



Evolution of sleep in relation to memory – a birds' brain view

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Sleep's role in memory consolidation is widely accepted. However, the role of the different sleep states and accompanying neurophysiological activity is still actively debated. Most theories of sleep-related memory consolidation are based on studies in a few mammalian species. Recent evidence from research in birds, which exhibit sleep states that are in most respects similar to those found in mammals (despite being distantly related) suggests that the way some types of memories are consolidated during sleep might be different in taxa other than mammals. This review will discuss how the recent sleep-related neurophysiological findings in birds inform our understanding of memory consolidation during sleep.

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Introduction

'Why do we need to sleep', is a question that is often asked, but has yet to be fully answered. Indeed, from an evolutionary perspective, sleep is a fascinating behavioral state, as it is a time when organisms are not fulfilling important activities like feeding or mating. Moreover, it is a state that renders an organism vulnerable to predation due to decreased awareness [1]. Hence, sleep undoubtedly serves an important function that cannot be omitted, but what this function or possible functions might be is still actively debated [1–4,5^o,6,7]. That sleep is, among

other functions, important for the consolidation of different types of memories, such as contextual (i.e. emotional, social, spatial, or temporal circumstances related to a certain event) and declarative (i.e. explicit memory for episodes and facts) memories is widely accepted (reviewed in Refs. [8–13]). However, how different sleep states and associated brain rhythms might play a role in memory consolidation is still a topic of active investigation. In this review we will discuss the evolution of sleep in relation to memory from an avian perspective.

Mammalian sleep

To date, the majority of sleep research has been conducted in mammals, which display two distinct types of sleep, rapid eye-movement (REM) and non-REM (NREM) sleep. Each of these sleep states are linked to specific brain activity patterns, with NREM sleep being characterized by a slow (<1 Hz) alternation in neuronal membrane potentials between hyperpolarized downstates with neuronal quiescence and depolarized upstates with action potentials giving rise to slow-waves in local field potential (LFP) and electroencephalogram (EEG) recordings, and REM sleep showing an activated pattern similar to that of wakefulness. Many theories of sleep's role in cognition, such as memory consolidation, are based on what is known about mammalian sleep states and related brain rhythms [5^o,8–10,12,14–18]. Various brain activity patterns occurring during NREM and REM sleep are proposed to play a role in processing information acquired during wakefulness.

During mammalian NREM sleep, the 'transfer' of information from the hippocampus to the neocortex (and perhaps vice versa [reviewed in Ref. [12]]) has been suggested to rely on the direct hippocampus-medial prefrontal cortex (PFC) connection [19] and bidirectional [20] communication through interacting neuronal rhythms (i.e. cortical slow-waves occurring in conjunction with hippocampal sharp-wave ripples (SWRs) and thalamocortical spindles) between these regions (e.g. Refs. [5^o,9,18]). The coordination of all three of these rhythms is thought to be required for the neuronal reactivation and transfer of memories (e.g. Refs. [12,18]). Specifically, their fine-tuned phase-locking is suggested to strengthen the cortical representation of the memory during NREM sleep (e.g. Refs. [12,18]).

Mammalian REM sleep is also proposed to facilitate the formation and consolidation of certain types of memory

[8]. The hippocampal theta rhythm occurring during mammalian REM sleep is, for instance, thought to be involved in the consolidation of emotional (reviewed in Refs. [21]), spatial (e.g. Refs. [22]) and contextual memories (reviewed in Refs. [15,23^{*}]). Notably, Boyce *et al.* [23^{*}] showed that disrupting the hippocampal theta rhythm during REM sleep without altering the time spent in REM sleep in mice impaired fear-conditioned contextual memory. This demonstrates that the rhythm *per se*, and not just the sleep state, plays a role in memory consolidation during sleep. In addition, another study in mice suggests that REM sleep may also function in facilitating motor learning and memory consolidation by selectively pruning and strengthening new synapses through calcium spike-dependent mechanisms [24]. Recently, it was furthermore shown that activation of melanin concentrating hormone-producing neurons (MCH neurons) during REM sleep impairs hippocampus-dependent memories [25]. Together these results show a role for REM sleep in both memory consolidation and forgetting.

Interestingly, although REM sleep is traditionally characterized by EEG activation, intra-cortical recordings of mice recently revealed that slow-waves can also occur in layer 4 of the primary sensory cortices during REM sleep and thus possibly gate sensory input to the neocortex during this sleep state [26]. Slow-waves during REM sleep were subsequently found, albeit in different brain regions, in humans [27]. Whether slow-waves occurring during REM sleep serve a role in memory or function to gate sensory input, as proposed by Funk *et al.*, is thus far unknown.

Taken together, the variety of brain rhythms occurring during both NREM and REM sleep serve important roles in memory consolidation. It is, however, less clear whether all of these brain rhythms occur and are linked to the same functions in other animals with similar sleep states and cognitive abilities.

Avian brain and cognition

Historically, birds have been considered to have lesser cognitive abilities than mammals. However, there are an increasing number of studies demonstrating that the cognitive capabilities of some bird species, such as parrots and corvids, actually exceed those found in mammals (reviewed in Refs. [28,29^{*}]). Manufacturing and using tools, problem solving, and vocal learning are just some examples of avian cognition (reviewed in Refs. [30]). Furthermore, some birds, like mammals, exhibit 'episodic-like' memory, which enables them to recall what happened where and when (reviewed in Ref. [31]). For example, food hoarding birds can remember what food they hid where and when (e.g. Refs. [32,33]).

Despite similarities in cognitive abilities, there are clear differences in brain organization between mammals and birds. Compared to primate brains of the same or larger size, the brains of some birds show higher neuronal density in the pallium; for instance, the pallium of a macaw weighs 14.38 g and contains 1.917×10^6 neurons, whereas the pallium (cortex) of a macaque weighs 69.83 g and contains only 1.710×10^6 neurons [34]. Moreover, the cytoarchitecture of the avian pallium shows pronounced differences compared to the mammalian neocortex [35]. Rather than being organized in the six-layered manner of the mammalian neocortex, homologous neurons in the avian brain are organized in large nuclei composed of small, densely packed stellate neurons [34] interconnected via axonal projections [35,36]. Even when such nuclei are layered one on top of the other, as in the hyperpallium, these 'pseudo-layers' lack pyramidal cells with long apical dendrites spanning the layers, as found in the neocortex. Despite these differences, in many respects the connections between nuclei are similar to those between mammalian cortical regions. One notable exception, particularly relevant to sleep's role in memory consolidation, however, involves the avian hippocampus and the nidopallium caudolaterale (NCL) — the functional analogue of the mammalian PFC, which is involved in higher-order multimodal processing and executive functions, such as decision-making (reviewed in Refs. [29^{*},37]). Unlike mammals which have a direct hippocampus-medial PFC connection [19], the avian hippocampus and NCL are not directly interconnected (reviewed in Refs. [15,38]). The available neuroanatomical and neurophysiological information thus suggests that there may be a fundamental difference between how hippocampal-dependent information is processed in birds and mammals (reviewed in Refs. [31]).

Avian sleep

Various studies show that, despite being distantly related to mammals and showing clear differences in neuroanatomy [34–36,38–43], birds exhibit sleep states that are in most respects similar to those found in mammals (reviewed in Refs. [15]). In addition, sleep in birds has been implicated in two types of developmental learning, namely filial imprinting in chicken chicks [44–46] and song learning in zebra finches [47–50]. In addition, sleep plays a role in processing auditory memories in adult starlings [51,52^{*}]. As none of these memories are known to involve the hippocampus, thus far nothing is known about sleep's possible role in processing hippocampal memories in birds (reviewed in Refs. [15]). Moreover, as of yet, it remains unknown how sleep-related brain rhythms in birds play a role in memory consolidation.

Avian NREM sleep-related brain activity

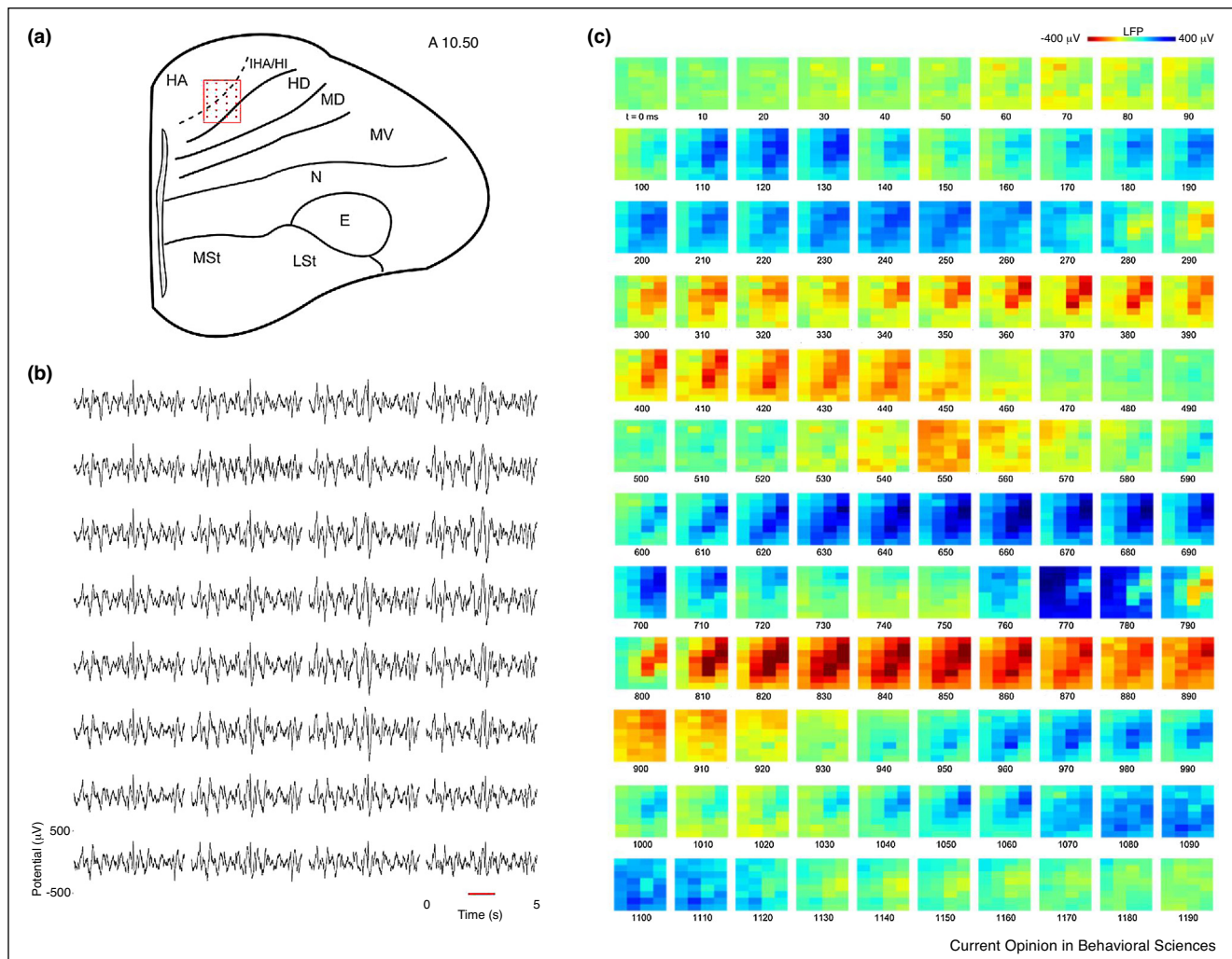
Previous research has shown that in birds, brain regions that are composed of pallial neurons homologous to neocortical (pallial) neurons (reviewed in Refs. [36,53])

display high-amplitude slow-waves during NREM sleep similar to those found during mammalian NREM sleep [54–56,57*]. Similar to mammals, avian NREM sleep EEG slow-wave activity (SWA, 0.5–4.5 Hz spectral power density) is homeostatically regulated in a local, use-dependent manner [56,58]. Until now, however, it is not known where these slow-waves are generated. In addition, until recently it was unclear if, as in mammals [59–61], slow-waves propagate through the avian brain. Furthermore, the existence of thalamocortical spindles was uncertain and little was known about sleep-related activity in the avian hippocampus (e.g. hippocampal

SWRs), and its possible relationship to activity in other pallial regions.

We recently showed that, as in mammals, traveling slow-waves can be found in the avian hyperpallium during natural NREM sleep [57*] (Figure 1). Slow-waves with similar propagation patterns also occur during isoflurane anesthesia in the hyperpallium, as well as other pallial regions [62,63]. Consequently, isoflurane seems to activate at least some of the same neural circuits that give rise to slow-waves during NREM sleep [64,65]. Interestingly, we have recently shown that slow-waves recorded in the

Figure 1



Traveling slow-waves in the pigeon hyperpallium during NREM sleep: **(a)** Schematic example of the location of the 32-channel silicon electrode array inserted in the hyperpallium. The hyperpallium primarily receives input from the nucleus geniculatus lateralis pars dorsalis (GLd; homologous to the mammalian lateral geniculate nucleus) to the interstitial part of hyperpallium apicale and the hyperpallium intercalatum (IHA/HI, collectively). The underlying hyperpallium densocellulare (HD) receives relatively little input from the GLd. The hyperpallium overlies and is interconnected with the dorsal and ventral mesopallium (MD/MV) and nidopallium (N). Abbreviations: entopallium (E), hyperpallium apicale (HA), striatum laterale (LSt), striatum mediale (MSt). **(b)** Five-second example of local field potentials (LFPs) recorded on the 4×8 grid of electrodes, showing the global distribution of oscillations during natural NREM sleep. **(c)** Red underlined episode of (b) is visualized in a sequence of image plots where pixels represent electrode sites and electrical potential is coded in color. Figure is reproduced from Van Der Meij *et al.* [57*] by permission of Oxford University Press.

hippocampus during isoflurane anesthesia likely do not originate from neural activity in this region, but are electrically volume conducted from the underlying nidopallium [83]. Thus, volume conduction may explain previous reports of slow-waves in EEG/LFP recordings of the avian hippocampus during NREM sleep. Although recordings of naturally sleeping birds are needed, this suggests that, unlike mammals, slow-waves do not appear to be present in the avian hippocampus [83]. This difference is especially interesting as traveling slow-waves are proposed to play a role in the processing of hippocampal memories during sleep in mammals [16,66]. Moreover, in naturally sleeping birds, the apparent absence of the two other rhythms — thalamocortical spindle [57^{*}] and hippocampal SWRs (reviewed in Ref. [15]) — implicated in hippocampal memory transfer in mammals, questions whether hippocampal memory consolidation takes place during avian sleep in the same way as in mammals. Although it is possible that these rhythms were missed in the few intra-cortical recordings of sleeping birds, their apparent absence might be related to limited connectivity between the avian hippocampus and pallial cortex-like regions. Indeed, the results from our lab's latest research [83], where hippocampal SWRs and slow-waves were not detected under isoflurane anesthesia and activity simultaneously recorded in the hippocampus and nidopallium was uncorrelated, suggests that the hippocampus and nidopallium do not work as a coordinated system during sleep. These results thus seem to suggest that the manner in which the avian hippocampus processes information may be fundamentally different from that of mammals during NREM sleep. This would fit with the fact that, even though the avian hippocampus is involved in storing certain types of information (e.g. spatial memories) however, there is so far no evidence for hippocampal memories being transferred to other brain regions for long-term storage (reviewed in Ref. [15]). Nonetheless, as suggested for the robust nucleus of the arcopallium in the songbird song network [67], hippocampal-dependent memory processing could be possible *within* the hippocampus during NREM sleep via, for instance, the reactivation or 'replay' of neuronal sequences activated during waking memory encoding without those memories being 'transferred' out of the hippocampus (reviewed in Ref. [15]).

Avian REM sleep-related brain activity

As in mammals, avian REM sleep is characterized by an activated (i.e. high-frequency, low-amplitude) EEG and LFP pattern associated with increased unit activity in the hyperpallium (i.e. the avian homologue of the mammalian primary visual cortex) relative to preceding NREM sleep [57^{*}]. Furthermore, avian REM sleep episodes alternate with NREM sleep episodes throughout sleep, usually becoming more frequent towards the end of the major sleep period [55,68]. Similar to altricial

mammals, the amount of time spent in REM sleep is the highest in young altricial birds before gradually declining to adult levels [69]. Our recent work in pigeons showed that slow-wave activity throughout the hyperpallium is low during REM sleep, with the greatest decrease taking place in the thalamo-recipient region of the hyperpallium, the region which shows the greatest SWA during NREM sleep [57^{*}]. This is particularly interesting in the light of recent observations made during REM sleep in mice wherein slow-waves persisted in the thalamo-recipient layers of primary sensory cortices, including the primary visual cortex [26], and during REM sleep in humans where two subtypes of slow-waves were found in different parts of the neocortex [27]. It is, however, unknown whether these opposing findings in pigeons and mice/humans are representative of all birds and mammals, respectively. Nonetheless, the results from pigeons indicate that the occurrence of slow-waves in primary sensory input layers is not a universal phenomenon in animals with REM sleep.

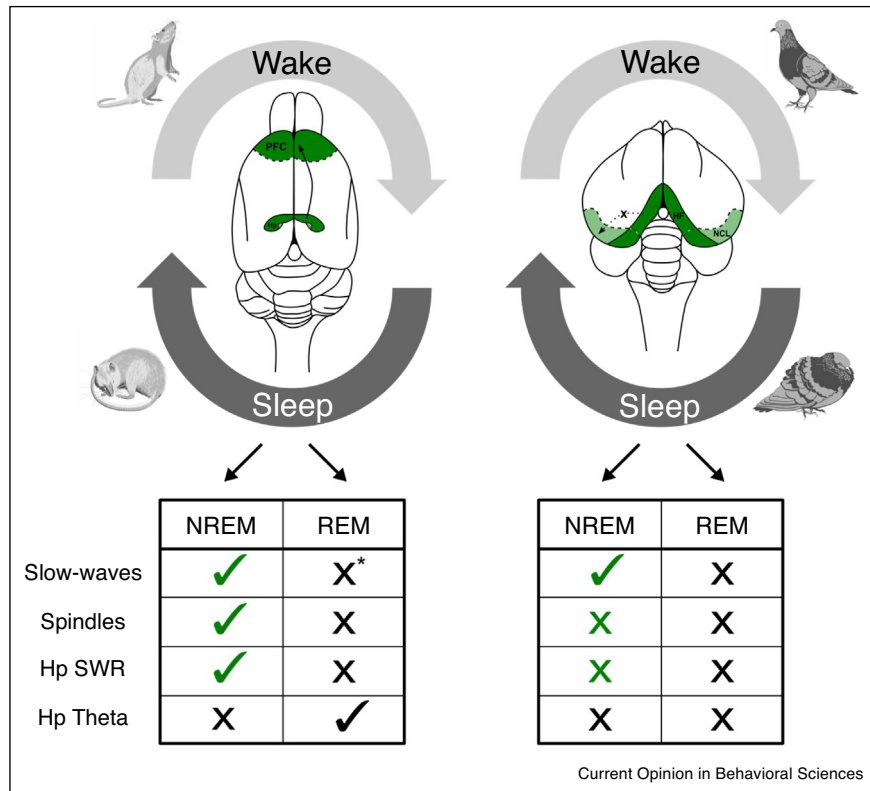
Additionally, REM sleep recordings in pigeons revealed localized gamma activity specific to the thalamo-recipient region of the hyperpallium during REM sleep [57^{*}]. REM sleep-related gamma activity has previously been shown in rodents [70] and humans [71,72], and has been suggested to play a role in memory retrieval (reviewed in Ref. [73]). Additional research, however, is needed to determine the exact region generating gamma in birds and its functional relationship to gamma reported during REM sleep in rodents and humans.

Another mammalian REM sleep-related rhythm, the hippocampal theta rhythm, which is implicated in the processing of emotional (reviewed in Ref. [21]), spatial (e.g. Ref. [22]) and contextual (reviewed in Ref. [15,23^{*}]) memories, has so far not been observed in the few studies that examined hippocampal activity during avian sleep (reviewed in Ref. [15]). Future recordings of the avian hippocampus during REM sleep will be needed to unravel potential differences between mammalian and avian brain rhythms, like theta, and their potential role(s) in the memory function of REM sleep.

A birds' brain view on sleep-related memory consolidation and cognition

There are numerous examples of birds showing similar cognitive abilities to those found in mammals. The current avian neurophysiological sleep data presented in this review, however, seem to suggest that memories, like the earlier discussed episodic-like memories, in birds might be processed differently during sleep compared to those in mammals. The apparent absence of thalamocortical spindles and hippocampal SWRs, both implicated in mammalian sleep-related hippocampal memory consolidation, during NREM sleep in birds combined with the

Figure 2



Schematic overview of the current knowledge about the similarities and differences between mammalian and avian NREM and REM sleep-related brain activity linked to memory consolidation. During mammalian NREM sleep, information transfer between the hippocampus (Hp) and neocortex is thought to involve the interplay of cortical slow-waves, thalamocortical spindles and hippocampal sharp-wave ripples (SWRs) mediated by a direct connection from the Hp to the prefrontal cortex (PFC; black arrow). Birds, on the other hand, so far seem to lack both spindles and SWRs during NREM sleep. Combined with the lack of connections between the hippocampal formation (HF) and the NCL (nidopallium caudolaterale; that is, the functional analogue of the mammalian PFC) (dotted arrow), and the absence of evidence of information transferring out of the hippocampus, this suggests that mammals and birds process hippocampal memories in a different way during sleep. In addition, REM sleep-related theta or slow-waves have not been found in birds. *Though REM sleep-related slow-waves have been shown in parts of the neocortex in mice (Funk *et al.* [26]) and humans (Bernardi *et al.* [27]) during REM sleep, many regions show an activated pattern similar to wakefulness. Rat and pigeon illustrations by Damond Kylo.

lack of connections between the hippocampus and the NCL (i.e. the functional analogue of the mammalian PFC (reviewed in Refs. [29*,37])), and the absence of evidence of information transfer out of the hippocampus, all point to a variance in how mammals and birds process memories during sleep (Figure 2).

Nonetheless, slow-waves might be involved in strengthening memories locally within pallial circuits [74,75], either via reactivation during fast activity occurring during the upstates of the slow oscillations [76] or via slow-wave induced synaptic downscaling which is thought to increase memory through increasing the signal-to-noise ratio in local circuits [17]. The potential for a local role for slow-waves in processing memories is supported by the fact that SWA is regulated in a local use-dependent manner in the mammalian neocortex [77] and avian hyperpallium [56,78]. Memory consolidation at the

systems level in birds could, nonetheless, take place between non-hippocampal/pallial regions like the hyperpallium, mesopallium and nidopallium [11,45]. Further research is needed to examine if and how (traveling) slow-waves and/or other rhythms play a role in this potential process in birds. In addition, more work is needed to determine if thalamocortical spindles and hippocampal SWRs during NREM sleep, and theta during REM sleep might have been missed in previous studies. Furthermore, the recent interest in sleep-related brain activity in other taxa of the evolutionary tree, like reptiles [79–81] and fish [82], has the potential to further inform our understanding of how sleep evolved and its potential role in memory.

Conflict of interest statement

Nothing declared.

CRedit authorship contribution statement

Jacqueline van der Meij: Writing - original draft, Visualization, Writing - review & editing. **Gianina Ungurean:** Writing - review & editing. **Niels C Rattenborg:** Writing - review & editing. **Gabriël J L Beckers:** Writing - review & editing.

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