of dream content along with the evidence from RBD patients in the clinic strongly suggest that SRM in humans is real, measurable, and emotionally consequential. What about for nonhuman animals? We, of course, do not know for sure whether SRM occurs in other animals. Although nonhuman animals may not experience "dreaming" as defined above (and that is an open empirical question), they very likely experience some types of emotional, perceptual, or imagistic SRMs in tandem with the two major sleep states. If, as happens in REM sleep, selected networks of the brain were activated to levels high enough to support mentation in humans, we would expect some sort of mental processes to engage after such activation in nonhuman animals that have REM sleep.

But how can we verify whether SRM experiences occur in nonverbal animals? The experiences of patients with RBD suggest one strategy. In the case of patients with RBD, we observed overt dream enactment behaviors occurring in tandem with REM sleep when the normal REM-associated spinal motor inhibition process was abolished by disease. What if that spinal motor inhibition process was experimentally abolished in animals? Would we see "dream" enactment behaviors in these animals?

Very early in the modern study of REM sleep physiology (in the 1960s), Jouvet and colleagues (Jouvet, Vimont, Delorme, & Jouvet, 1964; described in Jouvet, 1999) managed to selectively lesion REM sleep-related spinal motor inhibition neurons in the brainstem of cats, thereby abolishing the normal REM sleep-associated muscle atonia in these animals. When the cats were observed to enter an episode of REM sleep, they began to enact their dreams. The cats hissed and arched their backs as if they were preparing to fight an imaginary enemy. Often they would act as if they were stalking an imaginary prey. These data indicate that other animals may experience something like dreams. At a minimum, the data suggests that there is a marked similarity in reactions at the behavioral level when REM biology is disinhibited.

Most of us have observed sleeping dogs yelp, bark, or growl in their sleep. Similar anecdotal reports of other animals of all kinds suggest that most animals experience hallucinatory and "emotional" imagery during sleep that is analogous to dreaming in humans. Even birds and reptiles emit vocalizations during sleep. As is the case with human beings, these sleep-related vocalizations may be functionally correlated with both SRM experiences and with the underlying sleep state the animal is in when it vocalizes.

The case of birds may be particularly instructive. Recent data on cellular activity levels in avian brain nuclei devoted to song shows that these cells are reactivated and perhaps resculpted during sleep. A form of apparent song replay may occur in selected sleep states in some birds. Dave and Margoliash (2000; see also Deregnacourt, Mitra, Feher, Pytte, & Tchernichovski, 2005), for example, showed that "spontaneous" activity of certain neurons known to be associated with song production during waking life are reactivated during sleep in a form that reproduces the sensorimotor activation patterns normally associated with song produced in waking life. In addition, the timing and structure of neuronal activity elicited in the bird's motor "cortex" by the playback of song during sleep matches neuronal activity during daytime singing. The authors concluded that, "these data suggest a model whereby sensorimotor correspondences are stored during singing but do not modify behavior, and off-line comparison (e.g., during sleep) of rehearsed motor output and predicted sensory feedback is used to adaptively shape motor output" (p. 812).

Is the bird "practicing" its song during sleep? Is the bird "hearing" or dreaming its song during sleep? How can we answer such questions? Some birds exhibit the typical mammalian pattern of muscle atonia during REM. If the REM-associated motor inhibition was experimentally abolished in one of these birds, would we see any form of dream enactment behavior? As far as we know, researchers have never investigated this possibility in birds. Complicating the picture is the fact that REM episodes in birds are quite short, typically lasting on the order of seconds. Moreover, song replay in birds is often associated with a non-REM form of sleep in these animals. Finally, most birds exhibit what is called "unihemispheric sleep," in which one hemisphere sleeps at a time (more about this later). Given this type of complexity regarding sleep processes in birds and in various types of other animals, investigation of SRMs in nonverbal animals is likely to be an arduous and complicated process.

Although investigation of SRM processes in nonhuman animals will certainly be difficult, such information can help us to better understand potential functions of sleep and dreams. If it turns out, for example, that other animals dream solely of potential predators or solely of potential mates or solely of potential prey, then that fact is one more clue that can be used to construct a theory of the functions of sleep itself. Data on existence and content of SRM in other animals might also throw some light on the vexed question of the origins and functions of thought and consciousness itself.

Thus, we are at an early stage in our understanding of whether other animals dream. Knowing the details of what they dream about is likely to be even further in the future. There are, however, data on the amount of REM sleep found in other animals, and this information can give us some clues as to the evolutionary history of at least one form of dreaming—REM dreaming, and of brain activation patterns during REM sleep. In humans, mentation can occur in tandem with both REM and NREM sleep states, but it is clear that REM-related mentation is more vivid and memorable. We will, therefore, focus this review on the phylogeny of *REM sleep*. We will return to the issue of SRM in nonhuman animals after reviewing the available data on comparative REM sleep. First, we consider how broad evolutionary patterns in sleep can be investigated by using the comparative method. Next, we examine broad patterns of sleep across vertebrates, with a special focus on mammals. Finally, we integrate these details on the distribution of sleep to formulate hypotheses for the origin of REM sleep and its links to dreaming. Our goals are to give an overview of interesting questions related to REM sleep and dreams and to provide this overview in a synthetic framework that allows for progress in answering questions about the phylogeny of SRM.

USING THE COMPARATIVE METHOD TO UNCOVER THE FUNCTION OF SLEEP

The study of variation in sleep patterns across species is an important method for studying potential adaptive functions of sleep. It is the only method we have for inferring the evolutionary history of sleep and the factors that have influenced variation in sleep patterns among animals. It is important, however, to keep in mind several points when considering the evolutionary history of something as complex as the mental functions associated with REM. Rattenborg and Amlaner (2002) point out that thinking on the evolution of sleep has to some extent been distorted by an assumption that mammals are more advanced than nonmammals. Yet in some respects, birds have developed innovations in cortical laminar structure not observed in mammals. Similarly, reptiles have developed quite complex neural systems specialized to transduce light information into neural impulses that regulate rest-activity cycles (e.g., a parietal eye, a complex pineal system, and a brain site homologous to the suprachiasmatic nucleus or SCN). Clearly, we should not be seduced by evolutionary stories that inevitably lead to big-brained species sitting at the top of "a great chain of being" as the most fit or successful. Nor should we deny the possibility that certain evolutionary transitions could have been crucial for development of big brains, resulting in the highly differentiated REM and NREM sleep states characteristic of primates. One can identify such transitions and innovations without necessarily assuming that earlier steps in the pathway represent evolutionary dead ends in the taxa in which those transitions occurred. Rather, it is likely that sleep traits in those taxa continued to evolve, sometimes slowly, sometimes rapidly, depending on selective pressures faced by the species. Thus, differences in sleep traits across different species may, as Rattenborg and Amlaner (2002) point out, "actually reflect alternative means of fulfilling similar functions, rather than indicating different levels of sleep evolution" (p. 7).

On the other hand, when one or more of the behavioral, physiologic, electrophysiologic, or functional components of, for example, primate sleep are identified in taxa whose divergence from primates can be accurately estimated (by using molecular phylogenies and comparative methods—see below), then we can make some reasonable estimates concerning when selected traits of REM and NREM emerged in the line leading to the primates. Furthermore, when selected sleep traits are found to be associated with significant ecologic, life history, or physiologic traits across taxa with similar biological characteristics, including brain structure, then it is reasonable to investigate those associations in hopes of revealing functional relationships.

In short, if we use appropriate methods—namely the comparative phylogenetic methods to be discussed next, then analyses of sleep variation can help us discern when a trait evolved, in how many lineages, how long it survived over evolutionary time, and what its consistent functional relationships are.

We need to discuss one final methodological point before summarizing the phylogenetic approach to comparative sleep analyses. Analyses of any kind are only as good as the input data they work with. So, we need to say something about the data used in these analyses. Phylogenetic comparative analyses are typically carried out on large-scale databases that contain data points on dozens of variables, including both sleep variables and variables hypothesized to be related to sleep, such as body size, metabolic rates, brain size, and so on. Previously constructed comparative databases suffered from a number of shortcomings related to the reliability and validity of the data contained in the databases. Campbell and Tobler (1984) published a dataset of total sleep durations for 168 species, but there were no values for REM and NREM. Zepelin (1989) constructed the largest published dataset on REM and NREM (rather than just total sleep) values (containing 84 species). Elgar, Pagel, and Harvey (1988) analyzed a dataset comprising 69 species. To control for phylogenetic associations, Elgar et al. (1988) calculated correlations across taxonomic families (by computing means for species within genera and then genera within families). This taxonomic approach reduced sample sizes to between 20 and 34. They found correlations between sleep quotas and body weight, metabolic rate, mode of development (altricial versus precocial), and latitude. Subsequently, Berger (1990) criticized this study on the grounds that a number of the species estimates were highly questionable. Elgar, Pagel, and Harvey (1990) responded correctly that comparative analysis is the only way to derive general conclusions about sleep, and largely replicated their original findings using a substantially reduced sample that omitted data not satisfying Berger's criteria for reliability (42 species, giving actual sample sizes of up to 30 families). Nevertheless, analyses on these comparative datasets have been stymied by inconsistent data collation and modest sample sizes.

Recent developments in comparative analytical methods can help address these methodologic problems concerning comparative sleep datasets. For example, use of the technique of phylogenetically controlled "independent contrasts" (Harvey & Pagel, 1991) obviates the need to exclude attention to variance below the level of the taxonomic family. Thus, we can avoid the problem of reduced sample sizes arising from a focus only at family-level analyses. In addition, a large proportion of the variance in comparative biological variables is commonly associated with two factors: body size (allometry) and, as mentioned previously, phylogeny. Allometry is the study of how a trait scales with body size. Previous studies of sleep quotas have found negative correlations between sleep durations and body size (Zepelin, 1994), but little attention has been paid to establishing quantitative scaling relationships, despite the fact that regularities in these relationships may be important for understanding sleep variation in general. For example, metabolic rate and body mass scale with an exponent of 0.75 predict similar scaling patterns for sleep traits under hypotheses involving metabolic functions.

With regard to the issue of phylogeny, problems arose in previous comparative analyses because it was not clear (using only standard multiple regression techniques) whether similarities/associations in sleep expression obtained between animals was because of common functional relationships or common phylogenetic ancestry. Animals that were related phylogenetically were all too often treated as wholly independent data points. Given that most statistical tests of sleep variables in the databases (implicitly) assumed independence of the species data, some of the results of these early analyses are likely to be invalid. One needs to take phylogeny into account to identify true functional relationships between sleep properties and some other non-sleep-related trait. Indeed, in order to properly describe even the allometric scaling of a sleep trait, it is necessary to take phylogenetic information into account (Harvey & Pagel, 1991; Nunn & Barton, 2000, 2001), yet this is rarely done in studies of sleep.

Properly conducted phylogenetic and allometric analyses can help us answer four fundamental questions about the evolution of REM sleep. First, do phylogenetically close species share similar REM properties (e.g., durations)? In other words, do sleep-related traits exhibit what Blomberg and Garland (2002) call "phylogenetic signal"? Second, which sleep-related traits are evolutionarily primitive for mammals and birds, which are derived, and which similarities have arisen through convergent evolution? Third, do groups of taxa exhibit different scaling relationships? A deeper understanding of allometric patterns can be accomplished through understanding such "grade shifts" (Nunn & Barton, 2000). Fourth, what general evolutionary relationships exist (a) between sleep traits and (b) between sleep traits and other aspects of behavioral biology and ecology? Have particular taxa evolved distinctively different patterns of sleep, and, if so, how do these patterns relate to other features of their biology?

We cannot yet answer these fascinating questions about the phylogeny of sleep states because no such phylogenetically controlled studies of comparative sleep values have yet been conducted. We mention the questions here to highlight these promising areas for future study.

THE PHYLOGENY OF SLEEP

We turn now to a survey of comparative sleep patterns, focusing mainly on mammals, but with a short excursus on reptiles and birds. Our aim is to reconstruct the basic picture of what is currently known about comparative patterns of sleep, particularly REM sleep. It will be necessary to keep this basic picture of the variability in expression of REM and NREM sleep patterns in mind so that we can ground our discussion of the evolutionary history of sleep related mentation firmly in the context of comparative sleep biology.

Reptiles

Electrophysiologic signs of active/REM sleep appear to be absent in most and perhaps all reptiles (Frank, 1999; but see Rial, Nicolau, Lopez-Garcia, & Almirall, 1993). Although behavioral signs of sleep are clearly observable in reptiles, correlations between these behavioral signs of sleep and selected EEG indices are difficult to evaluate given the complexities of recording sleep EEGs from the reptilian scalp and brain. Early studies by Flanigan and others (Flanigan, 1973; see review in Rial et al., 1993) reported an association between behavioral sleep and intermittent high-voltage spikes and sharp waves recorded from various brain structures in crocodilians, lizards, and turtles. Other investigations found no such association between behavioral sleep and high-amplitude spikes and sharp waves in the same animals. Hartse (1994) argued that high-amplitude spikes and sharp waves define a reptilian sleep state homologous with mammalian slow wave sleep (SWS).

High-voltage slow waves superimposed on the waking and sleeping EEG in reptiles has been proposed as a precursor of SWA found in the sleep of mammals. The equation of reptilian high-voltage slow waves (HVSW) with mammalian SWA is supported by findings (Flanigan, 1973) of compensatory rebound of sleep-related processes, including EEG spikes after sleep deprivation in reptiles. The latency to behavioral sleep was increased and the duration of behavioral sleep was increased as well after sleep deprivation in reptiles.

With respect to REM, the consensus at this point is that reptiles do not exhibit REM sleep. When Frank (1999) reviewed the literature on reptilian sleep, he concluded that no convincing evidence had yet been produced of REM-like states in reptiles. Rattenborg and Amlanar (2002) also called the evidence for REM in reptiles "equivocal." Even when investigators claim to have found signs of REM in a reptile, they have hitherto failed to report whether those signs were observed while the animal was unresponsive to the environment (that is, whether arousal thresholds were elevated) or other crucial signs of behavioral sleep. Thus, it may be that putative REM-like episodes in reptiles were actually brief arousals into waking or some form of waking. On the other hand, crocodilian sharp waves and spike activity in the context of HVSW may be a kind of indeterminate or mixed form of what is called in mammalian species REM and NREM, thus these reptiles may exhibit protoforms of REM.

Avian Sleep

As is the case with mammals, birds can be either monophasic (with one consolidated period of sleep per day) or polyphasic sleepers (with several short episodes of sleep per day). Birds appear to exhibit a special form of SWA and very little REM-like sleep. SWA in birds does not appear to be homeostatically regulated. SWA in NREM sleep in pigeons does not decline in the course of the dark period, suggesting that SWA in these animals is not building up chemicals that are depleted during waking. Moreover, SWA does not appear to increase after sleep deprivation. Unlike mammals, sleep spindles are absent during NREM in birds. In addition to this unusual form of SWA, birds also display sleep states that simultaneously combine features of both wakefulness and SWA. As in aquatic mammals, unilateral eye closure and unihemispheric SWA also occur in birds (reviewed in Rattenborg, Amlaner, & Lima, 2000a, 2000b).

Avian REM-like sleep states are associated with desynchronized EEG, impaired thermoregulation, and higher arousal thresholds, but they last only seconds and are cumulatively only one-quarter the amount typically reported for mammalian species. Moreover, there appears to be no REM rebound following REM sleep deprivation.

Mammals

Monotremes

Composed of three extant species (two species of echidna and the duck-billed platypus), monotremes are thought to have diverged from the main mammalian line before the divergence of marsupials and placental mammals. Allison, Van Twyver, and Goff's (1972) original polysomnographic study of the short-beaked echidna (*Tachyglossus aculeatus*) revealed unequivocal SWA but no EEG evidence for REM. Siegel, Manger, Nienhuis, Fahringer, and Pettigrew (1996) investigated activity of brain stem reticular neurons in the same species. Patterned reticular neuronal activity varies consistently in REM and NREM states. Discharge rate is high and irregular during REM and low and regular during SWA. Siegel et al. (1996) found irregular reticular discharge patterns during SWA in the short-beaked echidna (that is, a mixture of REM and NREM signs). REMs were also later recorded in the duck-billed platypus despite no overt EEG signs of REM. Thus, the monotremes appear to exhibit a mixed, indeterminate form of sleep containing elements of both REM and NREM mammalian sleep states. Siegel and others have suggested that mammalian sleep states emerged out of this primordial hybrid state of indeterminate sleep with SWS and REM segregating into independent brain states dependent on the central nervous system organization of the animal. Therefore, they assume that monotremes are primitive in their sleep pattern.

Nicol, Andersen, Phillips, and Berger (2000) reported REM characteristics in short-beaked echidnas. This conclusion was based on evidence for concurrent cortical activation, reduced tonic electromyogram (EMG) activity, and REMs under low, thermo-neutral, and high-ambient temperatures. Some investigators have suggested that the REM sleep episodes reported by Nicol et al. (2000) actually reflect a quiet waking state in these animals. These studies of REM in monotremes have led some researchers to acknowledge that some REM-like electrophysiologic activity occurs in these animals, but the work also confirms previous impressions that REM without signs of SWA does not occur in monotremes.

Marsupials

Marsupials show more definite signs of REM sleep. Affani, Vaccarezza, and Abellone (1967) and Van Twyver and Allison (1970) were the first to document abundant signs of REM in a marsupial—the opossum. Cicala, Albert, and Ulmer (1970) found evidence for REM in the red kangaroo. Walker and Berger (1980) obtained sleep and wakefulness recordings from infant opossums, aged 48 to 79 days, while they were in their mothers' pouches. The ontogenesis of sleep in this marsupial was similar to that of placental mammals: quiet sleep increased from 13 percent sleep time at 48 days to 55 percent at 79 days; conversely, active sleep decreased from 87 percent to 45 percent, respectively. The amplitude of the EEG during quiet sleep increased with age and quiet sleep could be categorized as SWA at 75 days. Active sleep could be identified as REM sleep at the same age.

Aquatic Mammals

Members of three different orders that contain aquatic mammals—cetaceans (dolphins, porpoises, and whales), carnivores (seals, sea lions, and otters), and sirenians (manatees)—typically engage in unihemispheric sleep (Manger, 2006; Rattenborg, Amlaner, & Lima, 2000b). Cetaceans exhibit a clear form of unihemispheric slow wave sleep (USWS) or SWS. EEG signs of REM are absent, but cetaceans show other behavioral signs of REM, including REMs, penile erections, and muscle twitching. The two main families of pinnipeds, Otariidae (sea lions and fur seals) and Phocidae (true seals), show both unihemispheric and bihemispheric forms of sleep. Phocids sleep underwater (obviously holding their breath) while both hemispheres exhibit either REM or SWS. Amazonian manatees (*Trichechus inunguis*) also sleep underwater, exhibiting three sleep states: bihemispheric REM, bihemispheric SWS, and USWS. Both hemispheres awaken to surface and breathe.

In addition, when REM occurs in marine mammals, it is always bihemispheric. The bilateral nature of REM may be considered one of its distinctive features, and the brain structure of certain marine mammals apparently cannot mediate this feature. Interestingly, even when REM occurs in aquatic mammals, it never occurs unihemispherically.

Explanations of the loss of EEG signs of REM and the emergence of unihemisphericity of SWS in some aquatic mammals tend to reference the supposed incompatibility of REM-related muscle atonia and breathing while underwater. Yet, as just described, other marine mammals with similar ecologic constraints (e.g., Phocidae) evidence bihemispheric REM sleep even while underwater. Given the alternative means of sleeping and breathing in water observed in pinnipeds, one would expect manatees (order Sirenia) to display either of these strategies. As noted, however, Amazonian manatees (*T. inunguis*) exhibit REM sleep, bihemispheric SWS, and USWS. Thus, unlike that in dolphins and Otariidae, USWS in manatees is not clearly linked to surfacing to breathe. Nor does the relatively advanced nature of the cetacean brain help explain the absence of REM in cetaceans. Other mammals with equally developed brains (such as primates) express abundant REM.

As in birds, unihemispheric sleep in aquatic mammals is associated with keeping one eye open during sleep, which is typically the eye contralateral to the hemisphere that is asleep. Goley (1999; quoted in Rattenborg & Amlaner, 2002) reported that when a group of sleeping Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) swim slowly side-by-side in a group, they preferentially direct the open eye toward the other dolphins, as if watching to maintain contact with the group. Interestingly, when the sleeping dolphins switched, on an hourly basis, from one side of the group to the other, the side with the open eye switched accordingly, as if allowing each hemisphere a turn to sleep. Many male dolphins form coalitions to monopolize access to fertile females (Connor, Smolker, & Richards, 1992). Therefore, the open eye may be monitoring the herded female.

Placental Terrestrial Mammals

Behavioral measures of REM in placental mammals include a species-specific body posture and sleeping site, reduced physical activity (quiescence), reduced muscle tone, reduction in neck/nuchal muscle tone, paralysis of the antigravity muscles in some species, increased arousal threshold, and rapid reversibility to wakefulness. Physiologic indices of REM sleep include significant lability in the autonomic nervous system (ANS), cardiovascular, and respiratory systems, along with increases in metabolism. Electrophysiologic measures of REM include low-voltage fast waves, REMs, theta rhythms in the hippocampus, and pontine-geniculo-occipital (PGO) waves. Electrophysiologic measures of NREM include HVSW, spindles, and k-complexes. Functional indices of sleep include increased amounts of sleep after sleep deprivation, and increased sleep intensity after sleep deprivation.

REM sleep accounts for about 22 percent of total sleep time in adult humans. Humans are about average among placental mammals in the amount of REM sleep they engage in. Although the cortex is activated in REM, arousal thresholds are higher in REM than in the waking state (or in SWS for that matter). The phasic aspects of REM, such as intermittent muscle twitching, ANS discharges, and REM, occur in some mammals in association with bursts of PGO waves. Placental mammals (with the possible exception of humans) also exhibit a theta rhythm in the hippocampal formation during REM. Like NREM sleep, REM deprivation results in a rebound phenomenon, indicating that a certain amount of REM is required and must be made up if lost.

Although REM of placental mammals engages both hemispheres, it respects a very selective pattern of brain activation. Certain brain sites are activated while others are deactivated. Recent positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies of the sleeping brain in both humans and nonhuman animals have revealed that REM demonstrates high activation levels in pontine, midbrain tegmentum, portions of the cingulate gyrus, temporal-limbic, and amygdaloid sites, and orbitofrontal cortex. Conversely, other brain regions are deactivated in REM, including dorsolateral prefrontal areas, portions of the parietal cortex, and the cingulate (Braun et al., 1997; Hobson, Stickgold, & Pace-Schott, 1998; Maquet & Franck, 1997; Maquet et al., 1996; Nofzinger, Mintun, Wiseman, Kupfer, & Moore, 1997).

Finally, when human subjects are awakened from REM, they generally report a narrative involving the dreamer, with vivid visual detail, unpleasant emotions, and occasional bizarre and improbable events (Domhoff, 2003; Hobson & Pace-Schott, 2002; Nielsen, 2000; Strauch & Meier, 1996). As mentioned above there is reason to believe that other placental mammals "dream."

The foregoing brief review of the phylogenetic distribution of the two major sleep states suggests that the emergence of distinct sleep states, and in particular of REM, began with the evolution of reptiles and reaches its most derived state in terrestrial placental mammals. Avian REM is peculiar in that it is brief and shows no rebound effects. Nor does Avian NREM show clear rebound effects. Avian NREM furthermore appears to be unihemispheric. Turning now to the reptiles, REM-like sleep states do not occur at all in reptiles. On the other hand, the presence of HVSWs, as well as sharp spikes in the EEG of reptilian sleep, suggests that what is now called SWA in mammals first appeared in reptiles. The fact that some aspects of EEG sleep in reptiles appear to exhibit rebound effects after sleep deprivation supports the argument that some form of SWA is present in reptiles. REM, however, does not occur in reptiles, with the possible exception of the crocodiles. Crocodiles themselves, however, seem to exhibit some behaviors of mammals (like play in the young and care for young). *It thus appears that REM-related mentation experiences—let's call them dreams for the rest of this chapter—appear to be evolutionary innovations of proto-mammalian and mammalian taxa.*

With the appearance of the monotremes, clear signs of REM begin to appear in the EEG, although they are mixed with signs of NREM. Following the evolution of marsupials, clear electrophysiologic signs of REM emerge but they are again partially mixed with NREM, and it is not clear whether one or both sleep states are uni- or bihemispherically expressed. Finally, with the emergence of placental mammals we get the derived state of bihemispheric REM sleep. Recall that our review of comparative patterns of REM expression revealed that REM never occurred in the unihemispheric state. Only NREM or SWA occurred when unihemispheric sleep was present in a species.

We, therefore, tentatively conclude that REM requires bihemispheric activation to occur, and this activation pattern must decisively influence the form of mentation that occurs in REM.

If REM is a uniquely bihemispheric phenomena, then REM sleep may also require a functioning corpus callosum in order to achieve its full expression. The corpus callosum connects the two hemispheres, thereby exponentially increasing brain connectivity and integration relative to unihemispheric functional states (Scamvougeras, Kigar, Jones, Weinberger, & Witelson, 2003). A functioning corpus callosum permits simultaneous bihemispheric activation and all manner of patterns of cross-hemispheric interactions. The corpus callosum is a unique feature of the brain of placental mammals (Aboitiz & Montiel, 2003). Although marsupials evidence enlarged anterior commissures, the corpus callosum is less developed in them than in placentals. Aquatic mammals without REM evidence unique and perhaps reduced (in size) forms of the corpus callosum (Gilissen, 2006). Avian REM, as far as we know, is not strictly analogous to mammalian REM. Nor does avian REM exhibit sleep rebound effects after sleep deprivation (as is the case with mammalian REM). Thus, while bird song appears to be a partially sleep dependent process, it is related to unihemispheric NREM forms of sleep and thus may not be like REM-related forms of mentation at all. The hemispheres in birds are not as densely connected as are the hemispheres in mammals. In birds, for example, there is no structure corresponding to the mammalian corpus callosum. If REM does indeed require bihemispheric activation to occur, it is not surprising then that REM sleep in birds is fleeting. On the other hand, very little is known about this area of research, thus the relation between mammalian REM/dreams to avian unihemispheric NREM mentation processes remains a question for future research.

Bihemispheric REM produces a very special form of mentation or consciousness. Indeed, REM sleep itself has been associated with increased gamma wave frequencies (30–80 Hz)—an index of binding during waking life (Kahn, Pace-Schott, & Hobson, 1997; Llinas & Ribary, 1993). However, while bihemispheric binding appears to be enhanced in REM, anterior-posterior connectivity is impaired in REM. Within REM sleep, gamma frequency oscillations become desynchronized between frontal and posterior perceptual areas (Corsi-Cabrera et al., 2003; Perez-Garci, del-Rio-Portilla, Guevara, Arce, & Corsi-Cabrera, 2001). The picture, therefore, is complex. While REM-related mentation appears to support integration of right-left contributions, REM does not allow for integration of anterior-posterior information sources.

Thus, REM-related mentation experiences are the expression of intense activation of the limbic and amygdalar centers as well as integration of right-left hemispheric sources, along with de-synchrony in frontal-parietal areas. The monotremes were the first to experiment with binding across the hemispheres, but the marsupials and terrestrial placental mammals developed it more fully. Bihemispheric integration of information is most fully expressed in the primate line and of course in humans. This bihemispheric integration of information processing resources yields additional computational power and new emergent forms of attentional capacities (Banich, 2003). When coupled with anterior-posterior de-synchrony or disconnection, bihemispheric cross-talk produces the new form of consciousness we call dreams. The purpose of this new form of consciousness is still unknown.

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