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Review

History and future of comparative analyses in sleep research

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ABSTRACT

The comparative methods of evolutionary biology are a useful tool for investigating the functions of sleep. These techniques can help determine whether experimental results, derived from a single or few species, apply broadly across a specified group of animals. In this way, comparative analysis is a powerful complement to experimentation. The variation in the time mammalian species spend asleep has been most amenable for use with this approach, given the large number of mammals for which sleep data exist. Here, it is assumed that interspecific variation in the time spent asleep reflects underlying differences in the need for sleep. If true, then significant predictors of sleep times should provide insight into the function of sleep. Many such analyses have sought the evolutionary determinants of mammalian sleep by relating the time spent in the two basic states of sleep, rapid eye movement (REM) and non-REM sleep, to constitutive variables thought to be functionally related to sleep. However, the early analyses had several methodological problems, and recent re-analyses have overturned some widely accepted relationships, such as the idea that species with higher metabolic rates engage in more sleep. These more recent studies also provide evolutionarily broad support for a neurophysiological role for REM sleep. Furthermore, results from comparative analyses suggest that animals are particularly vulnerable to predation during REM sleep, a finding that lends further support to the notion that REM sleep must serve an important function. Here, we review the methodology and results of quantitative comparative studies of sleep. We highlight important developments in our understanding of the evolutionary determinants of sleep and emphasize relationships that address prevailing hypotheses for the functions of sleep. Lastly, we outline a possible future for comparative analyses, focusing on work in non-mammalian groups, the use of more physiologically meaningful variables, and electrophysiological sleep studies conducted in the wild.

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1. Introduction

The toolkit of sleep researchers is ever-increasing. Investigations into sleep were once achieved only through behavioral observation (Piéron, 1913) or low resolution measures of brain activity (Loomis et al., 1937; Aserinsky and Kleitman, 1953). However, recent technological advances, such as the use of functional magnetic resonance imaging (fMRI, Kaufmann et al., 2006) and high-density electroencephalography (EEG, Tucker, 1993) allow us to see how activity varies across different parts of the brain during wakefulness and sleep (Huber et al., 2004; Massimini et al., 2004; Gais et al., 2007). Moreover, advances in molecular genetics (Tafti and Franken, 2002; Mackiewicz and Pack, 2003) indicate that, compared to wakefulness, sleep favors the expression of different classes of genes, some of which appear to be evolutionarily conserved (Cirelli, 2003; Cirelli et al., 2004). The recent development of miniature digital technology for measuring the EEG from free-ranging animals in the wild (Vyssotski et al., 2006) will allow the exploration of sleep under ecologically realistic circumstances (Rattenborg et al., 2008a). In addition to this suite of techniques, sleep researchers also have the comparative methods of evolutionary biology as a tool for investigating the functions of sleep.

Although sleep appears to serve a vital function, there is still no consensus on the specific functions of sleep (Siegel, 2005; Stickgold, 2005; Tononi and Cirelli, 2006; Krueger et al., 2008; Mignot, 2008). Ideally, the most straightforward way to determine sleep's function would be to identify animals that sleep and those that do not, and then identify traits that are unique to each group. Unfortunately, all species studied sleep, making such comparisons impossible (Cirelli and Tononi, 2008; Lesku et al., 2009). A second strategy for illuminating the function of sleep is to compare species that sleep differently in some way, and then identify the factors responsible for maintaining those differences. One popular and potentially insightful approach is to determine why some species sleep a great deal and others only very little. Such among-species (or interspecific) variation has been best documented in the time that mammals spend in rapid eye movement (REM) and non-REM (or slow wave) sleep (McNamara et al., 2008), the two basic types of sleep in mammals. For example, large hairy armadillos (*Chaetophractus villosus*) spend 16 h per day in non-REM sleep (Affanni et al., 2001), whereas horses (*Equus caballus*) spend just 2 h in non-REM sleep (Ruckebusch, 1972); Virginia opossums (*Didelphis virginiana*) engage in REM sleep for more than 7 h per day (Walker and Berger, 1980a), but sheep (*Ovis aries*) spend just half an hour in that state (Ruckebusch, 1972). If we assume that such interspecific variation reflects underlying differences in the need for sleep, then identifying the evolutionary factors responsible for maintaining such variation should provide clues to the functions of sleep. This is the essence of comparative sleep research. A unique strength of this comparative approach is that it can be used to assess whether the results from experiments obtained from only a single or few species might be applied to a broader group of animals. Exploratory comparative analysis can also be of value for the identification of new (potentially unexpected) relationships that might lead to new hypotheses for the function of sleep, much as genome-wide screening has been used to identify novel genes that are only expressed in the brain during sleep (Cirelli, 2005).

Here, we review the methodology and results from quantitative comparative studies of sleep, beginning with the influential work of Zepelin and Rechtschaffen (1974), the first large-scale statistical analysis of interspecific variation of mammalian sleep. Throughout, we highlight important developments in our understanding of the evolutionary determinants of sleep and emphasize relationships that address prevailing hypotheses for the functions of sleep. We also discuss recent results from comparative work on birds. Lastly, we outline a possible future for comparative analyses of sleep that includes using more physiologically meaningful variables and conducting EEG-based sleep studies in the wild.

2. History of comparative analyses in sleep research

The value of a comparative approach to understanding sleep has been recognized for at least four decades (e.g., Weiss and Roldán, 1964; van Twyver, 1969). The first comparative studies analyzed sleep times in only a handful of species, hence their results were necessarily descriptive in nature. Perhaps the most substantive contribution of these early studies was simply the identification of interspecific variation in some aspects of EEG-defined sleep (Weiss and Roldán, 1964; van Twyver, 1969), suggesting that at least some features of sleep are (in part) genetically determined (see also Tafti and Franken, 2002; Mackiewicz and Pack, 2003), a necessary prerequisite for traits used in comparative analyses. Subsequent work would expand greatly upon these first (descriptive) studies by quantifying relationships among sleep parameters and constitutive (Section 2.1) and ecological (Section 2.2) variables.

2.1. The first quantitative comparative sleep analysis: Zepelin and Rechtschaffen

Zepelin and Rechtschaffen (1974) provided the first formal comparative analysis of sleep. Their chief motivation was to determine whether hypotheses for the function of mammalian sleep applied broadly across mammals. Such hypotheses included the idea that sleep in some way promotes longevity, and that sleep plays a role in reducing energy expenditure through enforcing inactivity and lowering the metabolic rate of an animal. As such, species with longer life spans and species with relatively higher metabolic rates were expected to engage in more sleep.

Zepelin and Rechtschaffen compiled a dataset based on electrophysiologically and behaviorally derived sleep data for 53 species. Their analysis was part hypothesis-testing and part exploratory; consequently, they included numerous variables beyond those required to evaluate the longevity and energy conservation hypotheses. The sleep-related variables included estimates of the time spent in non-REM sleep and REM sleep per 24 h day, total sleep time, and the percentage of total sleep time allocated to REM sleep (or %REM sleep). %REM sleep could be particularly informative if there are constraints on the amount of time an animal can sleep. Presumably, under such a constraint, the allocation of time to one sleep state would increase at the expense of the other, reflecting a tradeoff between the specific costs and benefits involved in engaging in more non-REM or REM sleep. These sleep-related variables were then correlated with variables related to anatomy (brain mass), physiology (mass-specific basal metabolic rate, BMR), and life-history (maximum life span and gestation period, the latter a proxy for postnatal brain maturity), collectively referred to as constitutive variables. As noted by Zepelin and Rechtschaffen (1974), these variables are not