



Review

An in depth view of avian sleep

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ABSTRACT

Brain rhythms occurring during sleep are implicated in processing information acquired during wakefulness, but this phenomenon has almost exclusively been studied in mammals. In this review we discuss the potential value of utilizing birds to elucidate the functions and underlying mechanisms of such brain rhythms. Birds are of particular interest from a comparative perspective because even though neurons in the avian brain homologous to mammalian neocortical neurons are arranged in a nuclear, rather than a laminar manner, the avian brain generates mammalian-like sleep-states and associated brain rhythms. Nonetheless, until recently, this nuclear organization also posed technical challenges, as the standard surface EEG recording methods used to study the neocortex provide only a superficial view of the sleeping avian brain. The recent development of high-density multielectrode recording methods now provides access to sleep-related brain activity occurring deep in the avian brain. Finally, we discuss how intracerebral electrical imaging based on this technique can be used to elucidate the systems-level processing of hippocampal-dependent and imprinting memories in birds.

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1. Introduction

A growing body of research on animals ranging from fruit flies to mammals to birds suggests that sleep is involved in processing information acquired during wakefulness (Abel et al., 2013; Donlea et al., 2011; Margoliash, 2010; Rasch and Born, 2013; Tononi and Cirelli, 2014). In mammals, the brain rhythms that occur during

sleep and its sub-states rapid eye movement (REM) and non-REM (NREM) sleep, have been implicated in processing information both locally within small neuronal assemblies and across brain regions (e.g. hippocampus and neocortex) at the systems-levels (Huber et al., 2004; Rasch and Born, 2013; Tononi and Cirelli, 2014). However, the exact nature of information processing and the role played by these rhythms remain actively debated (Frank, 2013; Rasch and Born, 2013; Tononi and Cirelli, 2012, 2014). Interestingly, despite lacking the laminar neuronal organization found in the neocortex (Medina and Reiner, 2000; Wang et al., 2010), birds exhibit similar sleep states and in many, but importantly not all, respects, similar sleep-related brain activity (Rattenborg et al., 2011). Although a growing body of research suggests that avian sleep also plays a

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role in processing information (Brawn et al., 2010; Derégnaucourt et al., 2005; Gobes et al., 2010; Jackson et al., 2008; Shank and Margoliash, 2009), when compared to mammals, little research has focused on the role sleep's sub-states and associated brain rhythms per se play in this process (Lesku et al., 2011), especially at the systems-level (Rattenborg et al., 2011). As such, birds provide a largely untapped opportunity to determine the functions of these brain rhythms in mammals through identifying shared functional targets and isolating potential *red herrings* that might arise from a strictly mammalian-based investigative approach.

The late Sir Gabriel Horn of Cambridge University also used this bird-based comparative approach to gain insight into basic neurobiological principles. In his case, Horn examined imprinting in chicken chicks to reveal the mechanisms of memory formation and consolidation at both the local and systems-levels (Horn, 2004). Interestingly, toward the end of his career, Horn also began to investigate the potential role sleep plays in processing imprinting memories (Horn et al., 2001; Jackson et al., 2008). Although neither of us ever met Horn, our interests recently converged on closely related topics (Beckers et al., 2014; Rattenborg et al., 2011). In addition, we recently began to use high-density brain recording methods that can be employed to gain further insight into the role sleep-related brain rhythms play in processing information in birds, including imprinting memories (Beckers and Gahr, 2010, 2012; Beckers et al., 2014). Consequently, we are in a position to both evaluate the significance of Horn's recent work on sleep, and to speculate on how it might continue to further our understanding of sleep and memory in the future.

2. Delving deep into the sleeping bird's brain

In mammals, many aspects of sleep-related brain activity can be measured from the surface of the brain, or even the scalp, as commonly done in humans with the electroencephalogram (EEG) (Massimini et al., 2004). Two neuroanatomical traits contribute to the large electrical fields detectable near the surface of the mammalian brain. First, neurons contributing to these fields comprise the neocortex, a laminar structure draped over the surface of the brain (Fig. 1A). Second, the cytoarchitecture of neocortical neurons favors the generation of large electrical fields detectable in the EEG. Specifically, the apical dendrites of pyramidal neurons point perpendicular to the surface of the brain. As a result, when activity is synchronized across large numbers of these neurons, large open electrical fields detectable in the EEG are generated (Buzsáki et al., 2012). These features of the mammalian brain and resulting descriptions of brain activity across states and neocortical regions, has led to several theories on how information is processed during wakefulness and sleep, both locally and across brain regions at the systems-level. At the systems-level, rhythms are thought to process information through coordinating the activity of distant brain regions (Colgin, 2011; Buzsáki et al., 2013; Sirota and Buzsáki, 2005; Steriade, 2006). In addition, the propagation of waves of activity between regions may also be involved in this process (Ermentrout and Kleinfeld, 2001; Nir et al., 2011; Wu et al., 2008).

In contrast to the mammalian neocortex, apparently homologous neurons in the avian brain are arranged in a largely nuclear manner (Fig. 1B) (Medina and Reiner, 2000; Wang et al., 2010). In addition, neurons in these nuclear structures are stellate, lacking the unidirectional apical dendrites found in the neocortex (Medina and Reiner, 2000; Watanabe et al., 1983). Despite these differences in neuronal cytoarchitecture, as in mammals, the avian brain orchestrates complex cognitive processes (Kirsch et al., 2008). Also as in mammals, the avian EEG shows homeostatically regulated high-amplitude slow-waves during NREM sleep (Lesku et al., 2011; Rattenborg et al., 2009) and low-amplitude, high-frequency activity

during REM sleep (Low et al., 2008; Scriba et al., 2013). Although the neuronal physiology underlying EEG slow-waves has been studied little in birds when compared to mammals, as in mammals, avian slow-waves appear to reflect the slow-oscillation (typically <1 Hz) of neuronal membrane potentials between depolarized “up-states” and hyperpolarized “down-states”, with and without action potentials, respectively (Reiner et al., 2001; Steriade, 2006). The presence of mammalian-like sleep-related brain activity despite the absence of neocortical-like neuronal cytoarchitecture in the avian brain, in-and-of-itself is interesting because it challenges the idea that the neocortex per se is required for the genesis of such EEG activity. Nonetheless, although the avian EEG can be used to identify sleep and its sub-states, due to the nuclear arrangement of neurons in birds, when compared to the mammalian EEG, it only provides a superficial view that likely misses processes occurring deeper in the sleeping bird's brain (Beckers et al., 2014). This is particularly problematic if our aim is to understand what is happening at the systems-level (Rattenborg et al., 2011). Clearly, intracerebral recording methods are needed to assess sleep's role in processing information in the avian brain at this level.

3. Recording deep brain activity using high-density multielectrodes

Intracerebral electrophysiological techniques in birds have generally focused on fields at the very local level ($\sim <50 \mu\text{m}$) through extra-cellular or even intra-cellular recordings using single electrodes (Ookawa, 2004; Reiner et al., 2001). The great advantage of this approach is that the activity of neurons – the fundamental building blocks of neuronal networks – can be studied directly. This is especially useful when cell types can be identified, but even lacking such identification, the measurement of cellular electrical activity in identified, localized brain regions, such as song system nuclei, have yielded fascinating insights into the mechanisms that underlie various behaviors, including sleep (Dave and Margoliash, 2000; Graber et al., 2013; Hahnloser and Fee, 2007; Hahnloser et al., 2006; Shank and Margoliash, 2009). Many of these insights are simply impossible to obtain from epidural EEG recordings, which are inherently much less local and, as noted above, only tap into structures near the brain's surface. Despite the success of intracerebral single-electrode techniques, their extremely local nature also has its limitations because it is blind to the interactions within larger populations of neurons that generate properties at the network or systems-level (Beckers et al., 2014).

A relatively recent technological development in neuroelectrical recording that combines many of the advantages of EEG and intracerebral single electrode techniques is that of high-density silicon multielectrode arrays (Buzsáki, 2004; Einevoll et al., 2013). Such arrays have one or more thin shanks containing multiple small electrodes (Fig. 2A). One obvious advantage of multielectrodes is that they can be used to record from many more neurons than was possible previously in the same recording session. However, their greatest benefit is qualitative: multielectrodes provide insight into the relationship between local electrical activity in many different sites, distributed over larger brain regions. As such, they provide a broader picture of how neurons are behaving as a system.

One of us recently started applying this recording technique to study auditory processing in the forebrain of zebra finches (*Taeniopygia guttata*) (Beckers and Gahr, 2010, 2012). In this work, the qualitative advantage of spatially distributed, parallel recordings at many sites ($n = 32$) over serial single-electrode recordings became very clear. The presentation of vocalizations that deviated from a sequence of identical vocalizations elicited action potential activity almost simultaneously across a large part of the auditory forebrain (Beckers and Gahr, 2012). From response to response, however, the

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