



Review

The energy allocation function of sleep: A unifying theory of sleep, torpor, and continuous wakefulness



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ABSTRACT

The energy allocation (EA) model defines behavioral strategies that optimize the temporal utilization of energy to maximize reproductive success. This model proposes that all species of the animal kingdom share a universal sleep function that shunts waking energy utilization toward sleep-dependent biological investment. For endotherms, REM sleep evolved to enhance energy appropriation for somatic and CNS-related processes by eliminating thermoregulatory defenses and skeletal muscle tone. Alternating REM with NREM sleep conserves energy by decreasing the need for core body temperature defense. Three EA phenotypes are proposed: sleep–wake cycling, torpor, and continuous (or predominant) wakefulness. Each phenotype carries inherent costs and benefits. Sleep–wake cycling downregulates specific biological processes in waking and upregulates them in sleep, thereby decreasing energy demands imposed by wakefulness, reducing cellular infrastructure requirements, and resulting in overall energy conservation. Torpor achieves the greatest energy savings, but critical biological operations are compromised. Continuous wakefulness maximizes niche exploitation, but endures the greatest energy demands. The EA model advances a new construct for understanding sleep–wake organization in ontogenetic and phylogenetic domains.

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Contents

1. Introduction	123
1.1. Prior theories on the functions of sleep	123
1.2. A unifying theory	124
2. Energy allocation, sleep, and life history theory	125
2.1. Background on life history theory	125
2.2. Wakefulness and energy allocation	125
2.3. Energy allocation and the function of sleep	126
2.4. Energy allocation and the function of REM sleep	128
2.5. Additional perspectives on the energy allocation model	130
3. Energy allocation and sleep deprivation	132
3.1. Sleep deprivation and physiological deficits	132
3.1.1. Sleep deprivation and central deficits	132
3.1.2. Sleep deprivation and peripheral deficits	133
3.2. Sleep deprivation and increased energy requirements	133
3.3. Adaptive responses related to cellular stress and thermoregulation	136
3.3.1. Cellular stress and adaptive responses	136

Abbreviations: BAT, brown adipose tissue; BI, biological investment; BMR, basal metabolic rate; CNS, central nervous system; EA, Energy Allocation; EE, energy expenditure; EEG, electroencephalogram; G, growth; M, maintenance; MCH, melanin concentrating hormone; NREM, non-rapid eye movement; REM, rapid eye movement; R, reproduction; SCN, suprachiasmatic nucleus; T_a , ambient temperature; T_c , core body temperature; T_{set} , set point for core body temperature; TE, thermoregulatory effort; WE, waking effort.

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3.3.2. Thermoregulatory control and adaptive responses	136
3.4. Sleep deprivation, energy allocation and homeostasis	138
3.4.1. Energy balance and prior theories of sleep homeostasis	138
3.4.2. The energy allocation model and sleep homeostasis	138
4. Phenotypes of energy allocation	139
4.1. Phenotype of sleep–wake cycling	140
4.2. Phenotype of torpor	140
4.3. Phenotype of predominant wakefulness	141
5. Phylogenetic considerations of the energy allocation model	142
5.1. Contributions of body size and energy constraints on sleep quotas	142
5.2. Altricial versus precocial species and REM sleep quotas	143
6. Summary	145
Acknowledgements	146
References	146

“The optimal animal, born with some amount of energy, proceeds through life gaining and expending energy according to some schedule that maximizes its total reproductive success.”
-Schoener (1971), p. 375

1. Introduction

Sleep remains the only universal behavior known to biology with no clear consensus regarding a fundamental underlying function. The recognition of sleep behavior across multiple phyla of the animal kingdom strongly suggests the presence of a shared or universal function. These diverse phyla include: insects (Hendricks et al., 2000; Huber et al., 2004b; Kaiser, 1985; Kaiser and Steiner-Kaiser, 1983; Shaw et al., 2000; Tobler and Neuner-Jehle, 1992), nematodes (Raizen et al., 2008), mammals (Zepelin et al., 2005), birds (Amlaner and Ball, 1989; Campbell and Tobler, 1984; Dewasmes et al., 1985), reptiles (Flanigan, 1973, 1974; Flanigan et al., 1973, 1974; Hartse, 1989), amphibians (Hartse, 1989; Lazarev, 1978; Segura, 1966), and fishes (Peyrethon and Dusan-Peyrethon, 1967; Shapiro and Hepburn, 1976; Zhdanova et al., 2001).

A universal need for sleep, however, has been questioned (Siegel, 2008). For example, although some species may exhibit prolonged periods of wakefulness with little or no sleep during seasonal mating (Lesku et al., 2012), migration (Rattenborg et al., 2004), or birthing (Lyamin et al., 2007; Lyamin et al., 2005), they show no apparent functional deficits during these times (Lesku et al., 2012; Rattenborg et al., 2004). Moreover, other species may forgo sleep for extended periods, such as during torpor or hibernation, when challenged by increased energy demands or limited energy supply. In light of these observations, the specific aim of this manuscript is to introduce a unifying theory of sleep function, including NREM and REM sleep, based on energy utilization or allocation, a theory that also integrates two additional behavioral phenotypes apart from sleep: torpor and continuous wakefulness.

1.1. Prior theories on the functions of sleep

Phylogenetic analyses of sleep and wakefulness across many orders of mammals (Allada and Siegel, 2008; Capellini et al., 2008a; Lesku et al., 2006; Lesku et al., 2008, 2009) and birds (Lima et al., 2005; Roth et al., 2006), as well as the great diversity in sleep expression in species with extreme specializations (Tobler, 1995), have led to a number of perceived contradictions with respect to identifying sleep's function. Complicating the search for a unifying function of sleep has been the historical recognition that endothermic birds and mammals exhibit two distinct stages of sleep, i.e., NREM and REM sleep (see Box 1 on Defining Sleep). Moreover, the characteristics of REM sleep are so diverse, ranging from muscle atonia to rapid eye movements and penile erections, that its

Box 1: Defining sleep.

Sleep in most species can be defined by behavioral criteria (Flanigan et al., 1973), including (1) species-specific posture, (2) behavioral quiescence, (3) elevated arousal threshold, and (4) rapid state reversibility. There is also a homeostatic regulatory capacity that includes compensation with increased sleep intensity or duration after loss (Tobler, 1995). The vast majority of species exhibit only one identifiable type of sleep, whereas endothermic birds and mammals exhibit two distinct sleep states with the appearance of rapid eye movement (REM) sleep. Non-REM (NREM) sleep or its equivalent is characterized by generalized immobility, regular respiration and heart rate, and, in species with a neocortex, a state of cortical electroencephalographic (EEG) slowing, often with high amplitude EEG slow waves. REM sleep, on the other hand, only occurs after bouts of NREM sleep and is characterized by a loss of thermoregulatory defense and the appearance of rapid eye movements, a generalized skeletal muscle atonia with intermittent muscle twitches of the distal extremities, penile or clitoral erections, cortical EEG activation resembling wakefulness, reports of vivid dreaming in humans and increased respiratory and heart rate variability. REM sleep is also referred to as paradoxical sleep or active sleep.

“descriptive features obviously fail to converge on a common function” (Rechtschaffen, 1998), let alone on an obvious function that may be similar to NREM sleep.

One of the most commonly cited theories on sleep function is that it conserves energy beyond what is attainable from quiet wakefulness (Berger and Phillips, 1993, 1995). This model has been viewed as a relatively passive process in which all biological functions are equally reduced during sleep, similar in concept to torpor or hibernation (Berger, 1984; Berger and Phillips, 1993, 1995; Siegel, 2009). Given, however, that REM sleep is a state of increased brain energy metabolism, REM sleep would appear to contradict this model. Moreover, because the amount of energy saved during sleep compared to wake is relatively small, some argue that it is inconsequential for energy conservation to be considered sleep's primary function (Horne, 1988; Rechtschaffen, 1998; Zepelin and Rechtschaffen, 1974).

Another longstanding theory is that sleep is a time for recovery or provides some recuperative process (Adam, 1980; Mignot, 2008; Oswald, 1980), but what is actually being recovered has remained elusive (Rechtschaffen, 1998). The findings that whole-body protein synthesis is actually greater during wakefulness than sleep and that protein synthesis is influenced by feeding (Clugston and Garlick, 1982a,b; Golden and Waterlow, 1977), have led to a refutation of the restorative hypothesis of sleep (Horne, 1980, 1988). Moreover, even though species with the largest bodies and brain sizes presumably require the greatest cellular or tissue recovery

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