Review

# An in depth view of avian sleep

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A B S T R A C T

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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## Contents

## 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 (∼<50 μm) 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
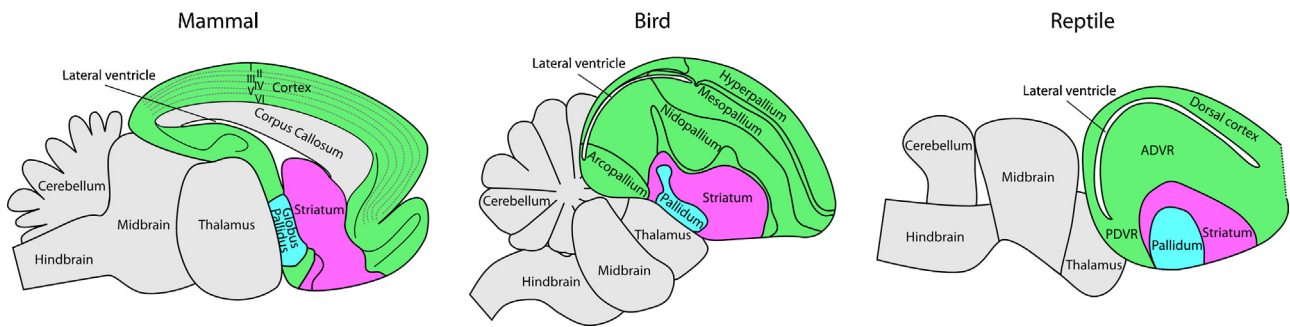
**Fig. 1.** Organization of the telencephalon in (A) mammals (rodent), (B) birds (songbird) and (C) reptiles (crocodile). Shown are sagittal views, with color-coding for the subdivisions pallidum, striatum, and pallium. *Abbreviations*: ADVR, anterior dorsal ventricular ridge; PDVR, posterior dorsal ventricular ridge. The olfactory bulb is long in the crocodile brain and is not shown here (cut at stippled line).
Figure adapted from Jarvis (2009) and Jarvis et al. (2013).

latency of this activity was highly variable. In serial single-electrode recordings, the spatially distributed nature of such event-related neuronal activity would be invisible, and it would be difficult if not impossible to localize such deep-brain activity in EEG recordings.

Because silicon multielectrodes are able to capture both local and more global aspects of neural activity with very high temporal resolution, this technique opens up new opportunities for the study of sleep-related neural mechanisms and functions in birds. We recently started characterizing sleep-related neural activity in the zebra finch, using 64-electrode recording of unit and local field potentials (Beckers et al., 2014). The small size of zebra finches has both drawbacks and benefits. Given the small size of this species, such intracerebral measurements are as yet not feasible for chronic recordings in freely behaving and spontaneously sleeping animals. Consequently, as a first step, we performed acute recordings in finches under isoflurane anesthesia, which is known to activate normal sleep-promoting regions in the mammalian hypothalamus (Moore et al., 2012). Moreover, in mammals, anesthetics induce neuronal oscillations comparable to those occurring during spontaneous NREM sleep (Chauvette et al., 2011; Steriade, 2006); although slow-waves are more synchronous, down-states are longer, and gamma (30–100 Hz) power is higher under ketamine-xylazine anesthesia (Chauvette et al., 2011). Finally, a benefit of the small size of the zebra finch brain is that it allows us to sample simultaneously with readily available multielectrode probes from more types of brain regions than would be possible in a bigger brained bird (Fig. 2B). This is particularly important when trying to get a broad overview of how the avian brain works as a system during sleep.

These recordings showed that slow-wave electrical activity within the zebra finch brain appears as a globally distributed process when viewed on longer time scales (i.e. seconds), with similar and apparently simultaneous oscillatory activity across many of the electrode sites of the array (Fig. 2D). However, when viewed on short time scales (i.e. tens of milliseconds), the peaks of the oscillations turn out to be time shifted across the array, showing that slow-waves are a traveling phenomenon in the avian brain (Fig. 2E), as has been established for slow-waves occurring during NREM sleep in mammals (Chauvette et al., 2011; Hangya et al., 2011; Luczak and Barthó, 2012; Massimini et al., 2004; Mohajerani et al., 2013, 2010; Murphy et al., 2009; Nir et al., 2011; Stroh et al., 2013; Volgushev et al., 2011). Importantly, the intracerebral multielectrode technique also provided new insights that would not have been gained with traditional techniques. First, because the array placement inside the brain can be varied, and measurements are not limited to a 2-D surface, as is the case in EEG, we were able to show that waves in the zebra finch brain propagate in highly variable directions in 3-D space. Second, in addition to local field potentials, we recorded action potential activity that propagated in concert with local field potential activity, indicating that slow-waves were occurring in the

immediate vicinity of the electrode sites (∼<50 μm) and did not constitute fields volume conducted from elsewhere in the brain. Third, the fact that the electrodes are distributed in a regular matrix arrangement (8 × 8, with 200 μm spacing in both directions), enabled us to move away from traditional multi-channel waveform plots which are difficult to interpret in terms of spatio-temporal dynamics, and instead to visualize slow-waves as a series of images (Fig. 2F) which can be played as videos, wherein pixels correspond to electrodes, color to activity levels (LFP or action potential firing), and time to time (either real-time or slowed-down; see Video 1). These videos revealed a complex storm of activity occurring in the depths of the sleeping avian brain that would have never been revealed with standard surface EEG methods.

In addition to broadening our understanding of the sleeping avian brain, this work also contributes to our understanding of the neocortex. First, the presence of traveling waves in the nuclear avian brain, demonstrates that the laminar arrangement of neurons in the neocortex is not required for waves to travel. Second, this suggests that the traveling nature of slow-waves does not subserve functions unique to laminar neuronal cytoarchitecture. Instead, the presumed function of this phenomenon must lie in more general traits shared by mammals and birds.

## 4. Future directions: systems-level memory processing in birds?

The high-density depth recording approach we used to record the temporospatial dynamics of neuronal activity at a relatively local level (1.4 mm × 1.4 mm), as well as other multi-electrode approaches in the avian brain (Guitchounts et al., 2013), can be expanded to record neural activity at a systems-level. The following section highlights two types of systems-level memory processing that would be important to explore using this deep brain approach. In addition, Box 1 discusses how this methodology could be used to resolve long-standing controversies in our understanding of reptilian sleep, and thereby the evolution of similar sleep states in mammals and birds.

### 4.1. Hippocampal memories

The following section reviews sleep's proposed role in the systems-level processing of hippocampal memories in mammals. Our objective here is not to provide a comprehensive review of the evidence supporting (Rasch and Born, 2013) or contradicting (Tononi and Cirelli, 2014) this model. Instead, our objective is to present the main framework of the model, so that it can be evaluated from a comparative perspective and potential avenues for future research can be explored.
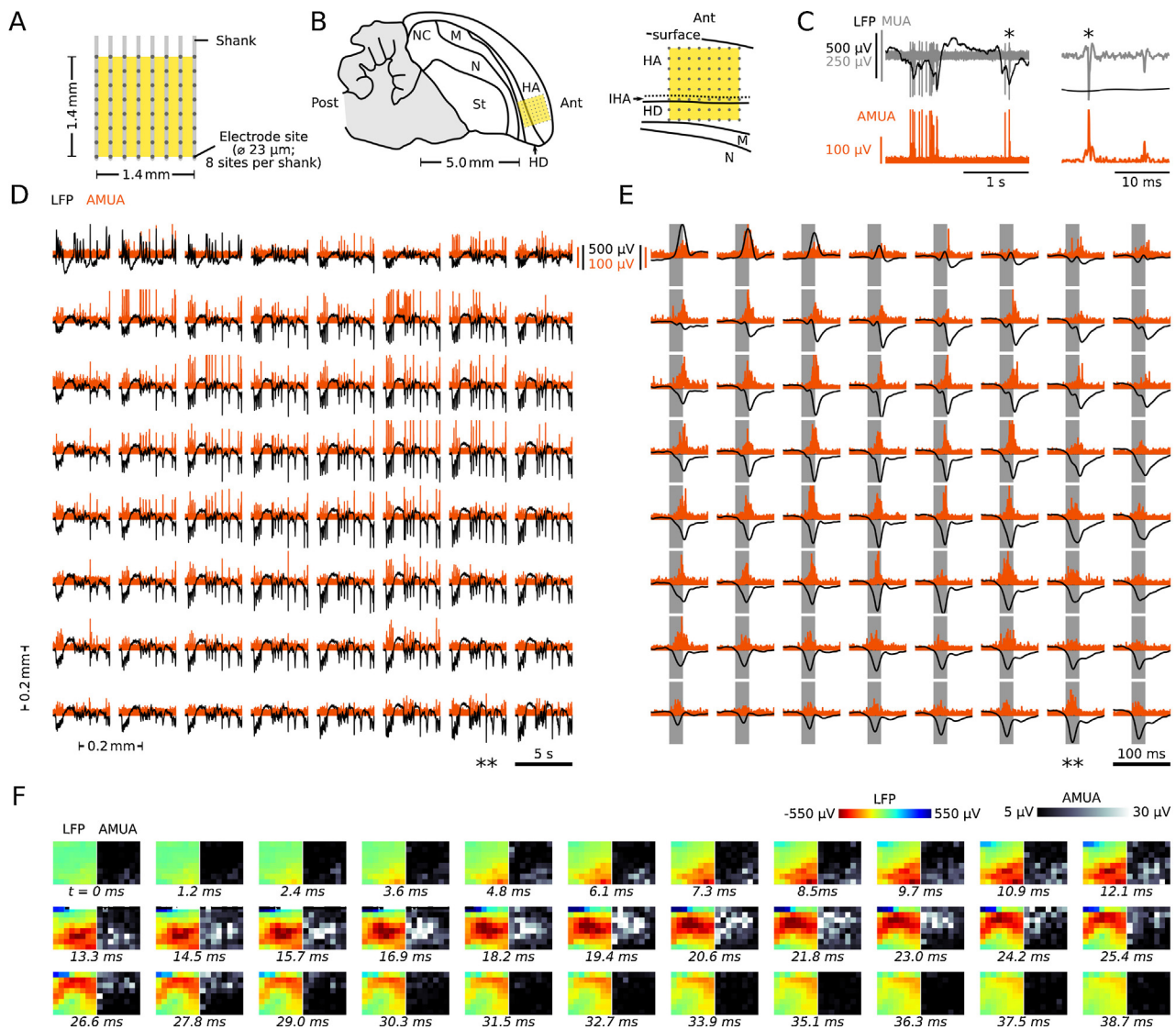
**Fig. 2.** High-density recording of slow-waves in the zebra finch forebrain. (A) The silicon multi-electrode probe consists of 8 shanks that are inserted into brain tissue. Each shank has 8 electrodes so that a total of 64 recording sites are organized in a regular grid with 200 μm inter-site spacing that extends over a 1400 μm × 1400 μm plane (yellow square). (B) Location of the silicon multi-electrode probe in the hyperpallium inserted sagittally to emphasize the coverage of the brain possible with readily available probes: the hyperpallium consists of the hyperpallium apicale (HA), the interstitial part of hyperpallium apicale (IHA), and the hyperpallium densocellulare (HD). The hyperpallium overlies and is interconnected with the mesopallium (M) and nidopallium (N). Recordings were made in this plane and horizontally in the same region as shown in (D). (C) Local field potential and multi-unit activity (MUA) from a single electrode showing the relationship between the two. Electrical potentials were recorded with a sampling rate of 14 kHz, and off-line filtered to obtain local field potentials (LFP, 0.1–350 Hz) and multi-unit action potentials (0.5–5 kHz). To obtain a signal that corresponds to the level of multi-unit action potential firing, the MUA signal is rectified and decimated (AMUA). (D) 5 s episode showing the temporal pattern of LFP and AMUA across the 8 × 8 grid of electrode sites. Oscillations appear to be globally distributed. (E) Detail of the LFP and AMUA peak indicated with two asterisks in (D). The peak of activity, both in LFP and AMUA signals, occurs at slightly different times across the electrode grid, first at sites in the bottom right corner and then later at sites in the top half of the grid. (F) The propagating nature of the activity peak is more easily seen when visualized in a sequence of image plots. Each image has 8 × 8 pixels corresponding to the 8 × 8 grid of electrode sites, and pixel color and gray levels correspond to LFP and AMUA magnitudes.
Figure adapted from Beckers et al. (2014).

According to a prominent model, NREM sleep-related brain rhythms are thought to orchestrate the systems-level processing of hippocampal-dependent memories in mammals (Rasch and Born, 2013). The model stems from the observation that damage to the hippocampus in humans causes amnesia for recent events, but not events that occurred in the distant past (Bayley et al., 2006; Eichenbaum, 2000; Frankland and Bontempi, 2005; Scoville and Milner, 1957; Smith and Squire, 2009; Teng and Squire, 1999). This suggests that recall of initially hippocampal-dependent memories shifts toward depending less on the hippocampus and more on the neocortex over time. This observation and the connectional neuroanatomy of the hippocampus and temporal lobe structures providing it with input led to the idea that during wakefulness the hippocampus serves as a convergence zone for input funneling in from virtually the entire neocortex (Eichenbaum, 2000, 2004; McClelland et al., 1995). The hippocampus is thought to use this input to quickly form an index of the neocortical circuits contributing to a certain event in a manner such that the recall of, or exposure to, portions of an experience can elicit the recall of the entire experience (i.e. an episodic memory). During sleep, the coordinated replay of past experiences in the hippocampus and neocortex is thought to lead to the strengthening of the neocortical representation of the memory and its integration within preexisting information stored in the neocortex. More recently, it has been suggested that the entire memory is not 'transferred' to the neocortex, but rather its episodic component remains dependent on the

**Box 1: Evolution of sleep in mammals and birds**

The presence of similar sleep states in mammals and birds either reflects the inheritance of comparable sleep states from their shared (stem amniote) ancestor, or a process of convergent evolution. Our understanding of the evolution of NREM and REM sleep in mammals and birds depends on an accurate assessment of sleep-related brain activity in non-avian reptiles [Note: as members of the taxon Dinosauria, birds are a type of reptile]. Unfortunately, in contrast to the situation in mammals and birds wherein most studies report largely similar sleep-related EEG activity, the non-avian reptile literature is rife with unresolved controversies. Reports of brain activity include mammalian/avian-like slow-waves occurring during behavioral sleep, slow-waves occurring during wakefulness, but not sleep, and intermittent sharp-waves arising from a low-amplitude background EEG pattern during sleep and, in some cases, wakefulness (*reviewed in* Hartse, 1994; Rattenborg, 2007). Many of the discrepancies are found between different research groups, even when working on the same species. Consequently, the lab-specific recording conditions and methods seem to contribute to the variation in reports; although the exact differences between labs remain poorly understood and likely include several factors.

Among the potential explanations, electrode placement may play an important role. In most cases, the EEG electrodes were reportedly placed on the dura overlying the dorsal cortex, a thin three-layered neocortex-like structure. However, the exact placement was only carefully described in a few studies, and as in birds, most of the neurons thought to be homologous to the neocortex are arranged in large nuclear structures well below the dorsal cortex (Fig. 1C). Consequently, it is conceivable that electrode placement contributed to the variation across studies, especially if different brain structures exhibit different activity patterns during sleep. The simultaneous recording of sleep-related brain activity in the dorsal cortex and underlying structures using the high-density depth recording methods described herein may serve as a powerful tool for resolving this long festering problem in comparative sleep research. Moreover, by using this approach to compare how the brains of Sauropsids (i.e. avian and non-avian reptiles) and mammals behave as systems during sleep, we may gain greater understanding of the evolution of systems-level memory processing.

hippocampus, whereas other components become represented in a more general manner as part of schemas in the neocortex (Lewis and Durrant, 2011; Preston and Eichenbaum, 2013; Winocur and Moscovitch, 2011).

Although the exact nature of such systems-level processing remains debated, the brain rhythms occurring during NREM sleep have been implicated in this process. During NREM sleep the hippocampus intermittently generates synchronous bursts of activity (sharp-waves) followed by high-frequency ripples. During such sharp-wave ripple (SWR) complexes, hippocampal and neocortical neurons that fired in a particular sequence during wakefulness 'replay' this sequence in a coordinated manner (Benchenane et al., 2010; Ji and Wilson, 2007; Peyrache et al., 2009). The timing of SWR complexes is influenced by the slow-oscillation of neocortical membrane potentials such that they occur during the up-state of the slow-oscillation when neocortical neurons are active. Thalamocortical spindles – intermittent waxing and waning 12–15 Hz rhythms – also occur during the up-state of the slow-oscillation (Steriade, 2006) and are thought to produce conditions conducive to the strengthening of the neocortical representation of the memory being 'replayed' (Isomura et al., 2006; Mölle et al., 2009; Sirota et al., 2003; Wierzynski et al., 2009). Over time this coordinated replay is thought to lead to reduced involvement of the hippocampus in the recall of memories. Finally, the presence of

direct projections from the hippocampus to the medial prefrontal cortex (mPFC) (Jay and Witter, 1991; Swanson, 1981; Thierry et al., 2000) and from the mPFC to regions providing input to the hippocampus, as well as several other lines of evidence suggest that the mPFC plays a key role in orchestrating or overseeing this process (Benchenane et al., 2010; Bontempi et al., 1999; Frankland et al., 2004; Gais et al., 2007; Mander et al., 2013; Maviel et al., 2004; Mölle and Born, 2009; Paz et al., 2007, 2009; Pelletier et al., 2004; Peyrache et al., 2009; Restivo et al., 2009; Takashima et al., 2006; *reviewed in* Colgin, 2011; Frankland and Bontempi, 2005; Huber and Born, 2014; Preston and Eichenbaum, 2013; Rattenborg et al., 2011).

Despite exhibiting mammalian-like NREM sleep, the available, albeit sometimes limited, evidence suggests that there are fundamental differences between how mammals and birds form and process hippocampal memories during wakefulness and sleep. Notably, SWRs and thalamocortical spindles have not been reported in birds, despite numerous studies using methods that readily detect such events in mammals (*reviewed in* Rattenborg et al., 2011). This apparent difference in neurophysiology may make some sense when one compares the nature of information reaching the avian hippocampus. In contrast to the mammalian hippocampus which receives highly processed high-order multimodal input funneling in from most of the neocortex, the avian hippocampus only receives information from a relatively small portion of the brain: the hippocampus and regions providing it with direct input only receive olfactory and visual information (Atoji and Wild, 2006; Shanahan et al., 2013). Moreover, most high-order association regions in the DVR, including the nidopallium caudolateral (NCL) – the functional analog of the mammalian PFC – do not provide direct input to or receive direct output from the avian hippocampus (Atoji and Wild, 2006; Kröner and Güntürkün, 1999; Shanahan et al., 2013). The NCL does receive direct projections from hyperpallium densocellulare (HD), which in turn is reciprocally connected to the hippocampus, but the NCL does not appear to project back upon the HD (Kröner and Güntürkün, 1999). The apparent absence of projections from the NCL to the HD (Kröner and Güntürkün, 1999), or other regions providing the hippocampus with input, seemingly precludes a role for the NCL in influencing the flow of information into and out of the hippocampus, as suggested for the mammalian PFC. Furthermore, as suggested by the limited input to the avian hippocampus, in contrast to mammals wherein the hippocampus is thought to function as a convergence node for forming episodic memories of what happened where and when, the avian hippocampus seems to be involved primarily in processing spatial information (Coppola et al., 2014). As such, behaviors suggestive of episodic-like memory in birds (Salwiczek et al., 2010) may depend on both hippocampal and extra-hippocampal brain structures (Rattenborg and Martinez-Gonzalez, 2011, 2013). Finally, in contrast to mammals, there is no solid evidence for the recall of memories initially dependent upon the hippocampus becoming dependent upon extra-hippocampal brain regions over time, as described in mammals (*reviewed in* Rattenborg et al., 2011). Collectively, these apparent differences between mammals and birds provide comparative support to the model proposed in mammals; lacking the mammalian-like flow of information into and out of the hippocampus, birds may have no need for the rhythms implicated in the systems-level processing of this information.

Although this comparison between mammals and birds suggests that there are differences at the systems-level in how hippocampal information is processed, avian sleep may nonetheless play a role in the systems-level processing of information. This could occur within the comparatively limited system within which the hippocampus functions, perhaps via different mechanisms/rhythms from those described in mammals. Sleep may also play a role in the systems-level processing of memories that do

not involve the hippocampus, including song learning (*reviewed in* Rattenborg et al., 2011). In either case, the high-density depth recording methods described herein may be used to identify candidate regions and rhythms involved in such processes through revealing coordinated sleep-related activity across brain regions.

### 4.2. Imprinting memories

Imprinting, the tendency for newly hatched precocial birds, such as chickens, to rapidly form memories of large moving objects (usually their parents) has served as a powerful model for investigating the mechanisms involved in memory consolidation. As extensively investigated by Horn and colleagues, visual imprinting involves processing at both the local and systems-level. Initially, for the first few hours after imprinting, recall of the imprinting stimulus depends on the intermediate and medial mesopallium (IMM). However, Horn's lesion studies have shown that after 4–6 h recall no longer depends solely upon this brain region, suggesting that the memory has been processed at a systems-level and other, as yet unknown, regions can support its recall (Cipolla-Neto et al., 1982; Honey et al., 1995).

Sleep may play a role in both the initial processing of the memory trace in the IMM and its subsequent systems-level processing. In a seminal paper published in *Current Biology* (Jackson et al., 2008), Horn and colleagues showed that sleep following exposure to an imprinting stimulus is important for the initial processing of imprinting memories. In this study, the chicks were divided into two experimental groups immediately following exposure to the imprinting stimulus. Chicks in one group were allowed to sleep undisturbed during a 6 h post-training session, and then, following a 1.5 h testing period, were disturbed for the next 6 h, presumably reducing their time spent sleeping. In the second group, the chicks were disturbed for the first 6 h and then allowed to sleep undisturbed during the last 6 h. The number of IMM neurons responding to the imprinting stimulus was assessed at the end of each session in both groups. Importantly, in chicks that were allowed to sleep first, more IMM neurons were responsive to the imprinting stimulus during the final testing period, than in chicks that were disturbed first and allowed to sleep second. Although sleep and the time spent in its sub-states were not quantified directly, the amount of 5–6 Hz power (perhaps occurring during NREM sleep) recorded in the IMM during the first session was greater in the group left undisturbed than in the disturbed group. Collectively, these findings indicate that sleep plays an important role in the initial consolidation of imprinting memories in the IMM. More generally, a major strength of this paper was that the authors were able to track sleep-related changes in the behavior of individual neurons contributing to a specific memory. Understandably, the potential role sleep plays in the systems-level processing of imprinting memories revealed by Horn's earlier IMM lesion studies was beyond the scope of this already comprehensive initial study.

Further insight into sleep's role in processing imprinting memories in the IMM, and its potential involvement in the systems-level processing of such information may be gained through using the high-density depth recording methods described herein. Specifically, regions exhibiting coordinated activity with the IMM during sleep, particularly during the time interval when the systems-level processing of the imprinting stimulus is thought to occur, would be prime candidates for extra-IMM regions supporting the recall of imprinting memories. More generally, the nature of the coordination and the rhythms employed might provide further insight into general principles that brains use to process information at a systems-level. In this respect, this extension of Horn's work might even inform our understanding of the systems-level processing of hippocampal memories in mammals, including ourselves.

## 5. Conclusions

The development of high-density recording methods serves as a powerful tool for exploring the depths of the avian brain. This method has already revealed a complex storm of activity occurring on a relatively local (1.4 mm × 1.4 mm) scale. By scaling up this approach, we hope to gain a greater understanding of how the avian brain works as a system of systems to process information during sleep. Comparing these findings in birds to those obtained from mammals and relating the results of such comparisons to similarities and differences in neuroanatomy, may reveal overriding principles of heuristic value for understanding the mammalian brain that might otherwise remain obscure using a strictly mammalian-based investigative approach. The extensive groundwork laid by Horn and his colleagues serves as a powerful system in which to apply this comparative approach to understanding sleep.

## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.neubiorev.2014.07.019.

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