REM sleep function: mythology vs. reality

Jerome M. Siegel

Professor of Psychiatry and Biobehavioral Sciences, UCLA Center for Sleep Research

Abstract

Since the discovery of REM (Rapid Eye Movement) sleep in 1953, misconceptions have arisen as to the evidence for its adaptive function and its relation to dreams. Eye movements recorded during REM sleep have not been consistently reported to mirror the eye movements predicted by dream reports. But evidence on eye movement and somatic motor expression from patients with REM sleep behavior disorder (RBD) is consistent with dream enacting behavior. The assumption that dreaming occurs only in REM sleep is incorrect, with numerous reports of nonREM dreaming. However, there may be qualitative differences between REM and nonREM dreams. Early studies that suggested a vital role for REM sleep in psychological well-being are refuted by studies of pharmacologically induced partial or complete REM sleep suppression. Studies of sleep across species show that the primitive monotreme mammals, platypus and echidna, have far more REM sleep than any other homeotherm group, whereas birds have far less REM sleep than any other homeotherm group. Human REM sleep amounts are not unusual, are correlated with nonREM sleep durations but are not correlated with intelligence. Across groups of homeotherms, REM sleep time is highly and inversely correlated ($r=-0.975$, $p=0.02$) with average core body temperature, suggesting that REM sleep cycles with nonREM sleep to regulate brain temperature during sleep. Cetacean mammals (dolphins and whales) do not have REM sleep despite their very large brain sizes and impressive cognitive abilities. Reports of “REM sleep like states” in arachnids, cephalopods and in zebrafish larvae are lacking critical evidence that the observed behaviors are occurring during sleep and that the behaviors are analogous to mammalian REM sleep.

THE DISCOVERY OF REM SLEEP

The discovery of REM sleep by Aserinsky and Kleitman[1] transformed the field of sleep research and our understanding of consciousness and dreams. This was followed by Dement’s discovery of a similar state in cats[2] and by Michel Jouvet’s investigation of the anatomy and physiology of this state[3,4]. An initial assumption was that REM sleep was a light stage of sleep, because of the waking-like activation of the EEG. Jouvet found that muscle tone was actively suppressed in REM sleep, beyond the reduction in muscle tone seen in nonREM sleep, in the state he termed “paradoxical” (i.e. REM) sleep. This active inhibition was inconsistent with the idea that REM sleep was a form of “light sleep.” The discovery of muscle tone reduction in REM sleep was later to find relevance in

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+1-818-891-8612 (office), jsiegel@ucla.edu, Neurobiology Research 151A3, 16111 Plummer St. North Hills, California, 91343, USA.
http://www.semel.ucla.edu/sleep-research

understanding and treating sleep apnea, which is elevated in REM sleep due to the reduction in tone of hypoglossal and pharyngeal musculature in individuals who are obese or have musculoskeletal disorders. A series of animal studies in which the brain was transected in the coronal plane at various levels led to the surprising conclusion that REM sleep, this “dream state” was generated in the brainstem rather than in the cortex[4,5]. Sastre and Jouvet found that relatively small bilaterally symmetrical lesions ventral to the locus coeruleus prevented the suppression of muscle tone in REM sleep. These lesions produced an unresponsive sleep-like state with dream-like or “oneiric” behavior[6]. This eventually led to the discovery of similar pathology in humans, termed REM behavior disorder, or “RBD.” RBD patients show vigorous motor activity during sleep which frequently injures the patient or bedmates. Upon awakening from a dream, RBD sufferers often describe dream imagery that corresponds to their behavior during the episode. Studies of RBD found that it was followed, in several years, in more than 80% of cases, by Parkinson’s disease[7,8]. This has raised the hope that Parkinson’s might be prevented by applying treatments as soon as RBD was diagnosed. The challenge of identifying a treatment that could delay or prevent this progression has not yet been met.

EYE MOVEMENT, ERECTIONS, DREAM CONTENT

Initial studies in which subjects were awakened during REM sleep and reported dreams, led to the tentative conclusion that awakening from REM sleep will always produce a dream report, and to the assumption that most or all dreams occur during REM sleep. These conclusions are clearly incorrect. It has been found that awakening from nonREM sleep produces frequent dream reports. The idea that such reports might be memories for a prior REM sleep period was contradicted by studies showing that awakening from nonREM sleep prior to the first REM sleep period frequently produced dream reports[9,10]. There may be subtle differences in the quality of REM and nonREM dream reports, with REM dream reports being more vivid that non-REM reports. Foulkes reported that rapid eye movement sleep awakenings revealed more statements involving affective, visual, and muscular content with less correspondence to residues of the subjects waking life, than non-REM awakenings[11]. However, late in the sleep period REM and nonREM dream reports are similar, suggesting that circadian related variables, such as rising brain and body temperature[12], rather than REM vs. nonREM states may determine the REM-nonREM differences in dream content[13].

It is difficult to determine if recorded eye movements correspond to presumed changes in the gaze of the dreamer. If for example, the subject is intensely focused on a long volley in a tennis match throughout the REM sleep dream, one might confidently identify the correspondence between eye movements and dream imagery. However, it is much more difficult to correlate eye movement data with a person’s typical dream reports, mixing thoughts and interactions. Early studies led Kleitman to conclude that there was no relation between the recorded eye movements and the eye movements predicted on the basis of the dream imagery in REM sleep (https://www.semel.ucla.edu/sleep-research/video/1995-kleitman-aserinsky-jouvet-dement-symposium-discovery-rem-sleep-celebrating). However, there is a general relation between eye movement frequency and the level of activity in the subject’s reported dream imagery[11,14]. Some people who consistently do not report dream imagery upon awakening from REM sleep nevertheless have REM sleep in normal amounts[15]. It has been shown that animals frequently awaken at the end of REM sleep, leading to the “sentinel hypothesis,” the idea that one adaptive feature of REM sleep is to periodically awaken animals to scan the environment[16]. Forebrain lesions in humans can prevent dreaming recall without affecting REM sleep parameters[10]. Conversely, posterior cortex activation is correlated with dreaming reports[17].

The more general issue of a correspondence between REM sleep motor activity and dream imagery received strong support from a study of REM behavior disorder[7]. Leclair-Visonneau and colleagues found that the “directional coherence between limbs, head and eye movements during rapid eye movement sleep behavior disorder suggests that, when present, rapid eye movements resemble scanning of the dream scene. Since the rapid eye movements are similar in subjects with and without rapid eye movement sleep behavior disorder, this concordance can be extended to normal rapid eye movement sleep[18].”

Erections are present in most REM sleep periods in young men, even in dreams without explicit sexual content[19,20]. Erections are such a consistent correlate of REM sleep in males, that they can be used to discriminate psychogenic and organic impotence. Erections are diminished in dreams whose reports indicate a high level of anxiety[21].

The hypothesis that REM sleep is vital for psychological stability[22] is contradicted by studies showing that the complete suppression of REM sleep (including rapid eye movements, dream reports and EEG activation during sleep) with monoamine oxidase inhibitors, for 14 to 40 night periods, is without deleterious psychological or cognitive correlates[23]. Antidepressant medication, which produces a consistent reduction in REM sleep amounts and can be beneficial in depressed patients[24], does not impair cognitive function[25].

ANIMALS, BRAIN SIZE, MEMORY, COGNITION, INTELLIGENCE QUOTIENT (IQ)

It has been assumed by some that only more intelligent animals have REM sleep, or that there is some greater amount or intensity of REM sleep in humans than in other animals. However, convincing evidence for this supposition is lacking. The champion REM sleepers are the egg laying (i.e. monotreme) mammals, duck billed platypus and the echidna. The platypus has 14 h/day of REM sleep compared to just 2 h/day on average in humans. Not only is the REM sleep amount in the platypus higher than that of all other mammals, the intensity of phasic activity during their REM sleep periods is very high[26]. A video of a platypus implanted with EEG and EOG recording electrodes can be seen at: https://www.semel.ucla.edu/sleep-research/video/sleep-monotremes-platypus-and-echidna. The echidna shows a mixture of nonREM EEG with REM sleep-like brainstem neuronal bursting throughout the sleep period[27].

Figure 1 illustrates the amounts of REM and nonREM sleep in representative mammals. Three relations are apparent. One is that human REM and nonREM sleep durations are not particularly high or low relative to other mammals. The second is that, in general, animals with high amounts of nonREM sleep, also have high amounts of REM sleep[28]. REM sleep typically follows nonREM sleep. The third is that there is no obvious positive correlation between REM sleep amounts and presumed intelligence, e.g. the baboon and the guinea pig have exactly the same amounts of REM and nonREM sleep[28].

Figure 2 shows the relative sizes of some of the most studied mammalian brains, along with the total amounts of sleep (**nonREM+REM durations in blue**) and REM sleep (**REM sleep durations in red**). It is unclear if elephants have REM sleep because surgical implants would be required to get an accurate reading of their EEG and eye movements during sleep. But their respiration is relatively regular throughout most of the sleep period, consistent with their having mostly nonREM sleep during their average 2.1 h daily sleep period. This figure shows that absolute brain size is not strongly correlated with sleep duration. Similarly, brain/body weight ratios are not strongly (or positively) correlated with sleep duration[29,30]. One study compared REM sleep amount across a variety of human subjects with their intelligence quotient (IQ). No significant relation was seen[31].

A recent study claimed that "jumping spiders" have REM sleep[32]. However, these authors did not present evidence that these animals were actually asleep, a standard test that could have been done by determining if arousal threshold was elevated during the observed eye movements. The "REM sleep" reported may have been a waking behavior. A similar problem exists for a claim of a REM sleep-like state in the octopus[33] or a claim that an octopus had a "nightmare," a study that had not yet been peer reviewed but that received substantial media exposure. A more recent study of sleep in the octopus provides evidence for an octopus state with "pronounced body movements" and "rapid changes in skin patterning and texture resembling those of waking and increased arousal threshold[34]." This state has certain aspects analogous to REM sleep and other aspects unique to the octopus. Another study implied that zebrafish larvae had a REM sleep-like state[35], although there have been no reports of REM sleep in adult zebrafish, and arousal thresholds, necessary to determine if the larvae were asleep, were not measured. It is important to be cautious in labelling variations in behavior as REM sleep, rather than describing and measuring a variety of behavioral parameters including arousal thresholds, heart rate, muscle tone, etc. in sleep and comparing them across species[28]. A study of neuronal activity in the pontine and caudal midbrain regions critical for the generation of REM sleep[4] of turtles found no evidence for REM sleep-like activation of these neuronal groups[36] in these reptiles. Nor is REM sleep present in cetaceans, including dolphins[37,38] or in fur seals during most of the year[39], i.e. REM sleep is not universally present in vertebrates, and should not be assumed to exist and serve similar functions to mammalian REM sleep in arachnids, fish and other non-homoeothermic species, without further evidence.

Although some studies have hypothesized that sleep in general and REM sleep in particular is important in learning, methodological problems complicate interpretation of such claims, which are largely derived from sleep deprivation studies. Certainly, sleep immediately after learning prevents interference of new learning with the just learned item produced and measured by the experimenter. But depriving subjects of several hours or a complete night's sleep, as is often done in "sleep-learning" experiments, can be expected to produce interference from learning during the extended waking period. This is typically not taken into account[28]. As reviewed above, total REM sleep suppression has no obvious effect on learning[23]. Despite claims that sleep parameters are affected by prior learning[40], a very large human study examining changes in REM, nonREM, sleep spindles and other parameters after learning found no significant relations[25].

BRAIN THERMOREGULATION

Is there any correlation between physiological parameters across homeotherm orders, including mammals and birds that explains the very large differences in REM sleep amounts? In particular, I wondered why the platypus and echidna have such high amounts of REM sleep. One parameter that distinguishes the monotreme mammals (platypus and echidna) from other homeotherms is their low body temperature (31°C). My recent analysis[28] plotted the relation between orders of mammals and of birds and the average amounts of REM sleep per day reported by each group. In general all animals within each order have very similar body temperatures. For example the elephant, human and mouse, all placental mammals, have about the same body temperature 37±0.5°C. Similarly birds have a body temperature of 41°C±0.5°C. Fig. 3 shows the very strong negative correlation across homeotherm orders: monotremes, marsupials and placentals and birds between core temperature (which is highly correlated with brain temperature) and REM sleep hours/day [28], $r=-0.975$, $p=0.02$, Fig 3. (Note that egg laying mammals (monotremes platypus and echidnas) have very low body temperature and very high level of REM sleep, while birds, who of course are also hatched from eggs, have very high body temperature compared to mammals, but very low body REM sleep amounts). In other words, it is temperature, not hatching from eggs, that is correlated with REM sleep duration in hours/day.

These data can be explained by the "brainstem thermoregulation hypothesis." It is well established that brain temperature, including brainstem temperature, decreases in nonREM sleep along with brain metabolism and brain energy consumption. Brain temperature rises in REM sleep[41,42]. According to the present hypothesis REM sleep warms the brainstem to reverse the cooling of the body and brain in nonREM sleep[16], thereby preparing the sleeping animal for alert awakening with waking-like brain temperatures[28]. The cooling of the brain and the reduction of the underling neuronal activity in non-REM sleep saves a considerable amount of energy, but makes animals more vulnerable if awakened during non-REM. This cooling is reversed by REM sleep[28]. The thermoregulatory hypothesis can explain the differences in REM sleep amounts between orders of mammals. The monotremes (platypus and echidna) have the lowest body and brain temperature of any order of homeotherms and the greatest amount of REM sleep. Because their waking body temperature is so low, I hypothesize that that they would be at risk if brain temperature fell still further in sleep. Marsupials have a higher level of body and brain temperature and a lower amount of REM sleep. This progression continues with placentals having a still higher body and brain temperature and lower amount of REM sleep. Birds have the highest body and brain temperature and the lowest amount of REM sleep of any of the homeotherm orders. This hypothesis also explains one of the most consistent findings of mammalian sleep studies: that smaller animals have a shorter nonREM-REM cycle than larger animals. Just as it takes longer to cool and heat a large object, the nonREM-REM cycles are longer in large animals with larger absolute brain sizes.

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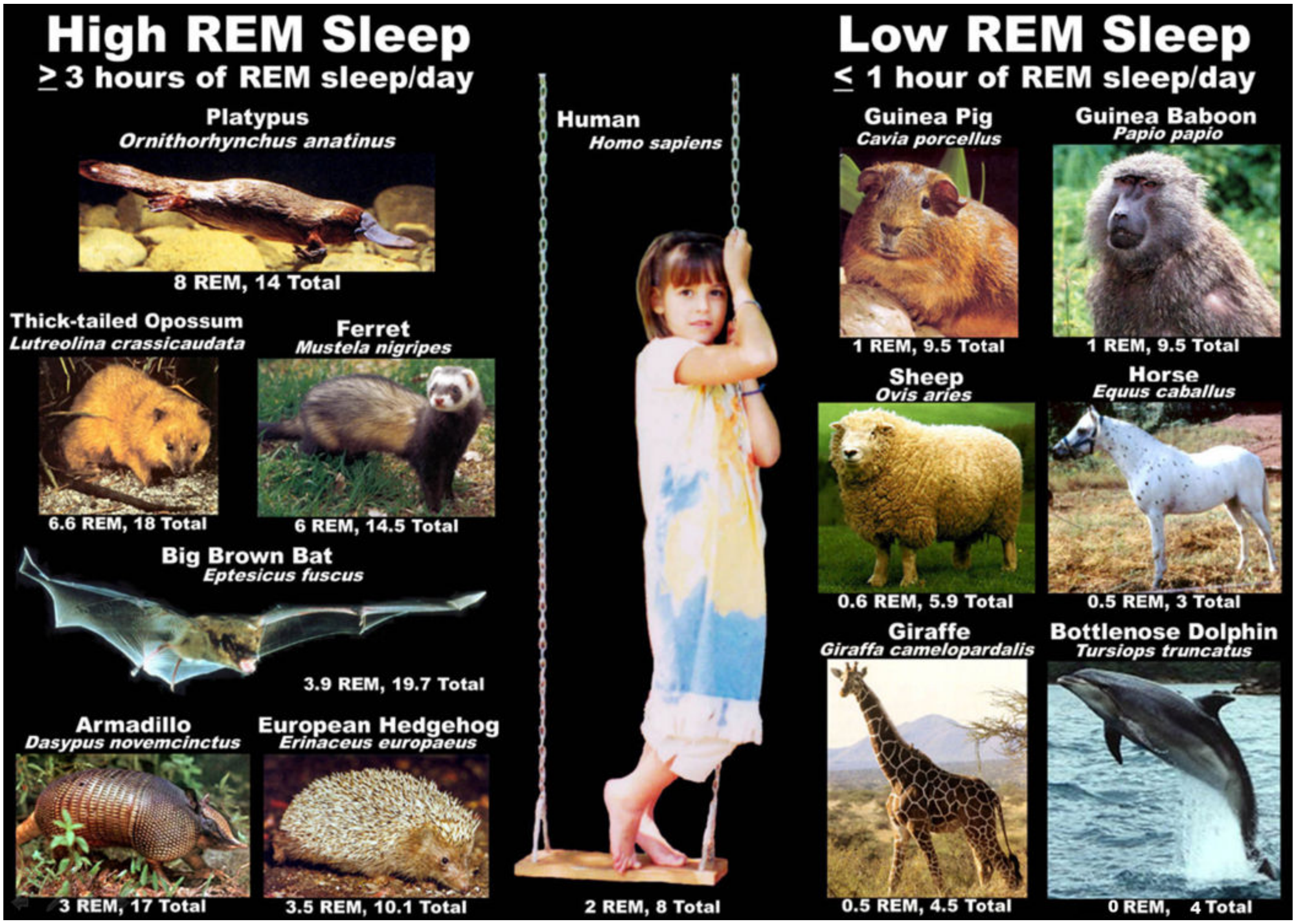

Fig 1.

Sleep in animals. Modified from [30]. Three points are illustrated by this figure and discussed further here[28]. 1. Human sleep and REM sleep is not unusually high of low compared to other animals. 2. Animals that have high amounts of REM sleep also have high amounts of nonREM sleep. 3. Animals with very different presumed cognitive capabilities do not necessarily have different amounts of sleep, e.g. the guinea pig has exactly the same amount of nonREM and REM sleep as the baboon (see [43] for further examples).

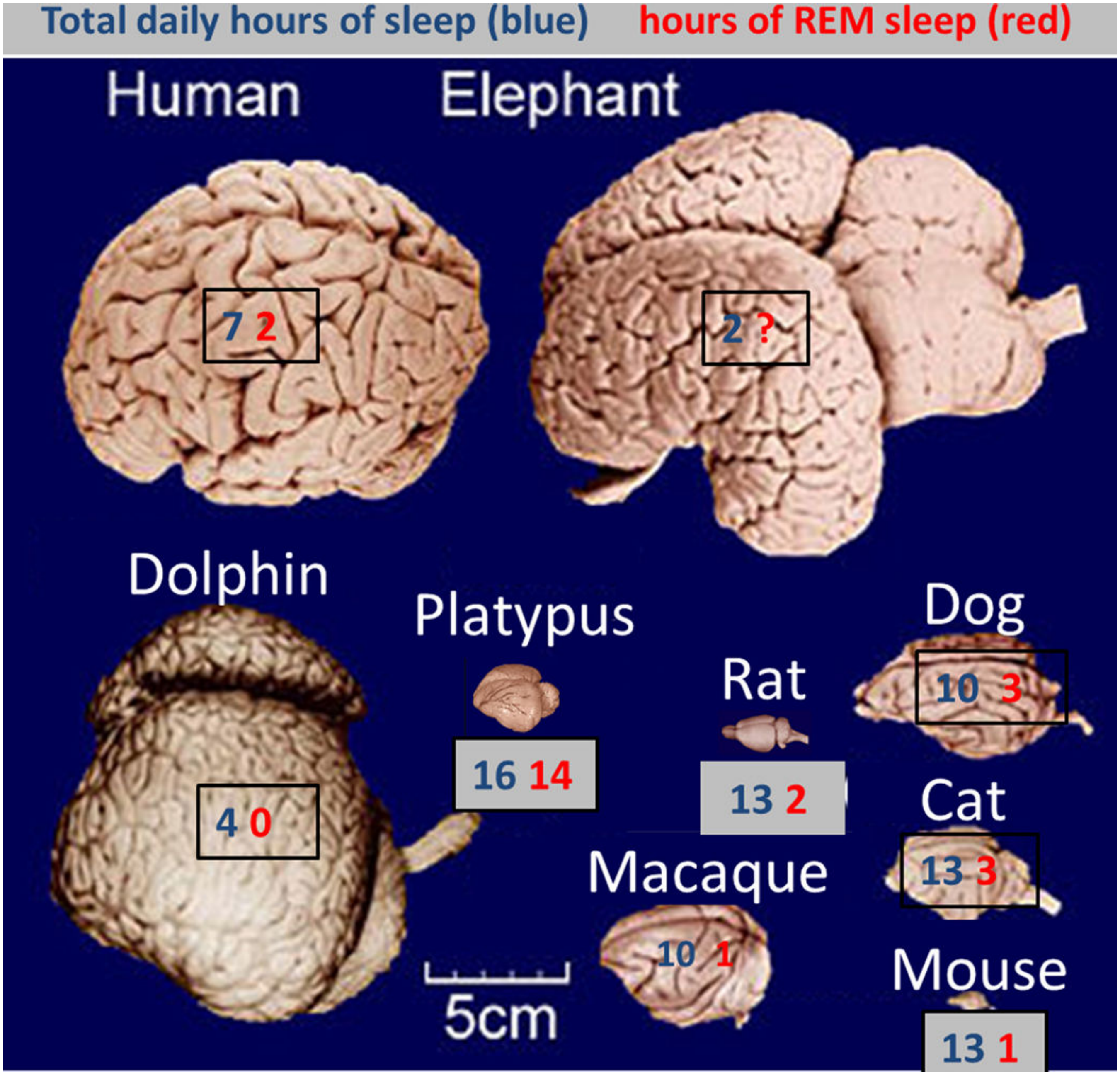

Fig 2.

Brain sizes of animals with documented sleep time. **NonREM+REM sleep time, in blue** and **REM sleep, time in red.** There is no strong relation between brain size (or brain body weight ratio[29]) and REM or nonREM sleep duration. Brain images from http://brainmuseum.org/index.html.

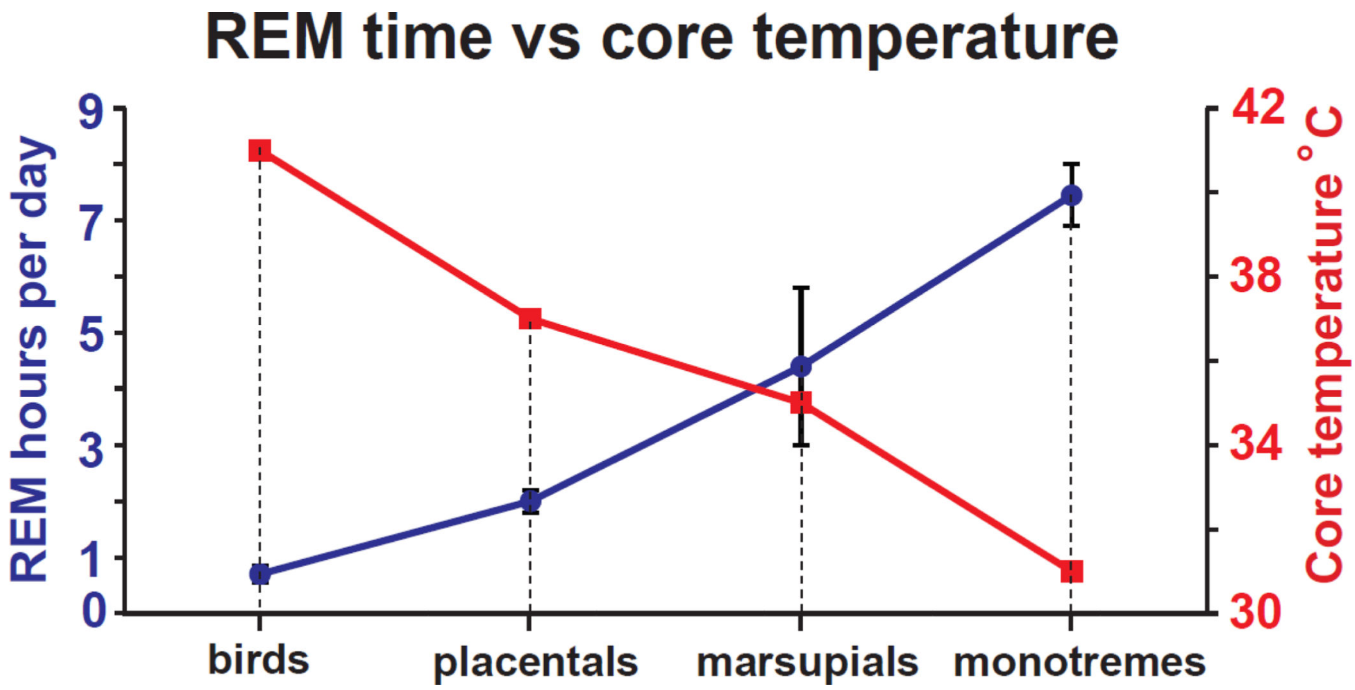

Fig 3.
Temperature across orders. REM sleep duration is strongly and inversely correlated with core (body and brain) temperature (r=−.975, p-0.02) modified from [28].