REVIEW ARTICLE

Two Types of REM Sleep: The Atonic and Brain REM Sleep

Zi-Jian Cai[1*]

[1]CaiFortune Consulting; No. 129, Building 6, Room 404, North Dongwu Road, Suzhou City, Jiangsu Province, 215128, PR China

ABSTRACT

With preliminary classification, there are five behavioral functions for rapid eye movement(REM) sleep after puberty, which are memory retention, drive dissipation, muscular efficiency, heat control and adaptive immobility. For these diversities, it is newly suggested in this mini-review to categorize the REM sleep into two types respectively as atonic and brain REM sleep. In concrete words, the atonic REM sleep was acquired early in platypus, ostrich, and reptiles, responsible for the adaptive immobility as rare exceptions to predation risk of sleep, for the important function recently proposed for improvement of muscular efficiency in most species, and for the heat control in some species, while the brain REM sleep were added later in evolution, responsible for conflict of emotional memories against disinhibited drives. In ecological aspects, this division of REM sleep is useful to pluralistically understand the diverse adaptive functions of REM sleep in various species. On inductive relation, the atonia is required for EEG activation from brain stem in REM sleep, consistent with the earlier origin of atonic sleep in evolution. On physiological paradox, the pathological high muscle tension in human depression results from the emotional stress from accumulated emotional memories processed in long REM sleep, therefore not contradictory with the atonic function of REM sleep. On stage interactions, these two types of REM sleep are different as coherent and counteractive with SWS respectively. In these respects, the REM sleep plays two types of qualitatively different functions in the atonic and brain REM sleep respectively.

Keywords: Rapid eye movement (REM) sleep, atonia, evolution, memory, depression, slow wave sleep

INTRODUCTION

There are various functions of rapid eye movement(REM) sleep for both brain and body. After puberty, the function of REM sleep for neural development has completed, and in this article it is only addressed to the functions of REM sleep in this post period.

The brain functions of REM sleep

On brain functions, it was early suggested that the REM sleep play functions in memory retention(Cai, 1991; 1995; 2015a; Smith, 1985) and retrieval(Cai, 1990; 1991; 1995; 2015a). Recently, many experiments have shown that the REM sleep plays roles in retention of emotional memories(Baran et al., 2012; Groch et al., 2013; Menz et al., 2013; Nishida et al., 2009; Popa et al., 2010). On the other hand, REM sleep deprivation has been reported as therapeutic against depression in humans(Vogel, 1975; 1983) and ameliorative against fear in rats(Hicks & Moore,

*Correspondence: hrsh8@126.com
No. 129, Building 6, Room 404, North Dongwu Road, Suzhou City, Jiangsu Province, 215128, PR China
Telephone: +86 512 65299403

1979), suggesting the REM sleep tend to disrupt the emotional balance toward depression(Goldstein & Walker, 2014; Palagini et al., 2013).

The brain functions of REM sleep have been a long historical subject. More than 100 years ago, Sigmund Freud published his book "The Interpretation of Dreams", suggesting that the instinctual wishes and drives conflict with the present and past ethics and realities in dreams. In 1968, Dement proposed that the REM sleep may function as energy or drive dissipation(Dement, 1969). In 1991 and 1995, Cai suggested that the REM sleep may function to complement the role of slow wave sleep(SWS) and shift the balance of emotion toward drive dissipation or even depression with retention of emotional memories(Cai, 1991; 1995; 2015a).

The peripheral functions of REM sleep

On peripheral functions, there are several possibilities. First, it was recently hypothesized that the REM sleep might play role in energy conservation together with SWS(Schmidt, 2014). Nonetheless, it was demonstrated in rodents that the REM sleep increased in duration simply with elevation of ambient temperature(Amici et al., 1998; Rosenthal & Vogel, 1993; 1994; Roussel et al., 1984), implicating the physiology of REM sleep be evolved against conservation of energy in response to temperature decrement. Likewise, it was also reported in humans that the REM sleep increased in duration from cool to moderate and to warm in temperature(Haskell et al., 1981; Karacan et al., 1978). In this regard, energy conservation may not be the function of REM sleep.

Second, it was recently suggested that, based on atonia, improvement of muscular efficiency may be a new function of REM sleep(Cai, 2015b), firstly in strength and secondly in skill. In phylogeny, this function of REM sleep is advantageous to explain the various exceptions of REM sleep, especially the absence of REM sleep in dolphins(Cai, 2015b; Lyamin et al., 2007; Madan & Jha, 2012; Sekiguchi et al., 2006; Siegel, 2008) and short duration of REM sleep in birds(Ayala-Guerrero et al., 1988, 2003; Cai, 2015b) in contrary to that in humans(Cai, 2015b; Floyd et al., 2007) and rodents(Cai, 2015b; Rechtschaffen et al., 1989), the absence of penile erections in REM sleep in

armadillo(Affanni et al., 2001; Cai, 2015b), as well as the higher voltage in EEG during REM sleep in platypus(Cai, 2015b; Siegel et al., 1998; 1999) and ostrich(Cai, 2015b; Lesku et al., 2011). In physiology, this function of REM sleep is advantageous to explain the association of REM sleep with the atonic episodes in SWS(Cai, 2015b; Tinguely et al., 2006; Werth et al., 2002), the absence of drastic menopausal change in duration of REM sleep(Cai, 2015b; Kalleinen et al., 2008; Orff et al., 2012; Shaver et al., 1988), and the different effects of ambient temperature on duration of REM sleep in rodents(Amici et al., 1998; Cai, 2015b; Rosenthal & Vogel, 1993; 1994; Roussel et al., 1984) and humans(Cai, 2015b; Haskell et al., 1981; Karacan et al., 1978). Obviously, improvement of muscular efficiency is an important and prospective function of REM sleep.

Third, it is necessary to consider the regulation of temperature. It is already known that the temperature regulation is suspended in REM sleep at the hypothalamic level(Libert, 2003; Parmeggiani, 2003). Despite the suspension, it is still necessary to consider that the increment of muscular efficiency may reduce and control the heat generation. At hot temperature, the REM sleep may make the animals adapt to warm environments via its atonic effects to improve the muscular efficiency(Cai, 2015b). In cold environments, it is meaningless for the REM sleep to decrease the muscle tension as the tension of muscles increases in response to cold in waking. In this regard, the function of REM sleep for muscular efficiency can partly account for the temperature regulation in animals, especially biased to heat control and warm adaptation rather than cold motivation(Cai, 2015b).

The ecological functions of REM sleep

On ecological functions, it was early suggested that sleep may help maintain immobility in animals choosing immobility as adaptive survival behavior(Meddis, 1975), which implicated that the REM sleep might cooperate with SWS in adaptive immobility in caves to avoid danger. In a few species, sleep is very long in duration, such as the armadillo(Affanni et al., 2001), bat(Zhao et al., 2010), owl monkey(Sri Kantha et al., 2009; Suzuki & Sri Kantha, 2006), and so on, so that immobility is obviously their

natural adaption. Nonetheless, Lesku et al. recently proposed that the REM sleep manifested inverse correlation with predation risk in most species(Lesku et al., 2006; 2009). In this regard, the adaptive immobility in caves to avoid danger is actually rare as exceptions. Besides, it is also difficult to use adaptive immobility to account for the REM sleep lengthy in carnivores which need predominate from more predation(Savage & West, 2007) while short in birds which need take rest(Ayala-Guerrero et al., 1988, 2003; Cai, 2015b). Whereas, as physiological studies suggested the REM sleep tend to disrupt the emotional balance toward depression(Goldstein & Walker, 2014; Hicks & Moore, 1979; Palagini et al., 2013; Vogel, 1975; 1983), so that nor supported the proposal of Lesku et al. which would predict the REM sleep to decrease fear(Lesku et al., 2006; 2009).

Sectional summary

In all, there are preliminarily five behavioral functions for REM sleep after puberty, which are memory retention, drive dissipation, muscular efficiency, heat control and adaptive immobility. In this review, it is attempted for the first time to further categorize these functions of REM sleep for the convenience to account for the functional and evolutionary variations of REM sleep.

Two types of REM sleep and evolutionary variations

Division of two types of REM sleep: The atonic and brain REM sleep

It is herein newly suggested that it is appropriate to categorize the functions of REM sleep into two types, the atonic and brain REM sleep. Acquired early in evolution in platypus(Cai, 2015b; Siegel et al., 1998, 1999), ostrich(Cai, 2015b; Lesku et al., 2011) and reptiles(Ayala-Guerrero & Huitrón Reséndiz, 1991; Ayala-Guerrero & Mexicano, 2008) without desynchronized cortical activation, the atonic functions of REM sleep are responsible for the improvement of muscular efficiency in most species(Cai, 2015b), for the heat control in some species(Cai, 2015b), and for the adaptive immobility to

avoid danger in caves in a few species(Meddis, 1975), while the brain functions of REM sleep requiring desynchronized cortical activation and acquired more recently in evolution responsible for assimilation of emotional memories(Baran et al., 2012; Groch et al., 2013; Menz et al., 2013; Nishida et al., 2009; Popa et al., 2010) and disinhibited drives(Cai, 1991; 1995; 2015a; Dement, 1969; Goldstein & Walker, 2014), and even for pathological generation of depression in humans(Dement, 1969; Goldstein & Walker, 2014; Palagini et al., 2013).

The REM sleep function in the species with short sleep duration

The REM sleep manifests phylogenetic variations in mammals and birds(Cai, 2015b; Lesku et al., 2006; 2009). REM sleep is absent in some dolphins(Cai, 2015b; Lyamin et al., 2007; Madan & Jha, 2012; Sekiguchi et al., 2006; Siegel, 2008), and very short in duration in many birds(Ayala-Guerrero et al., 1988, 2003; Cai, 2015b). Obviously, the function of REM sleep is unnecessary in these animals. Dolphins and birds are spatially free in swimming, flying or running. Speed, force and agility are advantageous to their adaptation in nature, while sophisticated skills with limbs of high accuracy, low rigidity and subtle movement are not possible to them due to possession of neither hands nor forepaws. This may be the reason why they are neither required to possess the atonic function of REM sleep for muscular efficiency, nor the practice of emotional memories in dreams.

Whereas, some mammals, such as horses and elephants(Savage & West, 2007; Williams et al., 2008), manifest REM sleep shorter in duration than carnivores(Savage & West, 2007) and pennipeds(Lyamin et al., 2002; 2012; Pryaslova et al., 2009), but longer than those in dolphins(Cai, 2015b; Lyamin et al., 2007; Madan & Jha, 2012; Sekiguchi et al., 2006; Siegel, 2008) and birds(Ayala-Guerrero et al., 1988, 2003; Cai, 2015b). They can partly improve their muscular efficiency with atonic REM sleep, but may not be able to fully reduce their muscle tone. Likewise, the Octodon degus were assessed to manifest stable REM sleep(Ocampo-Garcés et al., 2013), but less in time than other squirrels in the same phylogenetic order. As Octodon degus are both

intelligent and social, the stable REM sleep of shorter duration in degus may implicate that they can partly improve their muscular efficiency with atonic REM sleep, but less in extent than other squirrels in the same phylogenetic order, presumably because their social forces surpass the muscular forces of individuals(Cai, 2015b).

In similar, it was reported(Lesku et al., 2011) that the episodes of REM sleep in ostriches lasted 27±7 s on average, and could last up to 5 min, the longest reported for birds typically less than 10s in duration(Lesku et al., 2011). This bird may also reduce their muscle tone a little further during the atonic REM sleep in assistance to SWS.

The REM sleep functions in the species with long sleep duration

Further longer in duration of REM sleep, in the mammals sleeping daily as long as carnivores(Savage & West, 2007) and pennipeds(Lyamin et al., 2002; 2012; Pryaslova et al., 2009), or even longer than they do, the effect of atonic REM sleep to improve the muscular efficiency should persist, notably for increasing the contractile strength in carnivores and pennipeds, but might become secondary as compared to other functions of REM sleep during the lengthy sleep. Especially, adaptive immobility(Meddis, 1975) is the most obvious function of REM sleep in the few mammals sleeping daily longer than carnivores and pennipeds, such as armadillo(Affanni et al., 2001), bat(Zhao et al., 2010), owl monkey(Sri Kantha et al., 2009; Suzuki & Sri Kantha, 2006), and so on.

It is necessary to point out that Lesku et al. recently proposed that the duration of REM sleep manifested inverse correlation with predation risk(Lesku et al., 2006, 2009). In this regard, it is strange for these few species to sleep very long a day. As the most plausibly correct explanation, these few species may resort to immobility of sleep in their caves to avoid danger(Meddis, 1975), therefore exceptional to the proposal of Lesku et al(2006; 2009). Whereas, in most animals, the duration of REM sleep is inversely correlated with predation risk(Lesku et al., 2006; 2009), so that immobility of REM sleep would bring disadvantage. Besides, it is also difficult to use

adaptive immobility to account for the REM sleep lengthy in carnivores which need predominate from more predation(Savage & West, 2007), while short in birds which need take rest(Ayala-Guerrero et al., 1988; 2003; Cai, 2015b). Improvement of muscular efficiency is the more likely function of REM sleep for them(Cai, 2015b).

Origin and evolution of REM sleep functions

It is also necessary to point out that, although the REM sleep manifests phylogenetic variations in mammals and birds(Cai, 2015b; Lesku et al., 2006; 2009), atonia is present in REM sleep in both of them, and even in more ancient species, such as platypus(Cai, 2015b; Siegel et al., 1998; 1999), ostrich(Cai, 2015b; Lesku et al., 2011), reptiles(Ayala-Guerrero & Huitrón Reséndiz, 1991; Ayala-Guerrero & Mexicano, 2008) and so on. In these ancient animals with atonia preserved, it is not present the desynchronized EEG activation for forebrain memory processing. Obviously, improvement of muscular efficiency is the common important function of their atonic REM sleep.

It is certainly necessary to mention the function of REM sleep on heat control. It is an accessory function of REM sleep as improvement of muscular efficiency(Cai, 2015b), biased to heat control and warm adaptation rather than cold motivation, which belongs to the same category in function of atonic REM sleep. Although the animals can control heat generation via its atonic effects to improve the muscular efficiency(Cai, 2015b), the muscle tension increases naturally in response to cold in waking, so that it is meaningless for the animals to adopt the atonic REM sleep to decrease the muscle tension. Heat control is an important function of atonic REM sleep in some small mammals such as rats and so on(Cai, 2015b), in contrary to pennipeds(Lyamin et al., 2002; 2012; Pryaslova et al., 2009) and birds(Ayala-Guerrero et al., 1988; 2003; Cai, 2015b).

Later in evolution, the atonic REM sleep acquired desynchronized EEG activation in brain, which made memory processing possible. It was reported that the atonic REM sleep in armadillo was long but absent of penile erections(Affanni et al., 2001; Cai, 2015b), implicating the animal was able to process emotional

memory but unable to release sexual drive during their immobile REM sleep. It is likely that the heavily armored armadillo might need the atonic function of REM sleep to improve the muscular efficiency to reduce heat and maximize the contractile strength(Cai, 2015b), together with the practice of emotional behaviors for optimization in usage. Whereas, the armored armadillo is accustomed to the immobile inescapable curling state in response to danger, so that it is unnecessary for the armadillo to use sexual drive to counteract the depressive state from accumulated emotional memories processed in REM sleep(Cai, 1991; 1995; 2015a).

Nonetheless in most mammals, such as rodents, carnivores and humans, penile erections occur together with desynchronized EEG activation in REM sleep(Cai, 2015b). As mentioned in the "Introduction", it was suggested by Cai(1991; 1995; 2015a) and was also the traditional view of Freudianism that the present and past ethics and realities directly conflicted with the instinctual wishes and drives in both waking and dreams. Obviously, in rodents, carnivores and humans, it is completed the natural conflict of emotional memories against disinhibited drives during the REM sleep. In this regard, it is herein reasonable to categorize these two brain functions of REM sleep added later in evolution as another type of REM sleep.

In parallel, the evolution of REM sleep was sketchily depicted recently(Cai, 2015b). The function of atonic REM sleep as improvement of muscular efficiency was early acquired in evolution in reptiles, ostrich and platypus. Later, the retention of emotional memories was added to the atonic REM sleep in armadillo to make use of the muscular efficiency. Finally, disinhibition of drives was added to the atonic REM sleep in rodents, carnivores and humans to assimilate the contractile strength and muscular skills.

Sectional summary

In all, the REM sleep after puberty is divided into two types respectively as atonic and brain REM sleep. The atonic functions of REM sleep, acquired early in evolution in platypus, ostrich and reptiles, are responsible for the improvement of muscular efficiency in most species, for the adaptive immobility in caves to avoid danger in a few species, and also for the heat control in some species. Whereas, the brain functions of REM sleep requiring desynchronized EEG activation and acquired later in evolution are responsible for both retention of emotional memories and dissipation of disinhibited drives. This division of REM sleep is useful to pluralistically explain the diverse adaptive functions of REM sleep in various species.

Two types of REM sleep in function, two types of interactions with SWS

In consistency with the categorization of REM sleep into two types as the atonic and brain REM sleep, the physiological processes underlying these functions also manifest bifurcation in interaction with other physiological processes and states.

REM sleep and menopause

Menopause in humans manifests as decrease and even withdrawal of sexual drive in women. Several reports indicated that, except more frequent awakening during sleep, most polysomnographic variables preserved with little change from premenopausal to postmenopausal period(Kalleinen et al., 2008; Orff et al., 2012; Shaver et al., 1988). In accordance, even though there is drastic decrease in sexual drive in menopause, there is little menopausal change in duration of REM sleep, disagreeing with the brain function of REM sleep for conflict of emotional memories against disinhibited drives in humans, while supporting the function of REM sleep as improvement of muscular efficiency relatively. As the REM sleep declines roughly with aging(Floyd et al., 2007), immobility is obviously neither the major function of REM sleep in humans.

REM sleep and depression

Depression is the disease in humans also with reduction in instinctual drives. Lengthy REM sleep tends to disrupt the emotional balance toward depression(Goldstein & Walker, 2014; Palagini et al., 2013), while REM sleep deprivation was shown to be

therapeutic against depression in humans(Vogel, 1975; 1983) and ameliorative against fear in rats(Hicks & Moore, 1979). However, it is the characteristics of depression to be both high in muscle tone and long in REM sleep, incompatible with the atonic function of REM sleep as improvement of muscular efficiency. Herein, it is pointed out that the high muscle tension in human depression results from the emotional stress from the accumulated emotional memories in long REM sleep(Cai, 1991; 1995; 2015a). In this way, the characteristics of depression in muscle tone are not contradictory with the atonic function of REM sleep to improve muscular efficiency. Different types of REM sleep produce different physiological effects.

Interactions of REM sleep and SWS

On peripheral aspect, the REM sleep is associative with SWS to regulate muscular efficiency. It was reported that episodes with low muscular tone also occurred in SWS as in REM sleep, and even associative with the occurrence of REM sleep(Cai, 2015b; Tinguely et al., 2006; Werth et al., 2002), implicating the atonia in REM sleep was required for the induction of EEG activation from brainstem, consistent with the earlier acquisition of atonic sleep in evolution. Besides, it was even demonstrated that daytime deprivation of REM sleep caused an enhancement of muscular atonia during the recovery SWS(Cai, 2015b; Werth et al., 2002), suggesting that the atonia in REM sleep would not function solely for the blockade of behavioral expression of dream contents in REM sleep, but rather implicating that improvement of muscular efficiency was the important function of REM sleep which could partly be compensated with the muscular atonia during the recovery SWS.

It is noticed that, together with the coherence of SWS and REM sleep in improvement of muscular efficiency, the function of REM sleep in heat control(Cai, 2015b) is also coherent with that of SWS. SWS is preferably initiated during the circadian phase of decreased heat production(Van Someren, 2006), while SWS-related behaviors such as relaxation, lying down can feed back to the thermoregulatory system to save energy(Kräuchi, 2007). Atonia in REM sleep may be more efficient than

SWS in saving peripheral energy and controlling heat, even though they are coherent in function.

It is necessary to point out that immobility is also the common characteristic of both SWS and REM sleep, so that it is obvious that they are coherent for adaptive immobility to avoid danger in caves(Meddis, 1975). Taken together, muscular efficiency, heat control and adaptive immobility, as the atonic functions of REM sleep acquired early in evolution, are all accomplished coherently with SWS.

On the other hand, the brain functions of REM sleep as retention of emotional memories and dissipation of disinhibited drives are both counteractive with SWS. With regard to memory processing, it was shown that SWS might help retention of declarative memory(Inostroza & Born, 2013; Rasch & Born, 2013), while impair memory in emotional learning tasks, because cueing during postlearning SWS impaired the memory acquired in aversive task(Hars & Hennevin, 1987), and SWS was the source of memory impairment caused by REM sleep deprivation(Rideout, 1979). In contrast, many experiments have shown that the REM sleep plays functions in retention of emotional memories(Baran et al., 2012; Groch et al., 2013; Menz et al., 2013; Nishida et al., 2009; Popa et al., 2010). At the cellular level, it was shown that SWS favored LTD(Yang et al., 2012a, 2012b) but not LTP(Bramham & Srebro, 1989; Leonard et al., 1987), while REM sleep was required for LTP(Ishikawa et al., 2006; Ravassard et al., 2009). There are some attempts recently suggesting that both memory retention and noise clearance occur in SWS to reconcile the diverse results(Giuditta, 2014). All these results clearly demonstrated that SWS and REM sleep manifested opposite and counteractive in memory processing.

The role of SWS in emotional regulation against depression was postulated by Cai together with memory processing(Cai, 1991; 1995; 2015a), while by Kupfer and Reynolds together with aging and dementia(Kupfer & Reynolds, 1989). SWS was shown to be related with depression(Kupfer et al., 1990; Mendlewicz & Kerkhofs, 1991; Spiegel et al., 1986), while deprivation of stage 4 SWS in humans produced a depressive or hypochondriacal state(Agnew et al., 1967), whereas

increase in SWS duration in early sleep ameliorated depression(Wehr et al., 1979). Besides, hippocampal lesion but not neocortical lesion caused impairment of SWS(Kim et al., 1971), while the neuronal activity in SWS increased in hippocampus but not in neocortex(Steriade & Hobson, 1976; Winson & Abzug, 1977). In contrast, the REM sleep tends to disrupt the emotional balance toward depression(Goldstein & Walker, 2014; Palagini et al., 2013). REM sleep deprivation was reported as therapeutic against depression in humans(Vogel, 1975; 1983) and ameliorative against fear in rats(Hicks & Moore, 1979). All these results clearly demonstrated that SWS and REM sleep manifested opposite and counteractive in emotional regulation.

CONCLUSIONS

In this review, it is preliminarily classified the behavioral functions for rapid eye movement(REM) sleep after puberty as memory retention, drive dissipation, muscular efficiency, heat control and adaptive immobility. It is newly suggested to categorize these functions of REM sleep into two types as the atonic and brain REM sleep. The atonic REM sleep with evolutionary origin early in platypus, ostrich, and reptiles is responsible for the important function as improvement of muscular efficiency in most species, the heat control in some species, as well as the adaptive immobility to avoid danger in caves in a few species as rare exceptions to predation risk of sleep. Whereas, the brain REM sleep added later in evolution is responsible for conflict of emotional memories against disinhibited drives. This categorization of REM sleep helps to pluralistically understand the evolutionary variations of REM sleep. In consistency, the atonia in sleep is required for the EEG activation of forebrain from brainstem in REM sleep, consistent with the earlier acquisition of atonic sleep in evolution. Besides, it is clarified that the high muscle tension in human depression is caused by the emotional stress from the accumulated emotional memories processed in the pathologically long REM sleep, not in contradiction with the atonic function of REM sleep. Finally, it is pointed out that these two types of REM sleep are also different in interaction with SWS as coherent and counteractive respectively.

Conflict of interest

The author declares no conflict of interest nor financial support for this work.

References

Affanni, J.M., Cervino, C.O., & Marcos, H.J. (2001). Absence of penile erections during paradoxical sleep. Peculiar penile events during wakefulness and slow wave sleep in the armadillo. *Journal of Sleep Research,* 10, 219-228.

Agnew, H.W. Jr., Webb, W.B., & Williams, R.L. (1967). Comparison of stage four and 1-REM sleep deprivation. *Perceptual & Motor Skills,* 24, 851-858.

Amici, R., Zamboni, G., Perez, E., Jones, C.A., & Parmeggiani, P.L. (1998). The influence of a heavy thermal load on REM sleep in the rat. *Brain Research,* 781, 252-258.

Ayala-Guerrero, F., & Huitrón Reséndiz, S. (1991). Behavioral and electrophysiological patterns of wakefulness-sleep states in a lizard. *Boletin de Estudios Medicos Y Biologicos,* 39, 9-14.

Ayala-Guerrero, F., & Mexicano, G. (2008). Sleep and wakefulness in the green iguanid lizard (Iguana iguana). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology,* 151, 305-312.

Ayala-Guerrero, F., Mexicano, G., & Ramos, J.I. (2003). Sleep characteristics in the turkey Meleagris gallopavo. *Physiology & Behavior,* 78, 435-440.

Ayala-Guerrero, F., Pérez, M.C., & Calderón, A. (1988). Sleep patterns in the bird Aratinga canicularis. *Physiology & Behavior,* 43, 585-589.

Baran, B., Pace-Schott, E.F., Ericson, C., & Spencer, R.M. (2012). Processing of emotional reactivity and emotional memory over sleep. *The Journal of Neuroscience,* 32, 1035-1042.

Bramham, C.R., & Srebro, B. (1989). Synaptic plasticity in the hippocampus is modulated by behavioral state. *Brain Research,* 493, 74-86.

Cai, Z.J., 1990. The neural mechanism of declarative memory consolidation and retrieval: A hypothesis. *Neuroscience & Biobehavioral Reviews,* 14, 295-304.

Cai, Z.J., 1991. The functions of sleep: further analysis. *Physiology & Behavior,* 50, 53-60.

Cai, Z.J., 1995. An integrative analysis to sleep functions. *Behavioural Brain Research,* 69, 187-194.

Cai, Z.J., 2015a. Extending psychoanalysis with theories on sleep functions. *Journal of Sleep Disorders & Therapy,* 4, 217.

Cai, Z.J., 2015b. A new function of rapid eye movement sleep: Improvement of muscular efficiency. *Physiology & Behavior,* 144, 110−115.

Dement, W.C. (1969). The biological role of REM sleep(circa 1968). In: A. Kales(Ed.), *Sleep: Physiology and Pathology*(pp. 245-265). Philadelphia: Lippincott.

Floyd, J.A., Janisse, J.J., Jenuwine, E.S. & Ager, J.W. (2007). Changes in REM-sleep percentage over the adult lifespan. *Sleep,* 30, 829–836.

Giuditta, A. (2014). Sleep memory processing: the sequential hypothesis. *Frontiers in Systems Neuroscience,* 8, 219.

Goldstein, A.N., & Walker, M.P. (2014). The role of sleep in emotional brain function. *Annual Review of Clinical Psychology,* 10, 679-708.

Groch, S., Wilhelm, I., Diekelmann, S., & Born, J. (2013). The role of REM sleep in the processing of emotional memories: evidence from behavior and event-related potentials. *Neurobiology of Learning and Memory,* 99, 1-9.

Hars, B., & Hennevin, E. (1987). Impairment of learning by cueing during postlearning slow-wave sleep in rats. *Neuroscience Letters,* 79, 290-294.

Haskell, E.H., Palca, J.W., Walker, J.M., Berger, R.J., & Heller, H.C. (1981). The effects of high and low ambient temperatures on human sleep stages. *Electroencephalography and Clinical Neurophysiology,* 51, 494-501.

Hicks, R.A. & Moore, J.D. (1979). REM sleep deprivation diminishes fear in rats. *Physiology & Behavior,* 22, 689-692.

Inostroza, M., & Born, J. (2013). Sleep for preserving and transforming episodic memory. *Annual Review of Neuroscience,* 36, 79-102.

Ishikawa, A., Kanayama, Y., Matsumura, H., Tsuchimochi, H., Ishida, Y., & Nakamura, S. (2006). Selective rapid eye movement sleep deprivation impairs the maintenance of long-term potentiation in the rat hippocampus. *European Journal of Neuroscience,* 24, 243-248.

Kalleinen, N., Polo-Kantola, P., Himanen, S.L., Alhola, P., Joutsen, A., Urrila, A.S., & Polo, O. (2008). Sleep and the menopause - do postmenopausal women experience worse sleep than premenopausal women? *Menopause International,* 14, 97-104.

Karacan, I., Thornby, J.I., Anch, A.M., Williams, R.L., & Perkins, H.M. (1978). Effects of high ambient temperature on sleep in young men. *Aviation, Space, and Environmental Medicine,* 49, 855-860.

Kim, C., Choi, H., Kim, J.K., Kim, M.S., Huh, M.K., & Moon, Y.B. (1971). Sleep pattern of hippocampectomized cat. *Brain Research,* 29, 223-236.

Kräuchi, K. (2007). The human sleep-wake cycle reconsidered from a thermoregulatory point of view. *Physiology & Behavior,* 90, 236-245.

Kupfer, D.J., Frank, E., McEachran, A.B., & Grochocinski, V.J. (1990). Delta sleep ratio. A biological correlate of early recurrence in unipolar affective disorder. *Archives of General Psychiatry,* 47, 1100-1105.

Kupfer, D.J., & Reynolds, C.F. (1989). Slow-wave sleep as a 'protective' factor, In: A.J. Stunkard & A. Baum (Eds.), *Perspectives in Behavioral Medicine: Eating, Sleeping, and Sex*(pp. 131-145). New Jersey: Lawrence Erlbaum.

Leonard, B.J., McNaughton, B.L., & Barnes, C.A. (1987). Suppression of hippocampal synaptic plasticity during slow-wave sleep. *Brain Research,* 425, 174-177.

Lesku, J.A., Meyer, L.C., Fuller, A., Maloney, S.K., Dell'Omo, G., Vyssotski, A.L., & Rattenborg, N.C. (2011). Ostriches sleep like platypuses. *PLoS One,* 6, e23203.

Lesku, J.A., Roth, T.C., Amlaner, C.J., & Lima, S.L. (2006). A phylogenetic analysis of sleep architecture in mammals: the integration of anatomy, physiology, and ecology. *The American Naturalist,* 168, 441-453.

Lesku, J.A., Roth, T.C., Rattenborg, N.C., Amlaner, C.J., & Lima, S.L. (2009). History and future of comparative analyses in sleep research. *Neuroscience & Biobehavioral Reviews,* 33, 1024-1036.

Libert, J.P. (2003). Thermal regulation during sleep. *Revue Neurologique (Paris),* 159(11 Suppl), 6S30-34.

Lyamin, O.I., Kosenko, P.O., Vyssotski, A.L., Lapierre, J.L., Siegel, J.M., & Mukhametov, L.M. (2012). Study of sleep in a walrus. *Doklady Biological Sciences,* 444, 188-191.

Lyamin, O.I., Mukhametov, L.M., Chetyrbok, I.S., & Vassiliev, A.V. (2002). Sleep and wakefulness in the southern sea lion. *Behavioural Brain Research,* 128, 129-138.

Lyamin, O., Pryaslova, J., Kosenko, P., & Siegel, J. (2007). Behavioral aspects of sleep in bottlenose dolphin mothers and their calves. *Physiology & Behavior,* 92, 725-733.

Madan, V., & Jha, S.K. (2012). Sleep alterations in mammals: Did aquatic conditions inhibit rapid eye movement sleep? *Neuroscience Bulletin,* 28, 746-758.

Meddis, R. (1975). On the function of sleep. *Animal Behaviour,* 23, 676-691.

Mendlewicz, J., & Kerkhofs M. (1991). Sleep electroencephalography in depressive illness. A collaborative study by the World Health Organization. *The British Journal of Psychiatry,* 159, 505-509.

Menz, M.M., Rihm, J.S., Salari, N., Born, J., Kalisch, R., Pape, H.C., Marshall, L., & Büchel, C. (2013). The role of sleep and sleep deprivation in consolidating fear memories. *Neuroimage,* 75, 87-96.

Nishida, M., Pearsall, J., Buckner, R.L., & Walker, M.P. (2009). REM sleep, prefrontal theta, and the consolidation of human emotional memory. *Cerebral Cortex,* 19, 1158-1166.

Ocampo-Garcés, A., Hernández, F., & Palacios, A.G. (2013). REM sleep phase preference in the crepuscular Octodon degus assessed by selective REM sleep deprivation. *Sleep,* 36, 1247-1256.

Orff, H.J., Meliska, C.J., Lopez, A., Martinez, F., Sorenson, D., & Parry, B.L. (2012). Polysomnographic evaluation of sleep quality and quantitative variables in women as a function of mood, reproductive status, and age. *Dialogues in Clinical Neuroscience,* 14, 413-424.

Palagini, L., Baglioni, C., Ciapparelli, A., Gemignani, A., & Riemann, D. (2013). REM sleep dysregulation in depression: state of the art. *Sleep Medicine Reviews,* 17, 377-390.

Parmeggiani, P.L. (2003). Thermoregulation and sleep. *Frontiers in Bioscience,* 8, s557-567.

Popa, D., Duvarci, S., Popescu, A.T., Léna, C., & Paré, D. (2010). Coherent amygdalocortical theta promotes fear memory consolidation during paradoxical sleep. *Proceedings of the National Academy of Sciences of the United States of America,* 107, 6516-6519.

Pryaslova, J.P., Lyamin, O.I., Siegel, J.M., & Mukhametov, L.M. (2009). Behavioral sleep in the walrus. *Behavioural Brain Research,* 201, 80-87.

Rasch, B., & Born, J. (2013). About sleep's role in memory. *Physiology & Behavior,* 93, 681-766.

Ravassard, P., Pachoud, B., Comte, J.C., Mejia-Perez, C., Scoté-Blachon, C., Gay, N., Claustrat, B., Touret, M., Luppi, P.H., & Salin, P.A. (2009). Paradoxical (REM) sleep deprivation causes a large and rapidly reversible decrease in long-term potentiation, synaptic transmission, glutamate receptor protein levels, and ERK/MAPK activation in the dorsal hippocampus. *Sleep,* 32, 227-240.

Rechtschaffen, A., Bergmann, B.M., Everson, C.A., Kushida, C.A., & Gilliland, M.A. (1989). Sleep deprivation in the rat: X. Integration and discussion of the findings. *Sleep,* 12, 68-87.

Rideout, B.E. (1979). Non-REM sleep as a source of learning deficits induced by REM sleep deprivation. *Physiology & Behavior,* 22, 1043-1047.

Rosenthal, M.S., & Vogel, G.W. (1993). The effect of a 3-day increase of ambient temperature toward the thermoneutral zone on rapid eye movement sleep in the rat. *Sleep,* 16, 702-705.

Rosenthal, M.S., & Vogel, G.W. (1994). The effects of a 3-day increase of ambient temperature on body temperature and REM sleep in an animal model of depression. *Sleep,* 17, 291-297.

Roussel, B., Turrillot, P., & Kitahama, K. (1984). Effect of ambient temperature on the sleep-waking cycle in two strains of mice. *Brain Research,* 294, 67-73.

Savage, V.M., & West, G.B. (2007). A quantitative, theoretical framework for understanding mammalian sleep. *Proceedings of the National Academy of Sciences of the United States of America,* 104, 1051-1056.

Schmidt, M.H. (2014). The energy allocation function of sleep: A unifying theory of sleep, torpor, and continuous wakefulness. *Neuroscience & Biobehavioral Reviews,* 47C, 122-153.

Sekiguchi, Y., Arai, K., & Kohshima, S. (2006). Sleep behaviour: sleep in continuously active dolphins. *Nature,* 441, E9-10.

Shaver, J., Giblin, E., Lentz, M., & Lee, K. (1988). Sleep patterns and stability in perimenopausal women. *Sleep,* 11, 556-561.

Siegel, J.M. (2008). Do all animals sleep? *Trends in Neurosciences,* 31, 208-213.

Siegel, J.M., Manger, P.R., Nienhuis, R., Fahringer, H.M., & Pettigrew, J.D. (1998). Monotremes and the evolution of rapid eye movement sleep. *Philosophical Transactions of the Royal Society B Biological Sciences,* 353, 1147-1157.

Siegel, J.M., Manger, P.R., Nienhuis, R., Fahringer, H.M., Shalita, T., & Pettigrew, J.D. (1999). Sleep in the platypus. *Neuroscience,* 91, 391-400.

Smith, C. (1985). Sleep states and learning: a review of the animal literature. *Neuroscience & Biobehavioral Reviews,* 9, 157-168.

Spiegel, R., Köberle, S., & Allen, S.R. (1986). Significance of slow wave sleep: considerations from a clinical viewpoint. *Sleep,* 9, 66-79.

Sri Kantha, S., Suzuki, J., Hirai, Y., & Hirai, H. (2009). Behavioral sleep in captive owl monkey (Aotus azarae) and squirrel monkey (Saimiri boliviensis). *Acta Neurobiologiae Experimentalis (Wars),* 69, 537-544.

Steriade, M., & Hobson, J. (1976). Neuronal activity during the sleep-waking cycle. *Progress in Neurobiology,* 6, 155-376.

Suzuki, J., & Sri Kantha, S. (2006). Quantitation of sleep and spinal curvature in an unusually longevous owl monkey (Aotus azarae). *Journal of Medical Primatology,* 35, 321-330.

Tinguely, G., Huber, R., Borbély, A.A., & Achermann, P. (2006). Non-rapid eye movement sleep with low muscle tone as a marker of rapid eye movement sleep regulation. *BMC Neuroscience,* 7, 2.

Van Someren, E.J. (2006). Mechanisms and functions of coupling between sleep and temperature rhythms. *Progress in Brain Research,* 153, 309-324.

Vogel, G.W. (1975). A review of REM sleep deprivation. *Archives of General Psychiatry,* 32, 749-761.

Vogel, G.W. (1983). Evidence for REM sleep deprivation as the mechanism of action of antidepressant drugs. *Progress in Neuro-Psychopharmacology & Biological Psychiatry,* 7, 343-349.

Wehr, T.A., Wirz-Justice, A., Goodwin, F.K., Duncan, W., & Gillin, J.C. (1979). Phase advance of the circadian sleep-wake cycle as an antidepressant. *Science,* 206, 710-713.

Werth, E., Achermann, P., & Borbély, A.A. (2002). Selective REM sleep deprivation during daytime. II. Muscle atonia in non-REM sleep. *American Journal of Physiology - Regulatory, Integrative and Comparative Physiology,* 283, R527-532.

Williams, D.C., Aleman, M., Holliday, T.A., Fletcher, D.J., Tharp, B., Kass, P.H., Steffey, E.P., & LeCouteur, R.A. (2008). Qualitative and quantitative characteristics of the electroencephalogram in normal horses during spontaneous drowsiness and sleep. *Journal of Veterinary Internal Medicine,* 22, 630-638.

Winson, J., & Abzug, C. (1977). Gating of neuronal transmission in the hippocampus: efficacy of transmission varies with behavioral state. *Science,* 196, 1223-1225.

Yang, Z., Zhang, W., Wang, M., Ruan, D., & Chen, J. (2012a). Effects of daytime, night and sleep pressure on long-term depression in the hippocampus in vivo. *Neuroscience Letters,* 511, 106-109.

Yang, Z., Zhang, W., Wang, M., Ruan, D., & Chen, J. (2012b). Effect of low intensity low-frequency stimuli on long-term depression in the rat hippocampus area CA1 in vivo. *Neuroscience Letters,* 523, 24-29.

Zhao, X., Sun, H., Tang, Z., Flanders, J., Zhang, S., & Ma, Y. (2010). Characterization of the sleep architecture in two species of fruit bat. *Behavioural Brain Research,* 208, 497-501.