ANIMAL BEHAVIOUR, 2007, **74**, 189–197
doi:10.1016/j.anbehav.2006.12.007

A behavioural shutdown can make sleeping safer: a strategic perspective on the function of sleep

STEVEN L. LIMA* & NIELS C. RATTENBORG†
*Department of Ecology and Organismal Biology, Indiana State University, Terre Haute
†Max Planck Institute for Ornithology, Seewiesen

*(Received 14 September 2006; initial acceptance 23 October 2006;
final acceptance 28 December 2006; published online 9 July 2007; MS. number: A10559)*

Sleep appears to effect some sort of neural maintenance, but a complete theory of the function of sleep must address why such maintenance requires a behavioural shutdown (or unconsciousness) that leaves an animal vulnerable to predators. We present a simple, strategic model to determine the degree of sleep that minimizes the risk of predation. We assume that the brain is composed of neural units that can, in theory, 'sleep' independently of each other, and that a given neural unit must go offline for maintenance/sleep. We also assume that the probability of detecting an attack depends on the fraction of neural units that are awake. We found that having all neural units offline simultaneously (i.e. shutdown sleep) is often the safest way to perform neural maintenance, even though partial sleep makes predators more detectable. This counterintuitive result reflects the assumptions that, in a state of partial sleep, (1) neural maintenance takes longer to complete and (2) predator detection is less effective than suggested by the proportion of neural units online. Partial sleep is a possible outcome when the risk of attack increases as more neural units are taken offline. Minimal sleep (with only one or a few units offline) is a possible outcome when the attack rate while awake is substantially higher than when asleep. Partial sleep of a sort is known to occur in some animals, but there is no apparent evidence for the idea of minimal sleep.

Keywords: antipredator behaviour; optimality theory; predation; sleep; vigilance

Sleep (broadly defined) is a widespread behavioural phenomenon in the animal world (Campbell & Tobler 1984; Tobler 2000; Rattenborg & Amlaner 2002). Many animals will spend much of their lives in this behavioural state (Campbell & Tobler 1984; Amlaner & Ball 1994; Zepelin 2000). Humans, for example, spend about one-third of their lives asleep. Despite the ubiquitous nature of sleep, however, the function or functions of sleep remain unclear (Rechtschaffen 1998; Rattenborg & Amlaner 2002; Siegel 2005). Some researchers justifiably view the function of sleep as one of the most important unanswered questions in biology (e.g. Krueger & Obál 2002).

The function of sleep is unknown not for lack of interest in the topic. In fact, many functions have been proposed for sleep (Rechtschaffen 1998; Siegel 2005). Although varied and eclectic, most explanations for the function of sleep are implicitly or explicitly based on one overriding idea: sleep puts an animal in a particularly vulnerable state; hence, there must be a good reason to sleep. Following Horne (1988) and Rechtschaffen (1998), these proposed functions might be categorized as related to the body or brain. Hypotheses related to the effect that sleep has on the body address factors such as energy conservation (Berger & Phillips 1995; Zepelin 2000), immune system function (Majde & Krueger 2005) and safety (Meddis 1975; Webb 1975). Those related to the brain deal one way or another with the possible maintenance or restorative effects of sleep. Such 'brain' hypotheses address metabolic activities (Benington & Heller 1995; Basheer et al. 2004; Gip et al. 2004), or the maintenance of synaptic function (Kavanau 1996; Krueger & Obál 2002; Cirelli 2005; Ganguly-Fitzgerald et al. 2006; Tononi & Cirelli 2006), including neurogenesis (Guzman-Marin et al. 2005) and memory consolidation and enhancement (Stickgold & Walker 2005; Steriade 2006; Tononi & Cirelli

Correspondence: S. L. Lima, Department of Ecology and Organismal Biology, Indiana State University, Terre Haute, IN 47809, U.S.A. (email: lslima@isugw.indstate.edu). N. C. Rattenborg is at the Max Planck Institute for Ornithology, Seewiesen, Postfach 1564, D-82305 Starnberg, Germany.

0003–3472/07/$30.00/0

2006). With ongoing applications of functional genomics to the study of sleep, we will undoubtedly see additional maintenance-related hypotheses (see Tafti & Franken 2002; Mackiewicz & Pack 2003; Cirelli 2005). All of the proposed functions have their adherents and detractors, but there appears to be a consensus among sleep researchers that the primordial function of sleep is related to neural maintenance (see Rattenborg & Amlaner 2002; Siegel 2003; Cirelli 2005).

Two problems combine to obscure the function of sleep. The first is the simple fact that an animal does nothing (outwardly) while it sleeps. Thus, unlike other behaviours that are obviously directed towards a clear goal (e.g. food acquisition, mating, thermoregulation, etc.), a sleeping animal does not readily indicate its 'intent' in engaging in sleep. This situation has naturally led to the development of techniques to probe the physiological and neural dynamics of the sleeping brain for insights into the function of sleep. These techniques have shown that the brain is hardly 'turned-off' during the unconsciousness of sleep, and that many processes are taking place in the sleeping brain (Steriade 2006). Many sleep researchers suspect that the function of sleep will be realized only from studies at the physiological or molecular/biochemical level (Rechtschaffen 1998; Benington 2000; Krueger & Obál 2002).

The second problem in understanding the function of sleep is that many of the proposed functions would appear to be achievable in the waking state as well (see Moorcroft 1995; Rechtschaffen 1998). In other words, it is not clear why an animal needs to be in such a vulnerable and unresponsive state to achieve the various functions posited for sleep. Some hypotheses, however, do address the reason for a behavioural shutdown. Some neural maintenance hypotheses (Kavanau 1996; Krueger & Obál 2002; Tononi & Cirelli 2006) posit that such a state enhances synaptic maintenance. The immobilization hypothesis (Meddis 1975) states that shutdown sleep is simply a safer way to pass unproductive time than is being awake and more active/detectable to predators. This hypothesis is unique in suggesting that sleep is the safer state (see also Lima et al. 2005).

We take an approach to explain the function of sleep that focuses more on the second problem than the first, namely the reason for a complete behavioural shutdown during sleep. In other words, rather than using the traditional approach of taking shutdown sleep as a given and then attempting to explain function, we will assume a (general) function, neural maintenance, and attempt to explain the behavioural shutdown. Our approach is motivated by a simple question. Why not take only a small portion of the brain offline to sleep while keeping the rest of the brain awake to achieve some degree of safety while sleeping? In attempting to answer this question, we develop the first formal evolutionary/strategic model to address the function of sleep, or, more specifically, the question of why the vulnerable behavioural shutdown exists.

BASIC MODEL

We develop a model that suggests that shutdown (unconscious) sleep may often be the safest way to achieve neural maintenance. Sleep shutdowns are enigmatic precisely because sleep compromises predator detection (Lendrem 1984; Dukas & Clark 1995; Rattenborg et al. 1999; Gauthier-Clerc et al. 2002; Mathews et al. 2006; see also Anderson 1998; Caro 2005; Lima et al. 2005), hence we focus our model on sleep and predator avoidance. Furthermore, we take the position held by at least the plurality of sleep researchers and assume that sleep functions to enhance neural maintenance (Krueger & Obál 2002; Siegel 2003, 2005; Hobson 2005; Tononi & Cirelli 2006; see also Lesku et al. 2006). We assume that an animal's evolutionary 'goal' is to maximize its Darwinian fitness, which in our simple model is the equivalent of maximizing survival. Our model is thus a strategic one in the tradition of (phenotypic) evolutionary modelling (Stephens & Krebs 1986; Mitchell & Valone 1990; Houston & McNamara 1999; Brown 2001) based on the strategic advantage of a given degree of sleep. This model is thus not a mechanistic model, such as the 'two process model' used to predict the dynamics of sleep states (Borbély & Achermann 2000). Our model also greatly simplifies brain structure to clearly present the basic strategic principles underlying our ideas. The general conceptual results outlined below, however, are nevertheless applicable to many hypotheses about the maintenance-related functions of sleep.

We assume that the brain is composed of distinct (but unspecified) neural units that are linked to other such units to perform various functions (see Fingelkurts et al. 2005 for related discussion). We do not specify the nature of the neural units themselves, but they could be organized at any level from entire hemispheres down to neurons. We assume further that these units can sleep separately from other units. Sleep in a given unit would require being taken offline much as envisioned by Krueger & Obál (1993, 2002). We acknowledge that some degree of neuronal synchrony gives rise to the EEG waves that characterize nonrapid eye movement (NREM) sleep in mammals and birds (Massimini et al. 2004; Rattenborg 2006; Steriade 2006), but there is also evidence that NREM sleep develops independently in separate neural units. For instance, in 'drowsy' monkeys (*Macaca fascicularis*), neurons in one portion of the cortex may show sleep-like activity while others remain awake and able to control goal-directed behaviour (Pigarev et al. 1997). Sleep in separate neural units may also occur in various human sleep disorders in which the boundary between sleep and wakefulness is blurred (Mahowald & Schenck 2001, 2005). Furthermore, recent work suggests that the intensity of NREM sleep may differ between cortical areas depending on recent regional brain activity (Huber et al. 2004; Vyazovskiy et al. 2004; Rector et al. 2005).

Assume a brain composed of N such neural units. For simplicity and for mathematical tractability (but without any loss of generality), assume that the brain sleeps n units at a time ($1 \le n \le N$). The proportion of the brain asleep at a given time is thus $p = n/N$. Shutdown sleep is indicated by $n = N$ or $p = 1$, whereas minimal sleep is indicated by $n = 1$ (this state would probably not be identified as sleep per se). Assume that a given neural unit must be offline for t units of time for maintenance. A sleeping unit cannot