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REVIEW



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Do all mammals dream?

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Abstract

The presence of dreams in human sleep, especially in REM sleep, and the detection of physiologically similar states in mammals has led many to ponder whether animals experience similar sleep mentation. Recent advances in our understanding of the anatomical and physiological correlates of sleep stages, and thus dreaming, allow a better understanding of the possibility of dream mentation in nonhuman mammals. Here, we explore the potential for dream mentation, in both non-REM and REM sleep across mammals. If we take a hard-stance, that dream mentation only occurs during REM sleep, we conclude that it is unlikely that monotremes, cetaceans, and otariid seals while at sea, have the potential to experience dream mentation. Atypical REM sleep in other species, such as African elephants and Arabian oryx, may alter their potential to experience REM dream mentation. Alternatively, evidence that dream mentation occurs during both non-REM and REM sleep, indicates that all mammals have the potential to experience dream mentation. This non-REM dream mentation may be different in the species where non-REM is atypical, such as during unihemispheric sleep in aquatic mammals (cetaceans, sirens, and Otariid seals). In both scenarios, the cetaceans are the least likely mammalian group to experience vivid dream mentation due to the morphophysiological independence of their cerebral hemispheres. The application of techniques revealing dream mentation in humans to other mammals, specifically those that exhibit unusual sleep states, may lead to advances in our understanding of the neural underpinnings of dreams and conscious experiences.

KEYWORDS

consciousness, mammalia, mentation, non-REM sleep, REM sleep, sleep evolution

INTRODUCTION 1

Muscle tone is normally suppressed in REM sleep. Jouvet and Delorme (1965) discovered, in cats, that damage to a small region below locus coeruleus prevented this muscle tone suppression producing an animal that, when in REM sleep, locomoted and appeared to be pursing and attacking imagined images (Jouvet, 1962; Jouvet & Delorme, 1965). In 1986, Schenck and colleagues discovered a similar syndrome in humans where elaborate behavioral enactments, including attacking bed partners and objects near the bed, often causing injuries to the sleeper and his (the disorder is more frequent in men)

bed-mate (Schenck, Bundlie, Ettinger, & Mahowald, 1986; Schenck, 2005, 2013; Leclair-Visonneau, Oudiette, Gaymard, Leu-Semenescu, & Arnulf, 2010; but see Blumberg & Plumeau, 2016). The episodes occurred in REM sleep and these patients report dream mentation corresponding to the observed movements. Thus, the well-studied animal phenomenon parallels the human dream state, with its accessible mentation.

Some arguments can be made against the possibility that animals, other than humans, dream. Lesions of parietal cortex and certain other cortical regions prevent dreaming in humans, even in individuals continuing to show normal REM sleep as judged by cortical EEG,

suppression of muscle tone, and rapid eye movements (Solms, 1997, 2000). If the human cortex is unique in its ability to generate dream mentation, it is possible that dream-like mentation is absent in all animals. Humans before age 6 do not clearly have dream mentation, despite copious amounts of REM sleep, perhaps because these cortical regions, that are heavily involved in the processing of visuo-spatial skills, have not yet fully matured (Foulkes, 2002). Conversely, if intact animal cortices are able to generate dream mentation, animal dreams may be possible.

We can never know for certain what other people think, but because of similar verbal reports, behavior, and physiology, we can conclude that they have similar mentation and dreams. Similarly, we cannot know if other species have the same mental experiences as humans, but to the extent that their physiology and behavior overlaps with ours, we can infer certain parallels in mentation. In that spirit we can address the issue of whether animals may dream, perhaps with some aspects that parallel the human dream experience.

The word dream has multiple meanings including an aspiration/ ambition/ideal, an unrealistic/self-deluding fantasy, or a person/ object/thing that is considered wonderful/perfect. These multiple meanings and the modern colloquial usage of the word dream likely derive from Freud's influential idea that dreams that occur during sleep are a reflection of wishes that we hope to have fulfilled (Freud, 1900, 1901): however, in this review we consider the word dream to represent the thoughts, images, sensations, emotions, and other happenings that occur in the mind during sleep (Domhoff, 2017) in a strictly physiological sense. By adhering to the physiological underpinnings of what we term dreams, we attempt to examine this mental phenomenon across mammalian species, specifically focusing on those species that show unusual patterns of sleep physiology. At the outset we must note that it is not a straightforward task to determine whether all people actually dream, as the earliest REM sleep deprivation study showed that not all people report dreams upon awakening from REM sleep (Dement, 1960). There are also the issues of non-REM sleep dream recall (Foulkes, 1962; Kales et al., 1967; Siclari et al., 2017) and what is termed white, or contentless, dreams (Fazekas, Nemeth, & Overgaard, 2019), both of which are important when examining the concept of whether nonhuman mammals dream. In addition, the regional distribution of slow waves during non-REM sleep may interfere with the generation of conscious experiences and thus dreams in humans (Massimini et al., 2005; Nieminen et al., 2016), and this has been shown to occur most consistently when these variations in slow waves occur in the parieto-occipital cortex during both non-REM and REM sleep (Siclari et al., 2017; Siclari, Bernardi, Cata-Idi, & Tononi, 2018).

Dreaming, or the accurate reporting of dreaming, might require the lexical or visuo-spatial abilities of a 6-year old human (Foulkes, 2002), or alternatively, animals might experience an evolutionary precursor of the mentation reported by humans during sleep. An often quoted, but apparently never published, study trained a monkey to bar press when seeing projected images. When the monkey slept, it bar pressed during REM sleep (Luce, 1976), suggesting that this sort of operational approach (perhaps using eye or respiratory movements) might someday be used to detect and better understand mentation during sleep in nonhuman mammals.

WHAT ARE DREAMS? 2

For the current purposes we consider dreams to be the result of patterns of neural activity, predominately within the cerebral cortex, that form transient imagery, experienced as conscious thought, that can be considered mental representations (Morgan, 2014), occurring during physiologically defined sleep. We consider dreams to be purely internal mental representations, as during sleep we are, for the most part, not conscious of sensory inputs from the outer world (Velluti, 1997). These mental representations may or may not be recalled upon awakening, indicating that these mental representations are potentially accessible to the waking conscious realm.

DREAMS IN HUMANS AND EEG STATES 3

One of the central difficulties in examining the idea of whether nonhuman mammals dream is the language impediment-only humans can verbally report whether or not they were dreaming. Human sleep can be readily divided into non-REM and REM sleep based on a range of physiological criteria, but essential to this subdivision is the structure of the EEG. Indeed, non-REM sleep in humans can be further parcellated into multiple different stages, while REM appears to be a more singular sleep state, although it can be divided into tonic and phasic sleep (Dement & Kleitman, 1957a; Grigg-Damberger, 2009). Typically, dreams are associated with REM sleep, these REM sleep dreams being the vivid, unfolding, narrative-type, mental representations recalled upon arousal (Aserinsky & Kleitman, 1953; Dement & Kleitman, 1957b; Jacobs, Feldman, & Bender, 1972; Leclair-Visonneau et al., 2010); however, subsequent studies have also shown that dreams occur during non-REM sleep (Foulkes, 1962; Hauri & van de Castle, 1973; Kales et al., 1967; McNamara et al., 2010; McNamara, McLaren, & Durso, 2007; Stickgold, Malia, Fosse, Propper, & Hobson, 2001; Suzuki et al., 2004). Indeed, it has been shown that non-REM sleep dream reports from late in the sleep period can be difficult to distinguish from REM sleep dream reports (Domhoff, 2017, 2019; Nir & Tonini, 2010; Siclari et al., 2018).

It appears that the major difference in terms of the content of REM dreams versus non-REM dreams is that REM dreams involve more emotional, visual and movement content, are longer, show more continuity and coherence, and are more vivid than non-REM dreams (Foulkes, 1962; Suzuki et al., 2004). Additionally, REM dreams are characterized by self-initiated aggressive social interactions, whereas non-REM dreams are characterized by self-initiated friendly social interactions (McNamara et al., 2007, 2010). Despite this difference in dream content between sleep stages, the neural activation patterns in the posterior regions of the cerebral cortex during both REM and non-REM dreams appear to have some similar aspects, and indeed can be predictive of the occurrence of dreams (Siclari et al., 2017).

This is in stark contrast to the state-defining subcortical neural activity associated with the cholinergic, noradrenergic, histaminergic, serotonergic, and orexinergic systems during non-REM and REM sleep (Siegel, 2004, 2017)— perhaps it is these differences that not only underlie the different EEG patterns in the different sleep stages, but also the variance in the content of non-REM and REM dreams? Nevertheless, it would appear that a cautious appraisal of current knowledge would suggest that in humans there are both non-REM and REM dreams, and that these are associated with distinct sleep stages defined most clearly by EEG patterns.

4 | SLEEP EEG STATES ACROSS MAMMALS

That all mammals sleep is well known (Siegel, 2005), and across the phylogenetic breadth of mammals, in general (see below for exceptions), sleep has been shown to be comprised of both REM and non-REM sleep stages (Lesku, Roth, Amlaner, & Lima, 2006; Tobler, 1995). While in frequently studied species (such as laboratory rodents and nonhuman primates) various non-REM stages have been described that have more or less in common with the various non-REM stages seen in humans (Lesku et al., 2006: Tobler, 1995), for the current purposes we refer to non-REM sleep as a unitary state due to the differences between classification systems and across species in terms of the non-REM sleep stages. Given this, one could postulate that indeed mammals do dream, likely having what could be considered both non-REM and REM type dreams as reported in humans. While this could only be proven beyond doubt by certain mammals breaking the proverbial lexical barrier (if a dog dreamt what would it tell us about its dreams?), it is also possible that if the findings and techniques being developed that reveal the neural correlates of dreaming in humans (e.g., Siclari et al., 2017) were applied to nonhuman mammals that, at the least, suggestive circumstantial evidence of both non-REM and REM dreams in mammals could be obtained. While this generalized conclusion is broadly applicable to mammals, there are several orders and species that have been shown to have sleep physiology or behavior that differs significantly from the "typical" mammal, including monotremes, cetaceans, and certain other species.

5 | DO MONOTREMES DREAM?

The monotremes (platypuses and echidnas, the egg-laying mammals) represent distinct physiological departures from the typical EEG states observed in sleeping mammals (Siegel et al., 1999; Siegel, Manger, Nienhuis, Fahringer, & Pettigrew, 1996, 1998). In the monotremes two distinct sleep states can be discerned, which include the traditionally defined non-REM sleep (which can be further subdivided into moderate and high voltage non-REM), and a clear REM sleep state (defined with muscle atonia, rapid eye movements, twitching and erratic ECG); however, REM sleep in the monotremes, while abundant (occupying up to 8 hr/day in the platypus, Siegel et al., 1999), is unusual. The brainstem and the body of the monotremes display clear signs of REM

sleep as indicated above, but unlike REM sleep in marsupial and placental mammals where the forebrain EEG is desynchronized with a low voltage activity, the forebrain of the monotremes during REM sleep frequently shows synchronized high voltage activity, much like that observed in non-REM sleep. This seeming disconnect between the brainstem/body and the forebrain during REM in the monotremes may be associated with a discontinuity in the cholinergic system (Manger, Fahringer, Pettigrew, & Siegel, 2002).

Given this background regarding the physiology of the EEG during sleep in monotremes and the associated sleep states, what can we conclude about dreams in monotremes? Quite simply put, it appears unlikely that monotremes would experience the vivid, narrative REM sleep type dreams; rather, if they dream, they might experience the less vivid, shorter, and disjunct dreams associated with non-REM sleep. Thus, despite the fact that monotremes spend an inordinate amount of time in REM sleep (Siegel et al., 1999), the disconnect between the brainstem/body and cerebral cortex during REM sleep would appear to preclude the possibility of REM sleep type dreams in these mammals.

6 | DO CETACEANS DREAM?

The second unusual departure from the typically mammalian sleep physiology has been observed in cetaceans (whales, dolphins, and porpoises; Lyamin, Manger, Ridgway, Mukhametov, & Siegel, 2008). Cetacean sleep is most prominently characterized by the presence of unihemispheric slow wave sleep (USWS), this being a state where one cerebral hemisphere shows desynchronized low voltage activity characteristic of wake, while the other cerebral hemisphere shows synchronized high voltage activity characteristic of non-REM sleep (Lyamin et al., 2008). Cetacean sleep is further characterized by movement during the quiescent period (the amount of gross bodily movement is greater in smaller species than larger species), unilateral eye closure (of the eye connected to the hemisphere showing non-REM slow waves), a reduction in the temperature of the hemisphere showing non-REM slow waves, a lack of any substantive signs of REM sleep, and the apparent lack of sleep during the first few months of life (Lyamin, Pryaslova, Lance, & Siegel, 2005). These unusual patterns of sleep are supported by an altered anatomy of the systems controlling sleep, likely facilitated by a notably large posterior commissure and small corpus callosum (Dell et al., 2016; Dell, Patzke, Spocter, Siegel, & Manger, 2016; Lyamin et al., 2008; Manger, Hemingway, Haagensen, & Gilissen, 2010).

The inability to demonstrate any form of REM sleep conclusively in the cetaceans allows the conclusion that the vivid REM sleep type dreams are likely to be completely absent in the cetaceans. In contrast, the unihemispheric nature of slow wave sleep in the cetaceans indicates that they possibly experience the less vivid non-REM type dreams observed in other mammals; however, this tentative conclusion is complicated by the unihemispheric nature of slow wave sleep in cetaceans—if the cetaceans experience non-REM dreams, they likely do this unihemispherically. When the small corpus callosum

(Manger et al., 2010) and small hippocampus (Patzke et al., 2015) are taken into account, this may mean that the potential non-REM dreams experienced by cetaceans are even less vivid than those in other mammals, as interhemispheric recruitment of neural activity to provide dream content would be reduced (see also Greenwood, Wilson, & Gazzaniga, 1977 regarding dreams in humans following commissurotomy), as would aspects of the neural underpinnings of the memories necessary to provide content to these possible non-REM dreams. In addition to this, non-REM dreaming during USWS may be quite difficult or very challenging to support for the cetaceans, as they would be perceiving both a real world (awake hemispheric) and fictive world (sleeping hemisphere) simultaneously, which would be very difficult to manage behaviorally. Thus, the cetaceans appear to be the least likely of all the mammalian species to experience any form of mental representations during sleep that could be readily defined as dreams.

7 DREAMS AND OTHER MAMMALS THAT SHOW ATYPICAL SLEEP PATTERNS

7.1 | African elephants

The free-ranging African elephant is the shortest sleeping mammal recorded to date, having only 2 hour of sleep on average each day (as determined through actigraphy of the trunk, as recording EEG from these animals is both technically and ethically problematic, Gravett et al., 2017). It was found that the majority of sleep in the two female matriarch African elephants recorded from occurred while standing, with lying down to sleep occurring only every third or fourth day. Despite the fact that EEG validation is lacking, it would appear reasonable to conclude that sleep while standing correlates with non-REM sleep, and that perhaps the periods when these animals lie down to sleep might include REM sleep, as muscle atonia is indicative of REM sleep in other mammals (Siegel, 2004, 2005, 2017), and muscle atonia would likely prevent the elephants from maintaining a standing posture. This conclusion is supported by behavioral observations of sleep in captive Asian elephants, where behavioral signs of REM sleep were only observed when the elephants under study were in a recumbent position (Tobler, 1992). It should also be noted here that the neural systems that have become the focus of sleep control in "lab mammals" are present in elephants, and do not differ significantly from that observed in other mammals apart from a potentially augmented drive for arousal facilitated by additional orexinergic and noradrenergic neurons (Maseko, Patzke, Fuxe, & Manger, 2013).

Given this background regarding the sleep of elephants, it is reasonable to conclude that if elephants dream, they probably experience both the non-REM and REM types of dreams. The non-REM type dreams might occur on a daily basis (except on the days when their sleep is disturbed, Gravett et al., 2017), but the REM type dreams might occur only every third or fourth day when the elephants take the opportunity to lie down to sleep, indicating muscle atonia associated with REM sleep. This potentially irregular occurrence of REM

sleep, and the absence of any clear form of REM sleep in cetaceans (see above), provide an important phylogenetic counter-argument to the hypothesized association between REM sleep and memory consolidation (Ackermann, Hartmann, Papassotiropoulos, de Quervain, & Rasch, 2014; Boyce, Glasgow, Williams, & Adamantidis, 2016; Humiston & Wamsley, 2018, 2019; Magidov et al., 2018; Rasch, Pommer, Diekelmann, & Born, 2009; Siegel, 2001; Stickgold, 2005; Tilley & Empson, 1978; Wyatt, Fram, Kupfer, & Snyder, 1971).

7.2 **Pinnipeds**

There are three families of pinnipeds, the Phocidae, Otariidae, and Odbenidae (which consists of one species, the walrus). The Phocids have a sleep pattern similar to that of terrestrial mammals, with exclusively symmetrical bilateral non-REM and REM sleep. When sleeping in water they hold their breath across non-REM and REM sleep periods. The walrus has both bilateral non-REM and REM sleep while in water and on land, similar to the Phocids (Lyamin & Siegel, 2019). In this sense, the potential for the generation and experience of dreams in the Phocids and walrus is similar to that observed in most other mammals (see above) but must be aligned with the specific occurrence and timing of both non-REM and REM in these species given their semi-aquatic life history.

The Otariidae present with a more complex picture of sleep, and thus potential dreaming, when compared to the other pinnipeds. When sleeping on land the Otariidae evince a sleep pattern resembling that of terrestrial mammals, this being mostly bilateral non-REM sleep followed by bilateral REM sleep in amounts similar to humans. However, when in water, where they spend up to 7 contiguous months of each year when living in their natural habitat, they undergo unihemispheric sleep resembling the USWS of cetaceans, with a nearly complete absence of REM sleep. Strikingly, when returning to land they show little or no "rebound" of REM sleep (Lyamin et al., 2018). Thus, during the period when the Otariid seals are most active and challenged to find and remember the location of food sources and avoid predators, they do not appear to have REM sleep. It appears then that when sleeping on land, the Otariid seals have the potential to experience both non-REM and REM type dreams like other mammals. In contrast, when they are in the water, the potential REM type dreams would likely be absent, and the potential non-REM type dreams may be more similar to that observed in cetaceans rather than other mammals.

7.3 Arabian oryx

The Arabian oryx inhabits one of the hottest and most arid regions on the planet, the Arabian desert, and during the summer needs to sleep when temperatures often exceed the thermoneutral zone for mammals. A recent study has shown that the Arabian oryx shows both typically mammalian non-REM and REM sleep, obtaining sleep in a manner that could be described as typical for an artiodactyl during the

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relatively cooler winter months, sleeping during the predawn hours (Davimes et al., 2018). However, in summer when the temperatures consistently exceed the mammalian thermoneutral zone, the Arabian oryx sleeps during the morning hours, between sunrise and noon, using the natural physiological loss of body temperature during sleep as a novel thermoregulatory mechanism (Davimes et al., 2018). Along with this seasonal switch in the timing of sleep, in summer the amount of REM sleep is substantially reduced to only a few minutes per day, presumably to prevent the brain overheating (Davimes et al., 2018). If the Arabian oryx do dream, it appears likely that they would experience both non-REM and REM type dreams. Interestingly, the incidence and potential length of REM type dreams would be significantly curtailed during the summer months when sleeping at temperatures that exceed the mammalian thermoneutral zone.

7.4 | Rock hyrax

Rock hyraxes are members of the superorder Afrotheria, being most closely related to the elephants and seas cows (manatees and dugongs). Sleep in the rock hyrax is somewhat unusual, while they maintain the typically mammalian non-REM and REM sleep stages, an additional sleep stage, termed somnus innominatus (SI), is also observed (Gravett, Bhagwandin, Lyamin, Siegel, & Manger, 2012). SI is a sleep state characterized as a form of low-voltage slow wave sleep, exhibiting behavioral quiescence, desynchronized EEG, and the presence of muscle tone similar to non-REM, but also exhibits a less regular heart rate (compared to non-REM) and a greater amount of theta activity (Gravett et al., 2012). Thus, SI appears to show mixed characteristics of both non-REM and REM sleep. This unusual sleep state may be related to the presence of parvocellular cholinergic neurons within the laterodorsal and pedunculopontine tegmental nuclei of the pons in the rock hyrax (Gravett, Bhagwandin, Fuxe, & Manger, 2009).

As there are both clear non-REM and REM sleep stages in the rock hyrax, it would be safe to conclude that if the rock hyraxes do dream, they would experience both dream types. Interestingly, the additional sleep state, SI, being characterized by physiological aspects of both non-REM and REM sleep, could indicate the possibility of an additional type of dream in the rock hyrax. This type of SI dream might, speculatively, be of a form intermediate to that experienced in non-REM and REM in the rock hyrax, potentially being more vivid, contiguous and narrative-like than the non-REM dreams, but less so that the REM dreams. The presence of SI in the rock hyrax indicates that it would be an interesting species in which to investigate the neural correlates of dreaming using the techniques being currently developed in humans (Siclari et al., 2017), and may provide additional information of importance to determining the underlying physiology of dreams.

7.5 | River hippopotamus

Sleep in the river hippopotamus has not be examined using polysomnographic techniques, but behavioral observations indicate that the typically mammalian non-REM and REM sleep stages should be present, although in what proportions are unknown at present (Lyamin & Siegel, 2005). Despite the seemingly typical mammalian sleep, there are two specific changes in the structure of the cholinergic system in the diencephalon and pons that hint at additional possibilities in terms of sleep states in the river hippopotamus. These two differences include the presence of cholinergic neurons in the laterally located intralaminar nuclei of the dorsal thalamus and additional parvocellular cholinergic neurons in the laterodorsal tegmental nucleus of the pons (Dell et al., 2016). These differences, which in one respect are similar to the neuroanatomy of the rock hyrax, hint at the possibility of an as yet undescribed sleep state in the river hippopotamus. Thus, for the river hippopotamus we could conclude that there is the potential presence of both non-REM and REM type dreams; however, there is the additional possibility of some other form of dream occurring during sleep in the hippopotamus. Unfortunately, unlike the rock hyrax, the river hippopotamus may not be amenable to the application of standard recording techniques that might reveal the neurological correlates of any dream-like mentation.

7.6 | Manatees

Physiological recordings of sleep have been made in two species of manatee, the Amazonian manatee, Trichechus inunguis (Mukhametov, Lyamin, Chetyrbok, Vassilyev, & Diaz, 1992), and the west-Indian manatee. Trichechus manatus (Sokolov & Mukhametov, 1982). Both non-REM and REM sleep were readily observed in the manatees, but slow wave activity was highly lateralized and asynchronous, approximating the USWS observed in cetaceans, and bihemispheric REM sleep only occupied around 15 min per day. Given this physiological data it is reasonable to conclude that both non-REM and REM type dreams could be experienced by manatees. Interestingly, the non-REM type dreams might be affected in a manner similar to that discussed for the cetaceans, but the corpus callosum of the manatees does not appear to be reduced in size as seen in cetaceans (Manger et al., 2010), indicating that interhemispheric communication during non-REM sleep may not be as substantially reduced as in cetaceans. This would mean that potentially the content and intensity of the non-REM dreams in manatees may not be as depauperate as potentially experienced in cetaceans, but also not as rich as potentially experienced in other mammals.

8 | CONCLUSION

Do all mammals dream? The answer to this question could be either yes or no, and this is strongly dependent upon the definition of dream that is used, based on the level of confidence that one places on the idea that reports of dreams following arousal from non-REM sleep can be considered dreams. We can thus take a hard-stance regarding the definition of dreams that indicates that only those mental representations that occur during REM sleep should be considered dreams,

or a soft-stance by including all mental representations occurring during sleep, both non-REM and REM sleep, as dreams. Each stance can then lead to different conclusions.

The hard-stance is perhaps the most straightforward, as in this viewpoint dreams are specifically associated only with REM sleep. If mental representations that precipitate dreams can only be generated during the period of neural activity defining REM sleep (the hard-stance), then it is safe to conclude that cetaceans (whales, dolphins, and porpoises), and otariid seals while at sea, do not dream. The likelihood that monotremes (platypus and echidnas) dream is reduced by the moderate to high voltage of the EEG during most of REM sleep (Siegel et al., 1999). While this hard stance regarding dreams would indicate that the vast majority of mammals have the possibility/capacity to experience dreams, there are certain unusual cases, where the timing or amount of time that the brain spends in a state from which dreams could emerge, can change. These changes may align with changes in the environment that cause changes in the expression of REM sleep, most notably temperature extremes when considering cetaceans, otariid seals and the Arabian oryx, with phylogenetic history when considering the monotremes and Afrotherians, and with body size when considering the African elephant and river hippopotamus.

The soft-stance, that all mental representations during sleep, including those during non-REM sleep, represent dreams is more complex. Initially, we can conclude that if we take the soft-stance, then all mammals dream, as all mammals undergo some form of non-REM sleep. In certain cases, such as during USWS in the cetaceans, manatees and otariid seals, the phenomenal content of the dreams during non-REM sleep might be far less complex than that observed in species that exhibit bihemispheric slow wave sleep, or when otariid seals are on land and sleeping bihemispherically. This potential lessening in the complexity of dream content would appear to be most exacerbated in the cetaceans due to the underlying neuroanatomy that would serve to make the cerebral hemispheres act as independent entities more so than in other species (see above). Thus, of all the mammals, the cetaceans appear to be the least likely candidates to experience complex mental representations during sleep that could lead to the production of dreams.

The last issue to address is the possibility of dreams occurring during sleep states that are neither non-REM or REM, such as the state termed SI in the rock hyrax and the potential novel state/s that the anatomy of the somnogenic systems indicate may be present in the river hippopotamus. These potentially quite different sleep states may, if one were to take the soft-stance regarding dream definition, lead to mental representations that may create dreams quite different to those experienced during non-REM and REM. While the potentially novel sleep states have not been defined in the river hippopotamus although indicated by their unusual anatomy (Dell, Patzke, Spocter, Bertelsen, et al., 2016), the state termed SI in the rock hyrax, along with its unusual anatomy (Gravett et al., 2009, 2012), may be an interesting species for investigation, as if SI does allow for the production of dreams, the rock hyrax has three different clearly defined physiological sleep states (non-REM, REM, and SI) that may lead to the production of three very different types of dreams. Investigating cortical activity during non-REM, REM and SI in the rock hyrax with high density electroencephalography, as employed by Siclari et al. (2017) in humans which is predictive of dreams in humans, or other methods under development in humans to understand dream content (e.g. Horikawa, Tamaki, Miyawaki, & Kamitani, 2013; Sterpenich, Perogamvros, Tononi, & Schwartz, 2019), may augment our understanding of the neural correlates of consciousness in humans and across mammals as a class. The comparative observations regarding the physiology of sleep, and by extensions dreams, in mammals thus provides not only interesting observations for thought experiments, but also reveals potentially informative model species that may rapidly increase our current understanding of the manner in which the brain produces, processes, and accesses conscious experiences.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

P.R.M. and J.M.S. conceptualized and wrote this mini-review.

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