Neuroscience and Biobehavioral Reviews 32 (2008) 1451–1484

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Review

Cetacean sleep: An unusual form of mammalian sleep

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ARTICLE INFO

Keywords:
Evolution
Rapid eye movement sleep
Slow wave sleep
Unihemispheric sleep
Thermoregulation
Laterality
Vigilance

ABSTRACT

Our knowledge of the form of lateralized sleep behavior, known as unihemispheric slow wave sleep (USWS), seen in all members of the order Cetacea examined to date, is described. We trace the discovery of this phenotypically unusual form of mammalian sleep and highlight specific aspects that are different from sleep in terrestrial mammals. We find that for cetaceans sleep is characterized by USWS, a negligible amount or complete absence of rapid eye movement (REM) sleep, and a varying degree of movement during sleep associated with body size, and an asymmetrical eye state. We then compare the anatomy of the mammalian somnogenic system with what is known in cetaceans, highlighting areas where additional knowledge is needed to understand cetacean sleep. Three suggested functions of USWS (facilitation of movement, more efficient sensory processing and control of breathing) are discussed. Lastly, the possible selection pressures leading to this form of sleep are examined, leading us to the suggestion that the selection pressure necessitating the evolution of cetacean sleep was most likely the need to offset heat loss to the water from birth and throughout life. Aspects such as sentinel functions and breathing are likely to be proximate evolutionary phenomenon of this form of sleep.

Contents

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doi:10.1016/j.neubiorev.2008.05.023

1. Introduction

That sleep is an essential part of the life of animals is well known; indeed, it has been demonstrated that under some conditions lack of sleep is fatal (Rechtschaffen et al., 1983; Shaw et al., 2002). Despite this, the answer to the function of sleep, at its most basic level, has not been discovered, i.e. we cannot yet say why animals need to sleep. Sleep, or sleep-like, behavior has been observed and measured in many animal species, both vertebrate and invertebrate, but the exact phylogenetic boundaries defining the occurrence of sleep, and types of sleep, have not yet been determined. In the class Mammalia, all studies directed towards observing sleep have found it, in varying amounts and with different sleep topographies, e.g. some mammals have more rapid eye movement (REM) sleep than others (e.g. Zepelin et al., 2005; Siegel et al., 1999). The studies of sleep amongst various mammalian species have yet to reveal any specific or definitive links related to phylogeny, phenotype, life history, or environment; however, it has been seen that immaturity at birth is related to increased amounts of REM sleep, and that larger body size is related to a lower total sleep time in land mammals (e.g. Zepelin et al., 2005; Siegel, 2003, 2005; Lesku et al., 2006), but these trends are not strongly predictive.

The present review focuses on the study of sleep in cetaceans, a group of mammals that, arguably, face an unusual, or even extreme, environment in which mammalian sleep must occur. Studies of cetacean sleep have led to one of the most unusual findings to date in respect of sleep in mammals, this being the unihemispheric nature of slow waves (Mukhametov, 1987; Mukhametov et al., 1977; Mukhametov and Polyakova, 1981; Ridgway, 2002; Lyamin et al., 2004), i.e. cetaceans have the slow waves in one half of their brain at a time, while the other half of the brain has low voltage activity. This asymmetrical EEG state occurs in all cetaceans studied to date, with each half of the brain exhibiting approximately 4 h of SWS per day in the bottlenose dolphin, *Tursiops truncatus* (the most intensively studied species). Added to this unusually lateralized sleep pattern has been the lack of finding of any distinct form of REM sleep in the Cetacea (Mukhametov, 1988, 1995), i.e. the polygraphic signs of REM sleep, if it exists, are rare or unclear. These findings have made the study of sleep in whales and dolphins one of the most interesting topics in terms of the life history of cetaceans and more generally for mammalian sleep evolution.

In the present review we outline the history of the discovery of lateralized SWS in cetaceans, examining the hints derived from early behavioral observations through to the definitive polygraphic recordings of sleep. We then detail what has been found in these and several more recent studies of cetacean sleep to build as complete a picture as possible of cetacean sleep phenomenology. Following this we compare what is known about the anatomy and physiology of the somnogenic system from representative mammals (mostly rats, cats, monkeys and humans) with what is known in cetaceans, highlighting areas where our knowledge in cetaceans is deficient and areas of interest for future studies. Finally, we examine the various hypotheses forwarded regarding the evolution of cetacean sleep phenomenology, and attempt to define what selection pressures may have been contributing or underlying factors in the positive evolutionary selection of this phenotypically unusual form of mammalian sleep.

2. History of finding USWS in cetaceans

2.1. Lilly's predictions

John Lilly, who pioneered early experimental physiological studies of dolphins, proposed several theories regarding dolphin physiology, including specific proposals regarding sleep in the dolphin, and in doing so generated many novel ideas (Lilly, 1964). Lilly proposed that respiration in dolphins was controlled at the thalamo-cortical level of the CNS rather than the respiratory centers located in the medulla and at the pontomedullary junction, surmising that dolphins and porpoises "lack our unconscious automatic, self-sustained breathing", having respiration that is "almost if not fully voluntary". Lilly also proposed that bottlenose dolphins do not breathe while asleep, suggesting that they wake up in order to surface for each breath. Lilly further noted, significantly, that dolphins sleep with one eye closed and one eye open, and thought that this may "assure that the animal is always scanning