


Review

# Understanding Sleep and Memory in the Avian Brain

Janie M. Ondracek<sup>1,\*</sup> <sup>1</sup>Chair of Zoology, TUM School of Life Sciences, Technical University of Munich, 85354 Freising, Germany\*Correspondence: [janie.ondracek@tum.de](mailto:janie.ondracek@tum.de) (Janie M. Ondracek)

Academic Editor: Bettina Platt

Submitted: 26 January 2026 Revised: 23 March 2026 Accepted: 7 April 2026 Published: 9 May 2026

## Abstract

How do neural circuits change to incorporate newly learned events? After decades of research, we now have a good understanding of the diversity and duration of memory types, the context-specifics of learning regimes, and the brain areas that are likely to be involved. However, we are still far from a mechanistic understanding of the neural activity required to transform new behavioral experiences into long term memory accessed during recall events. What kind of network activity is required to affect these wide-spread changes in neuronal circuitries? Among current theories of memory in mammals, one of the most intriguing is concerned with the role of large-scale synchronous neural activity, which is thought to enable the transfer of information from the hippocampus to numerous regions of the neocortex. In this contribution, we first review sleep, learning, and memory in birds before highlighting evidence that large-scale synchronous neural activity also exists in the avian brain, making the case that by examining these questions from a comparative research perspective, we gain important insight into the canonical features of memory consolidation.

**Keywords:** sleep; birds; memory; memory consolidation; learning; hippocampus

## 1. Introduction

Given the importance of sleep to animal life, it is surprising how little we know about its function. Although the scientific study of sleep began in the mid-19th century [1], research was limited to humans and other mammals for over one hundred years [2,3]. Only in the 1960s did studies of sleep in non-mammalian animals start appearing [4–6], and through this comparative approach, we have learned that sleep serves a vital function. Across the animal kingdom, a lack of sleep can detrimentally affect development [7], cognitive abilities [8], and life span [9].

Recent innovations in recording techniques [10] and animal tracking software [11,12] have revitalized the study of sleep in non-mammalian animals, and recent publications have reported sleep in animals as diverse as octopus [13] and bearded dragons [14]. What is sleep, exactly, and what can we learn by studying sleep (and its functions) in non-mammalian brains? This is the topic of this short review.

## 2. Literature Review

### 2.1 What is Sleep?

While we all know what it feels like to be asleep, how do we go about determining whether an animal is asleep? In the field of comparative sleep research, sleep is usually defined using two frameworks. One framework involves a behavioral definition of sleep. This definition was first described by Piéron in 1913 [15] and later extended by Flanagan and Tobler in the 70s and 80s into a set of operational criteria including: (1) the presence of a specific sleeping site; (2) a typical body posture; (3) physical quiescence;

(4) elevated arousal threshold; (5) rapid state reversibility; and (6) regulatory capacity, i.e., (homeostatic) compensation after loss [16–19]. Using this behavioral framework, it became possible to investigate sleep-like behavior in a number of non-mammalian vertebrates and invertebrates.

In particular, the measurement of arousal thresholds has been instrumental in a large body of comparative sleep research, especially for work in invertebrates like fruit flies, nematodes, and even jellyfish [20–22]. Typical responses show that when an animal is engaged in sleep, more intense stimuli are needed to elicit a behavioral reaction than when it is engaged in drowsiness or in quiet waking. However, the use of arousal thresholds to identify sleep is not without its pitfalls: stimulus modality, salience, and contextual relevance are highly variable across different animal species, highlighting the problem with assigning a universal “high arousal threshold” metric across species. Furthermore, while behavioral definitions of sleep offer important guidelines that are appropriate in most cases, they may not be suitable for describing complex sleep patterns such as those found in aquatic mammals or migrating birds engaged in unihemispheric sleep.

The electrophysiological state of the brain provides another framework to describe sleep. Despite the (often) reduced external behavior during sleep, the sleeping brain remains highly active. The first electrophysiological studies of brain activity during sleep in humans revealed clear electroencephalographic (EEG) correlates of brain states [3], and researchers now divide sleep EEG patterns into two main types: (i) rapid eye movement (REM) sleep and (ii) non-REM (NREM) sleep. These two states of sleep have



been documented in numerous non-mammalian animals, including birds [23–27], reptiles [14,28,29], zebra fish [30], and cephalopods [13]. Similar to mammals, REM sleep states in these animals are characterized by low amplitude and aperiodic electrical activity that is highly similar to the awake brain state, whereas NREM sleep is characterized by the emergence of periodic ‘slow-wave activity’ (SWA; 1–4 Hz oscillations) during slow-wave sleep (SWS).

## 2.2 Characteristics of Avian Sleep

Although there are more than 18,000 species of birds by some counts [31] electrophysiological signs of sleep have been investigated in only a handful of these animals: chickens and pigeons [5]; geese [32]; multiple species of songbirds, including the white-crowned sparrow [33], zebra finch [25,26], and blackbird [34]; parrots (budgerigars) [23]; sandpipers [35]; burrowing owls [36], and ostriches [37] to name a few.

Sleep in birds is generally similar to mammalian sleep due to the largely uncontested presence of both SWS sleep and REM sleep, although the duration of REM sleep epochs are usually much shorter, the differences between sleep states are much smaller than in mammals [38–40], and sleep spindles, a hallmark of mammalian NREM, have not been observed during avian sleep [23,25].

Given the electrophysiological similarity between REM sleep and the awake state (as is also true for mammals), it is important to differentiate between true REM sleep and short bouts of wakefulness in birds. Decreased skeletal muscle tone, concomitant eye movement, and irregular heart rate are all features that accompany REM sleep in mammals. These mammalian co-indicators of REM sleep are present to varying degrees in non-mammalian species [41]. For example, while eye movements are present during REM-like sleep in reptiles [14] and many bird species, they are generally absent in burrowing owls [36]. Many birds remain vigilant during sleep, opening one or both eyes during SWS, and only closing both eyes during REM sleep [36,42,43]. Similarly, REM-related atonia in birds is often a function of the specific sleeping posture, and large variability is present in sleep-related electromyography (EMG) readings across avian species [23,37]. Such findings have led to an observable technology shift in the quantification of avian sleep, in which contemporary studies have replaced classical EMG and electrooculography (EOG) recordings of the eye with non-invasive accelerometry or video recording analysis to assess body movement and posture, and/or eye state (see Table 1 for a review (Ref. [5,23–25,32,33,35–37,44–50])).

Further complicating the issue of avian sleep is that in addition to bilateral phases of SWS and REM, where both hemispheres exhibit the same sleep state, many species of birds show bouts of unilateral SWS (USWS) - the condition where one hemisphere shows unambiguous waking EEG activity while the other shows unambiguous SWS activity.

Birds engaged in long migratory flights demonstrate both bilateral sleep as well as USWS [44]. USWS activity has been linked to unilateral eye opening, such that the awake EEG activity accompanies contralateral eye opening, and some authors have posited that USWS is under facultative control in birds and may have a role in heightening vigilance against predators [42,51].

The widespread activity that occurs in the brain during sleep has a purpose; however, there is still no consensus on what that might be. Non-mutually exclusive hypotheses range from energy conservation [52], brain thermoregulation [53], detoxification [54], and tissue restoration [55]. One view, which is well supported by data, is that sleep benefits memory [56].

## 2.3 What is Memory?

In psychological terms, memory is defined as the ability to encode, store, and subsequently retrieve information and past experiences [57]. Memory is the sum total of what we remember, and it endows us with the capability to learn and adapt from previous experiences. Over the years, psychologists have established three main categories of memory: short-term memory, which can only hold limited information; long-term memory, which can store an indefinite amount of information; and sensory memory, which is not consciously controlled [58].

There are also different types of memories: declarative memories are consciously acquired and include memories of experiences (i.e., episodic memory) and facts (i.e., semantic memory). In contrast, non-declarative memories are implicitly acquired and include procedural skill learning and behavioral conditioning (i.e., classical or operant conditioning [59]). While evidence suggests that non-declarative memories involve the basal ganglia and motor cortex, declarative memories involve the hippocampus [60].

Newly formed declarative memories require consolidation, a process by which they are transformed and stabilized into long-term memory [61,62]. While the initial encoding of a memory is a rapid (milliseconds) process, its long-term maintenance requires processes that continue to modify it over hours to years, as long-term memory representations are distributed over brain circuits. Compelling evidence in humans [63–65] and rodents [66–68] has shown that these processes occur during sleep and are collectively known as *memory consolidation*.

Research suggests that the consolidation of declarative and non-declarative memory differentially depends on the sleep state. For example, studies have shown that humans perform better in declarative memory-related tasks after sleep compared to wakefulness [63,64,69] and that this improvement is linked to SWS [70–72]. On the other hand, REM sleep has been shown to be important for perceptual tasks [73] and motor/visuomotor tasks in humans [74,75], and for procedural memories acquired through behavioral

**Table 1. Summary of avian sleep studies and methodologies over the past 60 years.**

Source	Bird species used	SWS presence	REM presence	EMG usage	EOG usage	Movement or accelerometer
Klein <i>et al.</i> (1964) [5]	Chicken and Pigeon	Present (as <i>sommeil lent</i> )	Present (as <i>sommeil hypotonique</i> )	Used (Neck muscles)	Used	Visual behavioral observation
Rojas-Ramírez & Tauber (1970) [45]	Hawk ( <i>Buteo jamaicensis</i> ); Falcon ( <i>Herpetotheres cachinnans</i> )	Present (as NREM)	Present (as REM)	Used (Neck muscles)	Used (Periorbital screws)	Scanning behavior and motor activity
Van Twyver & Allison (1972) [46]	Pigeon ( <i>Columba livia</i> )	Present	Present (as Paradoxical Sleep)	Used (Neck muscles)	Used	CCTV monitoring
Berger & Walker (1972) [36]	Burrowing Owl ( <i>Speotyto cunicularia</i> )	Present	Present (as Desynchronized Sleep)	Used (Neck and eye muscles)	Used (Orbital screws) to confirm absence of REM	Strain gauge and infrared CCTV
Walker & Berger (1972) [47]	Domestic Pigeon ( <i>Columba livia</i> )	Present	Present (as REM)	Used (Identical to owl study)	Used	Head movements recorded
Dewasmes <i>et al.</i> (1985) [32]	Goose (landaise strain)	Present	Present	Used (Neck muscles)	Used	CCTV/Behavioral observation
Szymczak (1989) [48]	Rook ( <i>Corvus frugilegus</i> ); Magpie ( <i>Pica pica</i> )	Present	Present (as Paradoxical Sleep)	Used (Electrographic)	Used (Electrographic)	Behavioral observation
Rattenborg <i>et al.</i> (2004) [33]	White-crowned sparrow ( <i>Zonotrichia leucophrys gambelii</i> )	Present	Present	Used (Neck muscles)	Not Mentioned	Infrared beam and video
Low <i>et al.</i> (2008) [25]	Zebra Finch ( <i>Taeniopygia guttata</i> )	Present	Present	Not Mentioned	Not Used	Video monitoring
Lesku <i>et al.</i> (2011) [37]	Ostrich ( <i>Struthio camelus</i> )	Present	Present (Mixed state)	Used (Neck muscles)	Used	3-axis head accelerometer and GPS
Lesku <i>et al.</i> (2012) [35]	Pectoral Sandpiper ( <i>Calidris melanotos</i> )	Present (as NREM)	Rarely Observed	Used (Neck muscles)	Not Used	Video and EMG-based activity
Rattenborg <i>et al.</i> (2016) [44]	Great frigatebird ( <i>F. minor</i> )	Present	Present	Not Used	Not Used	3-axis head accelerometer and GPS
Tisdale <i>et al.</i> (2017) [49]	Elegant crested tinamou ( <i>Eudromia elegans</i> )	Present	Present	Used (Neck muscles)	Used	3-axis head accelerometer and video
van Hasselt <i>et al.</i> (2020) [50]	European Starling ( <i>Sturnus vulgaris</i> )	Present (as NREM)	Present	Not Used	Not Used	3-axis head accelerometer
Canavan & Margoliash (2020) [23]	Budgerigar ( <i>Melopsittacus undulatus</i> )	Present	Present	Not Used (Atonia considered unreliable)	Used	Video and automated motion detection
Libourel <i>et al.</i> (2023) [24]	Chinstrap penguin ( <i>Pygoscelis antarcticus</i> )	Present	Present	Used (Neck muscles)	Not Used	3-axis head accelerometer, GPS, and pressure sensors

Atonia and EMG: Earlier studies (1960s–1980s) almost exclusively used neck EMG to identify the reduction of muscle tone during REM. More recent studies have omitted EMG leads because REM atonia is considered an unreliable indicator in birds. SWS, slow-wave sleep; EMG, electromyography; EOG, electrooculography; REM, rapid eye movement; NREM, non-REM; CCTV, closed-circuit television; GPS, Global Positioning System.

training in rodents [66–68]. These results demonstrate that memory consolidation during sleep may require different modes of brain activity. In this review, we will focus on memory consolidation involving the hippocampus and the brain oscillations known as sharp-wave ripples.

#### 2.4 Sharp Wave-Ripples and Memory Consolidation

During phases of SWS, large-scale synchronous neural activity is thought to enable the transfer of information from the hippocampus to numerous regions of the neocortex [76]. These sharp wave-ripple (SWR) events result from the coordinated firing of many neurons, and in the rodent hippocampus, the neural activity that initiates a SWR is well understood: massive excitation of neurons in the Cornu Ammonis 1 (CA1) subfield by the pyramidal neurons in the CA3 subfield causes a synchronization of inhibitory interneurons, which generates a ripple in the pyramidal layer [77].

Importantly, the spiking activity associated with SWRs is highly structured across neurons. In mammals, this activity reflects a temporally compressed version of sequential neuronal firing patterns experienced by the awake animal [78]. Specifically, in the rodent hippocampus, firing patterns in place cell assemblies are “replayed” in the same temporal order as that which occurred during the awake task performance [79,80], and many studies have documented replay events during SWRs, where sets of hippocampal place cells that fired together during exploration are more likely to fire together afterwards during sleep or awake rest [78,81,82].

Notably, studies in rodents have demonstrated that SWRs have a causal role in memory consolidation [83–86]. In these experiments, animals that underwent SWR suppression during sleep performed significantly worse in spatial memory tasks compared to control animals. These results highlight the functional role of SWRs in the consolidation of spatial memories.

The local network activity within the hippocampus is also coordinated with distant cortical activity [87], and neural coordination between brain areas provides a likely substrate for the network activation and reactivation required for learning and memory. Through its large-scale synchronous activity, SWR output brings about sequential activations in the prefrontal cortex, leading to a systems-level transformation of new experiences into stable memory traces. SWRs appear to be conserved throughout mammalian evolution: they have been found in every mammal investigated so far, including humans [79].

#### 2.5 How Neural-Circuit Homology Informs Function

How do the avian brain and the mammalian brain compare? The “sameness” of neural circuits or brain areas that is due to common evolutionary origin across animals is known as “homology” [88]. The identification of homologies across brain areas in different animals remains an

active area of research that has been revitalized by recent advances in transcriptomic methods [89]. The goal is that by studying homologies across neural circuits, we can gain considerable insight into their canonical function across animals.

During embryonic development, a remarkably similar “bauplan” exists across all vertebrate brains [90]. First, the primordial telencephalon develops into the pallium and the subpallium. Then the pallium further differentiates into a number of subregions that give rise to different brain structures in different animals [91]. Sometimes, these brain areas are similar across structure and function; for example, in both birds and mammals, the medial pallium gives rise to the hippocampal formation. In birds, the hippocampal formation receives visual input from the Wulst [92], and general characteristics such as connectivity, neuron types, and the presence of adult neurogenesis seem to be conserved between birds and mammals [93]. Similar to mammals, spatial learning in birds (see next section, “Models of memory and learning in birds”) also seems to rely on the function of the hippocampus.

Sometimes, however, embryonic development gives rise to very different neural architectures in mammals and birds. In mammals, for example, the dorsal pallium gives rise to the 6-layered neocortex, whereas in birds, the dorsal pallium becomes a structure known as the hyperpallium. Although the mammalian neocortex and avian hyperpallium derive from the same dorsal pallial structure, there is very little resemblance between the two structures in terms of morphology or function [94]. Indeed, the cognitive functions that are associated with the 6-layer mammalian neocortex seem to be seated in another brain area altogether in birds known as the “dorsal ventricular ridge” (DVR).

In mammals, parts of the ventral pallium give rise to the amygdalar complex [95]. In birds and reptiles, the ventral pallium gives rise to the DVR. This large pallial region dorsal to the basal ganglia is unique to reptiles and birds. In general, the anterior DVR consists of spatially segregated neuronal types specialized in processing visual, auditory, or somatosensory stimuli [96], whereas the posterior DVR is thought to be homologous with the mammalian claustrum and amygdala [97]. In birds, the DVR is subdivided into the mesopallium, nidopallium, entopallium, and arcopallium (Fig. 1A).

Although the regions of the DVR have no direct mammalian counterpart, recent advances using imaging technology, viral tools, and single-cell transcriptomics seek to better understand the relationship between the avian DVR and mammalian brain structures. The emerging story is complicated.

For example, although the avian DVR appears to lack a laminar structure, a recent imaging study showed that the sensory DVR displays radially and tangentially organized fibers, similar to the canonical microcircuit of the mammalian neocortex [98]. On the other hand, recent experi-

ments that used single-cell transcriptomics to characterize gene expression patterns in the avian DVR revealed that the avian DVR and the mammalian neocortex derive from fundamentally different neurodevelopmental regions and are therefore not homologous structures [99].

The story is also complicated at the cellular level. A recent study used optogenetic tools to specifically target excitatory and inhibitory neurons in the avian DVR and found physiological and computational similarities with mammalian excitatory and inhibitory neocortical neurons [100]. However, experiments using single-cell sequencing found that the entire songbird pallium is populated by a type of interneuron that is largely absent in the neocortex [99], suggesting that “cortical-like” microcircuits described in the avian DVR may engage an entire class of interneurons that has no counterpart in the mammalian neocortex [101]. These contrasting results highlight the dearth of knowledge about the cell types, anatomical connections, and computations of the avian DVR.

Although the anatomy of avian DVR is fundamentally different from the mammalian networks that underlie memory consolidation, its placement as a nexus of sensory input within the avian telencephalon might make DVR networks well-suited for a role in learning and memory, allowing avian intelligence to arise from neural circuitry fundamentally similar to that of the neocortex. And indeed, many of the impressive learning abilities of birds rely on networks within the DVR.

## 2.6 Models of Memory and Learning in Birds

### 2.6.1 Avian Learning and the DVR

The avian DVR is often compared to the mammalian neocortex [102], and indeed, the avian DVR has received renewed attention in recent years because of its role in multiple avian learning paradigms. For example, high-level cognition in corvids has been linked to a nidopallial area of the DVR (nidopallium caudolaterale [NCL]; Table 2, Ref. [33,103–139]). NCL has been compared to mammalian neocortex [102,103], and neurons in NCL have been shown to encode information ranging from numerosity [104] to abstract behavioral rules [105] to sensory consciousness [106].

Similarly, key elements of vocal learning in songbirds rely on brain areas in the DVR. During vocal learning, juvenile zebra finches use auditory feedback and motor learning to transition from acoustically simple songs to complex and stereotypical adult songs [140], a complex memory task that involves the formation of auditory memories (the “template”), sequences of motor output, and associative higher-order representations of learned vocalizations [141–143]. Vocal learning requires a set of interconnected brain nuclei that share analogies with brain areas involved in human language learning [144], and several areas within the DVR have been implicated in vocal learning. For example, immediate early gene studies have suggested that neurons

in a nidopallial area of the DVR (nidopallium caudomedial [NCM]) may encode the memory of the “tutor” song during vocal learning [107–110]. Similarly, neurons in mesopallial parts of the DVR have been shown to have a role in auditory object recognition [111] (the caudal mesopallium [CM]) and to encode stimulus surprise [112] (caudal lateral mesopallium [CLM]), whereas neurons in another small cluster of neurons embedded in the CM (Avalanche) have been shown to have a role in juvenile song copying [113]. Finally, neurons in the arcopallial part of DVR, in a nucleus known as the robust nucleus of the arcopallium (RA) have been shown to spontaneously reactivate during sleep [114–116], highly similar to the replay observed in mammalian hippocampus.

Filial (visual) imprinting also involves brain areas in the mesopallial part of the DVR. Young, visually naive domestic chicks quickly learn the characteristics of certain visually conspicuous objects upon being exposed to them. This imprinting memory critically relies on the left intermediate and medial mesopallium (IMM; formerly known as the intermediate and medial hyperstriatum ventral [IMHV] [117,118,145]): destruction of this region before training impaired imprinting [119,120]; destruction after training eliminated an acquired preference [121]. Furthermore, biochemical studies have shown that several features of the IMM undergo changes as a result of visual imprinting, including an increase in the size of post-synaptic densities percentage in IMM neurons and upregulation of N-methyl-D-aspartate (NMDA)-type glutamate receptors [117], highlighting a molecular mechanism for visual imprinting in the DVR.

### 2.6.2 Avian Learning and the Hippocampus

Spatial learning refers to the process by which an animal acquires a mental representation of its environment, and in humans, it is considered to be a form of declarative memory [146]. Tasks that query spatial learning have long been the preferred method for investigating memory consolidation in rodents, and decades of research have culminated in an understanding that the hippocampus is essential for memory consolidation. However, it is clear that non-mammals such as birds are also capable of learning and forming memories, and a significant amount of memory research has focused on the avian hippocampus, known as the “hippocampal formation”.

Similar to the spatial learning tasks commonly performed in rodents and which rely on the hippocampus, experiments investigating spatial learning in birds typically involve measuring the effect of hippocampal lesions on spatial memory tasks. For example, zebra finches that received ibotenic acid lesions in the hippocampus were impaired in their ability to remember the location of hidden seeds [122]. Similar studies conducted in Japanese quail [123,124], homing pigeons [125,126], as well as a seed-

**Table 2. Examples of learning and memory research in birds, and the corresponding brain regions of interest.**

Learning modality	Bird	Abbreviation	Brain region	Brain area	References
Vocal Learning	Zebra finch	NCM	nidopallium caudomedial	DVR - nidopallium	[107–110]
		CM	caudal mesopallium	DVR - mesopallium	[111]
		CLM	caudal lateral mesopallium	DVR - mesopallium	[112]
		Av	Avalanche, caudal mesopallium	DVR - mesopallium	[113]
		RA	robust nucleus of the arcopallium	DVR - arcopallium	[114–116]
Avian Cognition	Carrion crow	NCL	nidopallium caudolaterale	DVR - nidopallium	[103–106]
Visual Imprinting	Chicken	IMM	intermediate and medial mesopallium	DVR - mesopallium	[117–121]
Spatial memory	Zebra finch	HF	Hippocampal formation	Hippocampus	[122]
	Chickadee	HF	Hippocampal formation	Hippocampus	[127–129]
	Homing pigeon	HF	Hippocampal formation	Hippocampus	[125,126]
	Quail	HF	Hippocampal formation	Hippocampus	[123,124]
Episodic memory	Chickadee	HF	Hippocampal formation	Hippocampus	[133]
	Jays				[130–132,137]
	Blue tit, great tit				[134]
Operant learning	Zebra finch				[138,139]
	Starlings				[135,136]
	White-crowned sparrows				[33]

DVR, dorsal ventricular ridge.

caching songbird, the black-capped chickadee [127–129], have all implicated the avian hippocampus in spatial learning.

Episodic memory also relies on the hippocampus, and it is often considered the “pinnacle” of the different types of memory [147]. Episodic memories are memories of experiences, and they provide the “what-when-where” content for an experience [148]. Although spatial memories provide a structural framework for episodic memories by encoding information about the location where an event may have occurred, episodic memories must also have an association of what happened and when it occurred in time.

Experiments that leveraged the seed caching abilities of some bird species highlight the evidence that episodic memory is not unique to humans [147,148]. For example, scrub jays were able to remember the locations of perishable and non-perishable food items and recover the food before it became inedible [130–132]. Recent work in another seed-caching specialist, the chickadee, was able to show that seed-caching involved event-specific “barcodes” of neural activity in the hippocampus, which encoded unique identifiers to episodic memory events [133]. Finally, evidence of episodic memory also appears in non-seed caching generalist foragers (like blue tits and great tits [134]) and hummingbirds [149].

### 2.7 Sleep, Learning, and Memory in Birds

A growing body of evidence has shown that sleep is an essential requirement for several learning and memory tasks in birds. During vocal learning, anecdotal evidence reports that juvenile birds tend to fall asleep after first exposure to the singing of an adult tutor [150] and furthermore, that the

initial tutor song exposure causes a circadian pattern of vocalization deterioration which continues into adulthood, but does not exist prior to tutor song exposure [151]. Immediate early gene expression increases during sleep in learning juveniles in a brain area thought to house the auditory memory of the tutor song, and this activation is related to the amount of tutor song exposure and accuracy of song performance during prior wakefulness [152]. Finally, neurons in a premotor brain nucleus involved in song learning (RA) showed an increase in high-frequency bursting activity during sleep in juvenile zebra finches [116], and spontaneous activity patterns recorded during sleep in adult zebra finches were highly similar to patterns recorded during daytime singing [114,153,154]. Interestingly, recordings from the muscles of the syrinx, the vocal organ of songbirds, also show song rehearsals during sleep [155].

Similarly, studies investigating visual imprinting have also highlighted a role for sleep. Specifically, neurons in the IMM become selectively responsive to a trained imprinting stimulus [117]. This stimulus selectivity is critically dependent on a period of SWS after exposure to the visual imprinting stimulus for the memorization of the stimulus to be successful [118].

Operant learning has also shown a requirement for sleep in birds. One study, in which starlings were trained to discriminate between different auditory stimuli, showed that sleep supported the consolidation of recent auditory memories [135], and furthermore, that sleep could improve learning for interference tasks as well [136]. Similarly, white-crowned sparrows which were trained on a pecking task performed less accurately after their sleep was restricted to 3 hours [33].

Although sleep has been shown to be required for spatial memory task performance in rats [156] and humans [157], scientific reports of its effects on spatial memory learning in birds remain rare. In one study which focused on mono-ocular sleep (sleep with one eye open), chicks were trained in a spatial learning task to find food in one of 4 containers, and chicks reportedly spent more time sleeping during learning compared to non-learning control chicks [158,159]. Altogether, this evidence highlights a critical role for sleep in a wide range of avian learning paradigms. However, the exact mechanisms of this sleep requirement remain unclear: how does sleep support learning in a brain that lacks the complex laminar neural-architecture that defines the mammalian brain?

## 2.8 Open Questions

Exactly how diverse memories are consolidated across the networks of the avian brain is not currently understood. In mammals, the process of memory consolidation involves specific interactions between two main brain areas: the hippocampus and the cortex. Is the specific neuronal hardware (e.g., neural circuits, physiological properties) a critical component of this process? Or alternatively, are there specific population patterns (i.e., SWRs) that are vital to memory consolidation and can arise from various neural-architectures? The latter theory is appealing, as it suggests that other brain areas that participate in the encoding of the animal's experience during behavior may use similar schemes to transfer and consolidate memories and experiences. In the following sections, I will review some of our recent findings to highlight the importance of studying sleep, learning, and memory in alternative animal models like birds.

## 2.9 SWR-Like Activity During Sleep in Songbirds

Through its large-scale synchronous activity, SWR output brings about sequential activations in the prefrontal cortex, leading to a systems-level transformation of labile experiences into stable memory traces [160]. We found evidence of SWR-like activity in the avian brain that is remarkably similar to mammalian hippocampal SWR activity [27,161] during SWS in birds. Importantly, we did not record SWR activity in the avian hippocampus [162] but rather in the avian DVR. Avian SWRs are characterized by a large, sharp wave in the local field potential (LFP), a fast ripple oscillation, and a burst in gamma-band activity [27]. Based on these results, I propose that avian SWRs have several attributes that likely facilitate memory consolidation in the avian brain.

### 2.9.1 Avian SWRs Occur During Sleep

In birds, it is possible to track the transitions between different phases of sleep by calculating the ratio of delta activity ( $\delta$ , 1–4 Hz) to gamma activity ( $\gamma$ , 30–140 Hz; Fig. 1B, Ref. [161]). This method is analogous to metrics that have

been used for rodents [163], but accounts for the dominant frequency bands present during avian sleep [25,26,164].

As is true in mammals, SWS phases in birds correspond to an increase in delta activity (Fig. 1C). Avian SWRs appear during phases of SWS in zebra finches, paralleling the situation in the rodent hippocampus, where SWR activity specifically occurs during bouts of rest and SWS [77]. Similar to mammals, sleep in birds likely provides an optimal “offline” period for memory consolidation due to the greatly reduced processing of external information [165].

### 2.9.2 Avian SWRs are Spatially-Distributed, Large-Scale Events

Avian SWRs can be recorded throughout a large expanse of the avian brain. Using 4-shank silicon probes in isoflurane-anesthetized zebra finches, we measured avian SWRs throughout the medial-lateral extent of the avian DVR. Avian SWRs were apparent at recording locations throughout this area; however, the shape of the sharp wave and the presence or absence of the ripple component appear to change as a function of spatial position (Fig. 1D). These findings were also replicated in our recent paper using Neuropixels 1.0 probes (IMEC, Leuven, Belgium) chronically implanted in the brains of male zebra finches [27], which revealed avian SWR activity that spanned more than 3 mm. By affecting neural activity over such a large part of the brain, avian SWRs have the capacity to synchronize the firing of many neurons in a powerful, population-wide event that can affect both local and distal neural activity.

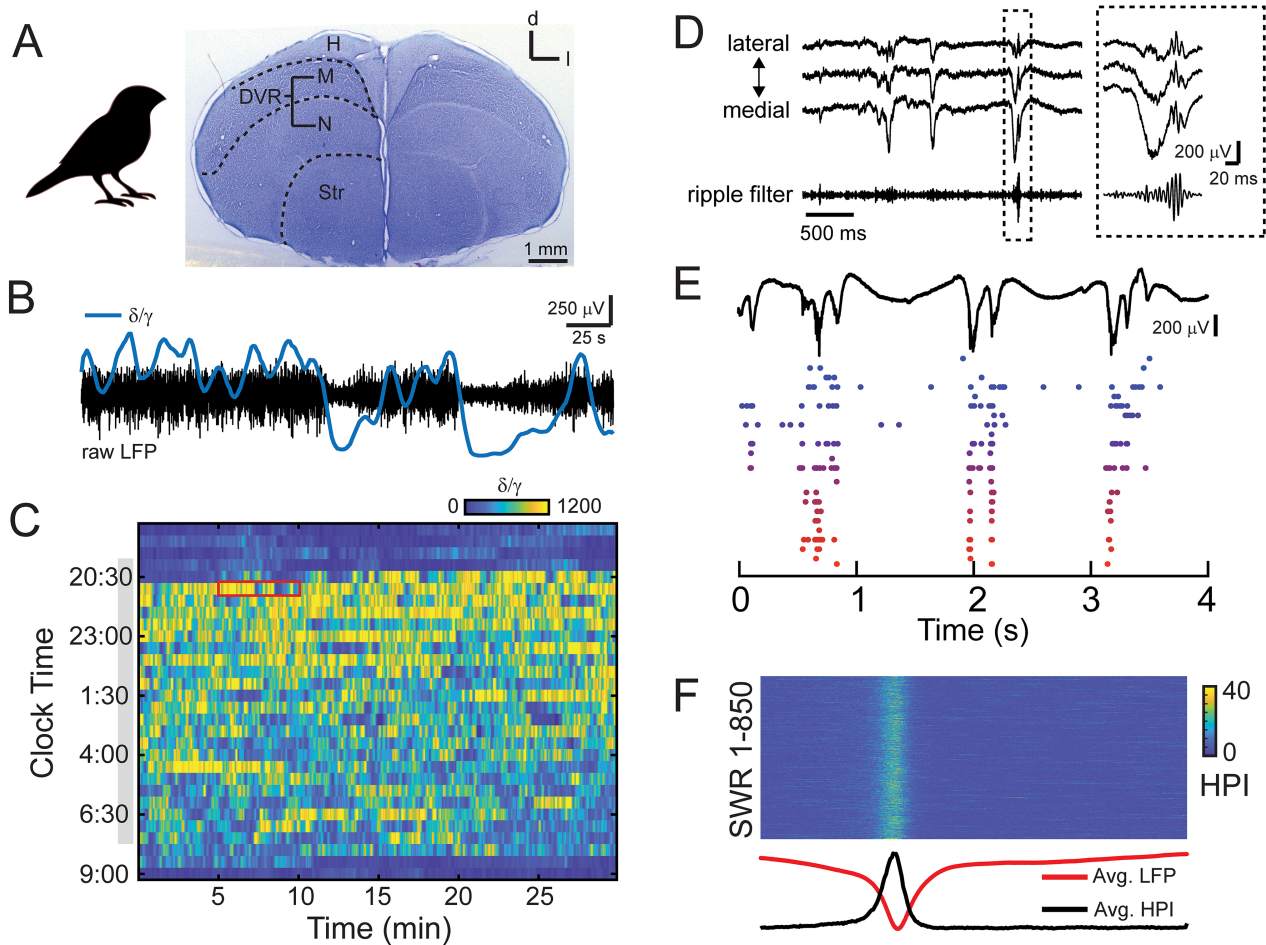
### 2.9.3 Avian SWRs are Associated With Sequences of Neural Activation

Avian SWRs are associated with increased neural activity, and across neurons, these firing patterns form distinct sequences of activity that could represent neural reactivation of events experienced during awake periods (Fig. 1E). These patterns are highly similar to the reactivation of neuronal firing patterns, or “replay” events, observed in the rodent hippocampus [77,79] and drive the population in a temporally locked spiking pattern (Fig. 1F).

## 3. Conclusions

In birds, the relationship between patterns of neural firing during SWRs and awake behavior remains unresolved. Furthermore, it remains unclear which behavioral experiences might be replayed during sleep in birds. Further work is required to specify how neural activity patterns that occur during awake behavior are recapitulated during SWRs in offline sleep phases.

Could it be that SWRs in avian brains are used for memory consolidation or memory transfer? If true, SWRs may constitute a basic mechanism for memory transfer that is shared across vertebrate brains. Importantly, similar SWR-like LFP patterns have also been recorded during sleep in the reptilian DVR [14,28,29]. The fact that SWR-



**Fig. 1. Sleep characteristics and sharp wave-ripple (SWR) activity in the avian brain.** (A) The zebra finch brain. Histological section stained with cresyl violet indicates the subdivision of the avian pallium. H, hyperpallium; M, mesopallium; N, nidopallium; Str, striatum; DVR, dorsal ventricular ridge. Entopallium and arcopallium are not pictured. Scale bar indicates 1 mm. (B) 5 minutes of raw local field potential (LFP) (black) recorded during natural sleep. Data corresponds to red box in (C). The LFP is composed of distinct states, as evident in the  $\delta/\gamma$  ratio (blue line), where large amplitude LFP coincides with high  $\delta$  power Ref. [161]. (C) NREM and REM sleep stages oscillate throughout the night, as indicated by the changes in the  $\delta/\gamma$  ratio. Vertical axis is the clock time; each row represents 30 minutes of data. Lights off: 20:00 to 8:00 (gray bar). (D) SWR activity recorded from the DVR of an anesthetized zebra finch. Raw LFP traces are organized from most lateral (top) to most medial (bottom). Electrode shanks are separated by 125  $\mu\text{m}$ . Bottom trace, ripple filter (120–250 Hz). SWR in the dotted box is enlarged (right). Vertical scale bar: 200  $\mu\text{V}$ ; horizontal scale bar: 20 ms. (E) Sequences of neural activity are associated with avian SWRs. Top: Raw LFP. Bottom: Colored dots indicate action potentials. Each color indicates a different unit. Vertical scale bar: 200  $\mu\text{V}$ . (F) 850 successive SWRs aligned, for each trace, on the peak negative LFP waveform. Averages for all SWR high pass intensity (HPI, black) and LFP (red) traces are shown below.

like activity patterns arise from both reptilian and avian DVR during sleep suggests that some version of the neural circuit that gives rise to mammalian hippocampal SWRs may also be present in the avian DVR – despite the absence of clear anatomical lamination in the DVR (although see [98]). However, the function of avian SWR-like activity is still a mystery. As proposed by Sherry and Schacter in their landmark paper [166], it is possible that an existing memory system may be co-opted for use in other situations than for which it had been evolutionarily selected. Further work is required to determine whether the SWR-like activity ob-

served in the avian DVR is an “epiphenomenon” related to the ongoing dynamics of the sleeping brain, or whether it has a true function in learning and memory. Experiments that build upon the recent approaches in rodents to block replay in birds would more clearly link the dynamics of replay and memory consolidation in avian models.

As others have highlighted [167], comparative approaches serve as powerful tools in assessing the validity of universal principles in neuroscience research. This is especially true when we consider that for the past decades, the field of neuroscience has been slowly converging on a

few selected model organisms. By diversifying the field of memory research to include alternative animal models and behaviors, we will deepen our existing knowledge about sleep, learning, and memory, and may thereby reveal foundational principles that underlie learning and memory for all animals.

## Disclosure

A previous German version of this paper was published as “Schlaf und Gedächtnis in neuronalen Nicht-Säugetier-Architekturen” in *Neuroforum* (e-ISSN 2363-7013), 2024, Volume 30, Issue 2, [https://nwg-info.de/sites/nwg-info.de/files/media/pdf/neuroforum/Neuroforum\\_02-2024.pdf](https://nwg-info.de/sites/nwg-info.de/files/media/pdf/neuroforum/Neuroforum_02-2024.pdf).

## Author Contributions

JMO prepared the figure and conducted the literature search for the manuscript and wrote the paper. JMO read and approved the final manuscript. JMO has participated sufficiently in the work and agreed to be accountable for all aspects of the work.

## Ethics Approval and Consent to Participate

Not applicable.

## Acknowledgment

The author would like to thank the two anonymous reviewers for their comments on a previous version of this manuscript as well as Harald Luksch for his support of her independent research at his Chair of Zoology at the Technical University of Munich.

## Funding

This research was funded by Deutsche Forschungsgemeinschaft (ON 151/1-1).

## Conflicts of Interest

The author declares no conflicts of interest.

## Declaration of AI and AI-Assisted Technologies in the Writing Process

The author used Google Notebook LM to assemble some of the information in Table 1. After using this tool, the author reviewed the information in the table and takes full responsibility for its contents.

## References

- [1] Davy J. XIV. On the temperature of man. *Philosophical Transactions of the Royal Society of London*. 1845; 319–333. <https://doi.org/10.1098/rstl.1845.0014>.
- [2] Borbély AA. Circadian rhythm of vigilance in rats: modulation by short light-dark cycles. *Neuroscience Letters*. 1975; 1: 67–71. [https://doi.org/10.1016/0304-3940\(75\)90014-2](https://doi.org/10.1016/0304-3940(75)90014-2).
- [3] Loomis AL, Harvey EN, Hobart GA. Cerebral states during sleep, as studied by human brain potentials. *Journal of Experimental Psychology*. 1937; 21: 127–144. <https://doi.org/10.1037/h0057431>.
- [4] Hobson JA, Goin OB, Goin CJ. Electrographic correlates of behaviour in tree frogs. *Nature*. 1968; 220: 386–387. <https://doi.org/10.1038/220386a0>.
- [5] KLEIN M, MICHEL F, JOUVET M. POLYGRAPHIC STUDY OF SLEEP IN BIRDS. *Comptes Rendus des Seances De La Societe De Biologie et De Ses Filiales*. 1964; 158: 99–103.
- [6] Tauber ES, Roffwarg HP, Weitzman ED. Eye movements and electroencephalogram activity during sleep in diurnal lizards. *Nature*. 1966; 212: 1612–1613. <https://doi.org/10.1038/2121612a0>.
- [7] Kayser MS, Yue Z, Sehgal A. A critical period of sleep for development of courtship circuitry and behavior in *Drosophila*. *Science (New York, N.Y.)*. 2014; 344: 269–274. <https://doi.org/10.1126/science.1250553>.
- [8] Chen P, Ban W, Wang W, You Y, Yang Z. The Devastating Effects of Sleep Deprivation on Memory: Lessons from Rodent Models. *Clocks & Sleep*. 2023; 5: 276–294. <https://doi.org/10.3390/clockssleep5020022>.
- [9] Mazzotti DR, Guindalini C, Moraes WADS, Andersen ML, Cendoroglo MS, Ramos LR, *et al.* Human longevity is associated with regular sleep patterns, maintenance of slow wave sleep, and favorable lipid profile. *Frontiers in Aging Neuroscience*. 2014; 6: 134. <https://doi.org/10.3389/fnagi.2014.00134>.
- [10] Jun JJ, Steinmetz NA, Siegle JH, Denman DJ, Bauza M, Barbarits B, *et al.* Fully integrated silicon probes for high-density recording of neural activity. *Nature*. 2017; 551: 232–236. <https://doi.org/10.1038/nature24636>.
- [11] Romero-Ferrero F, Bergomi MG, Hinz RC, Heras FJH, de Polavieja GG. idtracker.ai: tracking all individuals in small or large collectives of unmarked animals. *Nature Methods*. 2019; 16: 179–182. <https://doi.org/10.1038/s41592-018-0295-5>.
- [12] Mathis A, Mamidanna P, Cury KM, Abe T, Murthy VN, Mathis MW, *et al.* DeepLabCut: markerless pose estimation of user-defined body parts with deep learning. *Nature Neuroscience*. 2018; 21: 1281–1289. <https://doi.org/10.1038/s41593-018-0209-y>.
- [13] Pophale A, Shimizu K, Mano T, Iglesias TL, Martin K, Hiroi M, *et al.* Wake-like skin patterning and neural activity during octopus sleep. *Nature*. 2023; 619: 129–134. <https://doi.org/10.1038/s41586-023-06203-4>.
- [14] Shein-Idelson M, Ondracek JM, Liaw HP, Reiter S, Laurent G. Slow waves, sharp waves, ripples, and REM in sleeping dragons. *Science (New York, N.Y.)*. 2016; 352: 590–595. <https://doi.org/10.1126/science.aaf3621>.
- [15] Piéron H. Le problème physiologique du sommeil. 1913.
- [16] Tobler I. Is sleep fundamentally different between mammalian species? *Behavioural Brain Research*. 1995; 69: 35–41. [https://doi.org/10.1016/0166-4328\(95\)00025-o](https://doi.org/10.1016/0166-4328(95)00025-o).
- [17] Tobler I. *Evolution and Comparative Physiology of Sleep in Animals*. *Clinical Physiology of Sleep* (pp. 21–30). Springer New York: New York, NY. 1988. [https://doi.org/10.1007/978-1-4614-7599-6\\_2](https://doi.org/10.1007/978-1-4614-7599-6_2).
- [18] Flanigan WF, Jr, Knight CP, Hartse KM, Rechtschaffen A. Sleep and wakefulness in chelonian reptiles. I. The box turtle, *Terapene carolina*. *Archives Italiennes De Biologie*. 1974; 112: 227–252.
- [19] Flanigan WF, Jr, Wilcox RH, Rechtschaffen A. The EEG and behavioral continuum of the crocodylian, *Caiman sclerops*. *Electroencephalography and Clinical Neurophysiology*. 1973; 34: 521–538. [https://doi.org/10.1016/0013-4694\(73\)90069-2](https://doi.org/10.1016/0013-4694(73)90069-2).
- [20] van Alphen B, Semenza ER, Yap M, van Swinderen B, Allada R. A deep sleep stage in *Drosophila* with a functional role in waste clearance. *Science Advances*. 2021; 7: eabc2999. <https://doi.org/10.1126/sciadv.abc2999>.

- [21] Nath RD, Bedbrook CN, Abrams MJ, Basinger T, Bois JS, Prober DA, *et al.* The Jellyfish *Cassiopea* Exhibits a Sleep-like State. *Current Biology*. CB. 2017; 27: 2984–2990.e3. <https://doi.org/10.1016/j.cub.2017.08.014>.
- [22] Cho JY, Sternberg PW. Multilevel modulation of a sensory motor circuit during *C. elegans* sleep and arousal. *Cell*. 2014; 156: 249–260. <https://doi.org/10.1016/j.cell.2013.11.036>.
- [23] Canavan SV, Margoliash D. Budgerigars have complex sleep structure similar to that of mammals. *PLoS Biology*. 2020; 18: e3000929. <https://doi.org/10.1371/journal.pbio.3000929>.
- [24] Libourel PA, Lee WY, Achin I, Chung H, Kim J, Massot B, *et al.* Nesting chinstrap penguins accrue large quantities of sleep through seconds-long microsleeps. *Science (New York, N.Y.)*. 2023; 382: 1026–1031. <https://doi.org/10.1126/science.adh0771>.
- [25] Low PS, Shank SS, Sejnowski TJ, Margoliash D. Mammalian-like features of sleep structure in zebra finches. *Proceedings of the National Academy of Sciences of the United States of America*. 2008; 105: 9081–9086. <https://doi.org/10.1073/pnas.0703452105>.
- [26] Yeganegi H, Ondracek JM. Multi-channel recordings reveal age-related differences in the sleep of juvenile and adult zebra finches. *Scientific Reports*. 2023; 13: 8607. <https://doi.org/10.1038/s41598-023-35160-1>.
- [27] Lorenz C, Das A, Centeno EGZ, Yeganegi H, Duvoisin R, Ursu R, *et al.* Sharp Waves, Bursts, and Coherence: Activity in a Songbird Vocal Circuit Is Influenced by Behavioral State. *The Journal of Neuroscience: the Official Journal of the Society for Neuroscience*. 2025; 45: e1903242025. <https://doi.org/10.1523/JNEUROSCI.1903-24.2025>.
- [28] Albeck N, Udi DI, Eyal R, Shvartsman A, Shein-Idelson M. Temperature-robust rapid eye movement and slow wave sleep in the lizard *Laudakia vulgaris*. *Communications Biology*. 2022; 5: 1310. <https://doi.org/10.1038/s42003-022-04261-4>.
- [29] Libourel PA, Barrillot B, Arthaud S, Massot B, Morel AL, Beuf O, *et al.* Partial homologies between sleep states in lizards, mammals, and birds suggest a complex evolution of sleep states in amniotes. *PLoS Biology*. 2018; 16: e2005982. <https://doi.org/10.1371/journal.pbio.2005982>.
- [30] Leung LC, Wang GX, Madelaine R, Skariah G, Kawakami K, Deisseroth K, *et al.* Neural signatures of sleep in zebrafish. *Nature*. 2019; 571: 198–204. <https://doi.org/10.1038/s41586-019-1336-7>.
- [31] Barrowclough GF, Cracraft J, Klicka J, Zink RM. How Many Kinds of Birds Are There and Why Does It Matter? *PLoS One*. 2016; 11: e0166307. <https://doi.org/10.1371/journal.pone.0166307>.
- [32] Dewasmes G, Cohen-Adad F, Koubi H, Le Maho Y. Polygraphic and behavioral study of sleep in geese: existence of nuchal atonia during paradoxical sleep. *Physiology & Behavior*. 1985; 35: 67–73. [https://doi.org/10.1016/0031-9384\(85\)90173-8](https://doi.org/10.1016/0031-9384(85)90173-8).
- [33] Rattenborg NC, Mandt BH, Obermeyer WH, Winsauer PJ, Huber R, Wikelski M, *et al.* Migratory sleeplessness in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). *PLoS Biology*. 2004; 2: E212. <https://doi.org/10.1371/journal.pbio.0020212>.
- [34] Szymczak JT, Kaiser W, Helb HW, Beszczyńska B. A study of sleep in the European blackbird. *Physiology & Behavior*. 1996; 60: 1115–1120. [https://doi.org/10.1016/0031-9384\(96\)00231-4](https://doi.org/10.1016/0031-9384(96)00231-4).
- [35] Lesku JA, Rattenborg NC, Valcu M, Vyssotski AL, Kuhn S, Kuemmeth F, *et al.* Adaptive sleep loss in polygynous pectoral sandpipers. *Science (New York, N.Y.)*. 2012; 337: 1654–1658. <https://doi.org/10.1126/science.1220939>.
- [36] Berger RJ, Walker JM. Sleep in the burrowing owl (*Speotyto cunicularia hypugaea*). *Behavioral Biology*. 1972; 7: 183–194. [https://doi.org/10.1016/s0091-6773\(72\)80198-6](https://doi.org/10.1016/s0091-6773(72)80198-6).
- [37] Lesku JA, Meyer LCR, Fuller A, Maloney SK, Dell’Omo G, Vyssotski AL, *et al.* Ostriches sleep like platypuses. *PLoS One*. 2011; 6: e23203. <https://doi.org/10.1371/journal.pone.0023203>.
- [38] Tobler I. Phylogeny of Sleep Regulation. In Kryger MH, Roth T, Dement WC (eds.) *Principles and Practice of Sleep Medicine* (pp. 112–125). 5th edn. Elsevier: St. Louis. 2011. <https://doi.org/10.1016/C2009-0-59875-3>.
- [39] Margoliash D. Song learning and sleep. *Nature Neuroscience*. 2005; 8: 546–548. <https://doi.org/10.1038/nn0505-546>.
- [40] Roth TC, 2nd, Lesku JA, Amlaner CJ, Lima SL. A phylogenetic analysis of the correlates of sleep in birds. *Journal of Sleep Research*. 2006; 15: 395–402. <https://doi.org/10.1111/j.1365-2869.2006.00559.x>.
- [41] Yamaguchi ST, Zhou Z, Norimoto H. Diversity of REM sleep. *Current Opinion in Behavioral Sciences*. 2024; 60: 101457. <https://doi.org/10.1016/j.cobeha.2024.101457>.
- [42] Rattenborg NC, Lima SL, Amlaner CJ. Half-awake to the risk of predation. *Nature*. 1999; 397: 397–398. <https://doi.org/10.1038/17037>.
- [43] Rattenborg NC, Amlaner CJ, Lima SL. Unilateral eye closure and interhemispheric EEG asymmetry during sleep in the pigeon (*Columba livia*). *Brain, Behavior and Evolution*. 2001; 58: 323–332. <https://doi.org/10.1159/000057573>.
- [44] Rattenborg NC, Voirin B, Cruz SM, Tisdale R, Dell’Omo G, Lipp HP, *et al.* Evidence that birds sleep in mid-flight. *Nature Communications*. 2016; 7: 12468. <https://doi.org/10.1038/ncomms12468>.
- [45] Rojas-Ramírez JA, Tauber ES. Paradoxical sleep in two species of avian predator (Falconiformes). *Science (New York, N.Y.)*. 1970; 167: 1754–1755. <https://doi.org/10.1126/science.167.3926.1754>.
- [46] Van Twyver H, Allison T. A polygraphic and behavioral study of sleep in the pigeon (*Columba livia*). *Experimental Neurology*. 1972; 35: 138–153. [https://doi.org/10.1016/0014-4886\(72\)90065-9](https://doi.org/10.1016/0014-4886(72)90065-9).
- [47] Walker JM, Berger RJ. Sleep in the domestic pigeon (*Columba livia*). *Behavioral Biology*. 1972; 7: 195–203. [https://doi.org/10.1016/s0091-6773\(72\)80199-8](https://doi.org/10.1016/s0091-6773(72)80199-8).
- [48] Szymczak JT. Influence of environmental temperature and photoperiod on temporal structure of sleep in corvids. *Acta Neurobiologiae Experimentalis*. 1989; 49: 359–366.
- [49] Tisdale RK, Vyssotski AL, Lesku JA, Rattenborg NC. Sleep-Related Electrophysiology and Behavior of Tinamous (*Eudromia elegans*): Tinamous Do Not Sleep Like Ostriches. *Brain, Behavior and Evolution*. 2017; 89: 249–261. <https://doi.org/10.1159/000475590>.
- [50] van Hasselt SJ, Rusche M, Vyssotski AL, Verhulst S, Rattenborg NC, Meerlo P. The European starling (*Sturnus vulgaris*) shows signs of NREM sleep homeostasis but has very little REM sleep and no REM sleep homeostasis. *Sleep*. 2020; 43: zsz311. <https://doi.org/10.1093/sleep/zsz311>.
- [51] Rattenborg NC, Lima SL, Amlaner CJ. Facultative control of avian unihemispheric sleep under the risk of predation. *Behavioural Brain Research*. 1999; 105: 163–172. [https://doi.org/10.1016/s0166-4328\(99\)00070-4](https://doi.org/10.1016/s0166-4328(99)00070-4).
- [52] Berger RJ, Phillips NH. Energy conservation and sleep. *Behavioural Brain Research*. 1995; 69: 65–73. [https://doi.org/10.1016/0166-4328\(95\)00002-b](https://doi.org/10.1016/0166-4328(95)00002-b).
- [53] McGinty D, Szymusiak R. Keeping cool: a hypothesis about the mechanisms and functions of slow-wave sleep. *Trends in Neurosciences*. 1990; 13: 480–487. [https://doi.org/10.1016/0166-2236\(90\)90081-k](https://doi.org/10.1016/0166-2236(90)90081-k).
- [54] Inoué S, Honda K, Komoda Y. Sleep as neuronal detoxification and restitution. *Behavioural Brain Research*. 1995; 69: 91–96. [https://doi.org/10.1016/0166-4328\(95\)00014-k](https://doi.org/10.1016/0166-4328(95)00014-k).

- [55] Adam K, Oswald I. Sleep is for tissue restoration. *Journal of the Royal College of Physicians of London*. 1977; 11: 376–388.
- [56] Maquet P. The role of sleep in learning and memory. *Science* (New York, N.Y.). 2001; 294: 1048–1052. <https://doi.org/10.1126/science.1062856>.
- [57] Squire LR. Memory and brain systems: 1969–2009. *The Journal of Neuroscience: the Official Journal of the Society for Neuroscience*. 2009; 29: 12711–12716. <https://doi.org/10.1523/JNEUROSCI.3575-09.2009>.
- [58] Zlotnik G, Vansintjan A. Memory: An Extended Definition. *Frontiers in Psychology*. 2019; 10: 2523. <https://doi.org/10.3389/fpsyg.2019.02523>.
- [59] Chambers AM. The role of sleep in cognitive processing: focusing on memory consolidation. *Wiley Interdisciplinary Reviews. Cognitive Science*. 2017; 8: 10.1002/wcs.1433. <https://doi.org/10.1002/wcs.1433>.
- [60] Moscovitch M, Rosenbaum RS, Gilboa A, Addis DR, Westmacott R, Grady C, *et al*. Functional neuroanatomy of remote episodic, semantic and spatial memory: a unified account based on multiple trace theory. *Journal of Anatomy*. 2005; 207: 35–66. <https://doi.org/10.1111/j.1469-7580.2005.00421.x>.
- [61] Dudai Y, Karni A, Born J. The Consolidation and Transformation of Memory. *Neuron*. 2015; 88: 20–32. <https://doi.org/10.1016/j.neuron.2015.09.004>.
- [62] Kandel ER, Dudai Y, Mayford MR. The molecular and systems biology of memory. *Cell*. 2014; 157: 163–186. <https://doi.org/10.1016/j.cell.2014.03.001>.
- [63] Rauchs G, Bertran F, Guillery-Girard B, Desgranges B, Kerrouche N, Denise P, *et al*. Consolidation of strictly episodic memories mainly requires rapid eye movement sleep. *Sleep*. 2004; 27: 395–401. <https://doi.org/10.1093/sleep/27.3.395>.
- [64] Aly M, Moscovitch M. The effects of sleep on episodic memory in older and younger adults. *Memory* (Hove, England). 2010; 18: 327–334. <https://doi.org/10.1080/09658211003601548>.
- [65] Stickgold R. Sleep-dependent memory consolidation. *Nature*. 2005; 437: 1272–1278. <https://doi.org/10.1038/nature04286>.
- [66] Smith C. Sleep states and learning: a review of the animal literature. *Neuroscience and Biobehavioral Reviews*. 1985; 9: 157–168. [https://doi.org/10.1016/0149-7634\(85\)90042-9](https://doi.org/10.1016/0149-7634(85)90042-9).
- [67] Smith C. Sleep states, memory processes and synaptic plasticity. *Behavioural Brain Research*. 1996; 78: 49–56. [https://doi.org/10.1016/0166-4328\(95\)00218-9](https://doi.org/10.1016/0166-4328(95)00218-9).
- [68] Smith C. Sleep states and memory processes. *Behavioural Brain Research*. 1995; 69: 137–145. [https://doi.org/10.1016/0166-4328\(95\)00024-n](https://doi.org/10.1016/0166-4328(95)00024-n).
- [69] Diekelmann S, Born J. Cueing fear memory during sleep—to extinguish or to enhance fear? *Sleep*. 2015; 38: 337–339. <https://doi.org/10.5665/sleep.4484>.
- [70] Alger SE, Lau H, Fishbein W. Slow wave sleep during a daytime nap is necessary for protection from subsequent interference and long-term retention. *Neurobiology of Learning and Memory*. 2012; 98: 188–196. <https://doi.org/10.1016/j.nlm.2012.06.003>.
- [71] Plihal W, Born J. Effects of early and late nocturnal sleep on declarative and procedural memory. *Journal of Cognitive Neuroscience*. 1997; 9: 534–547. <https://doi.org/10.1162/jocn.1997.9.4.534>.
- [72] Yaroush R, Sullivan MJ, Ekstrand BR. Effect of sleep on memory. II. Differential effect of the first and second half of the night. *Journal of Experimental Psychology*. 1971; 88: 361–366. <https://doi.org/10.1037/h0030914>.
- [73] Karni A, Tanne D, Rubenstein BS, Askenasy JJ, Sagi D. Dependence on REM sleep of overnight improvement of a perceptual skill. *Science* (New York, N.Y.). 1994; 265: 679–682. <https://doi.org/10.1126/science.8036518>.
- [74] Maquet P, Laureys S, Peigneux P, Fuchs S, Petiau C, Phillips C, *et al*. Experience-dependent changes in cerebral activation during human REM sleep. *Nature Neuroscience*. 2000; 3: 831–836. <https://doi.org/10.1038/77744>.
- [75] Vertes RP. Memory Consolidation in Sleep: Dream or Reality. *Neuron*. 2004; 44: 135–148. <https://doi.org/10.1016/j.neuron.2004.08.034>.
- [76] Buzsáki G. Two-stage model of memory trace formation: a role for “noisy” brain states. *Neuroscience*. 1989; 31: 551–570. [https://doi.org/10.1016/0306-4522\(89\)90423-5](https://doi.org/10.1016/0306-4522(89)90423-5).
- [77] Girardeau G, Zugaro M. Hippocampal ripples and memory consolidation. *Current Opinion in Neurobiology*. 2011; 21: 452–459. <https://doi.org/10.1016/j.conb.2011.02.005>.
- [78] Wilson MA, McNaughton BL. Reactivation of hippocampal ensemble memories during sleep. *Science* (New York, N.Y.). 1994; 265: 676–679. <https://doi.org/10.1126/science.8036517>.
- [79] Buzsáki G. Hippocampal sharp wave-ripple: A cognitive biomarker for episodic memory and planning. *Hippocampus*. 2015; 25: 1073–1188. <https://doi.org/10.1002/hipo.22488>.
- [80] Skaggs WE, McNaughton BL. Replay of neuronal firing sequences in rat hippocampus during sleep following spatial experience. *Science* (New York, N.Y.). 1996; 271: 1870–1873. <https://doi.org/10.1126/science.271.5257.1870>.
- [81] Pavlides C, Winson J. Influences of hippocampal place cell firing in the awake state on the activity of these cells during subsequent sleep episodes. *The Journal of Neuroscience: the Official Journal of the Society for Neuroscience*. 1989; 9: 2907–2918. <https://doi.org/10.1523/JNEUROSCI.09-08-02907.1989>.
- [82] O’Neill J, Senior TJ, Allen K, Huxter JR, Csicsvari J. Reactivation of experience-dependent cell assembly patterns in the hippocampus. *Nature Neuroscience*. 2008; 11: 209–215. <https://doi.org/10.1038/nn2037>.
- [83] Girardeau G, Benchenane K, Wiener SI, Buzsáki G, Zugaro MB. Selective suppression of hippocampal ripples impairs spatial memory. *Nature Neuroscience*. 2009; 12: 1222–1223. <https://doi.org/10.1038/nn.2384>.
- [84] Ego-Stengel V, Wilson MA. Disruption of ripple-associated hippocampal activity during rest impairs spatial learning in the rat. *Hippocampus*. 2010; 20: 1–10. <https://doi.org/10.1002/hipo.20707>.
- [85] Khodagholy D, Gelinas JN, Buzsáki G. Learning-enhanced coupling between ripple oscillations in association cortices and hippocampus. *Science* (New York, N.Y.). 2017; 358: 369–372. <https://doi.org/10.1126/science.aan6203>.
- [86] Norimoto H, Makino K, Gao M, Shikano Y, Okamoto K, Ishikawa T, *et al*. Hippocampal ripples down-regulate synapses. *Science* (New York, N.Y.). 2018; 359: 1524–1527. <https://doi.org/10.1126/science.aao0702>.
- [87] Siapas AG, Wilson MA. Coordinated interactions between hippocampal ripples and cortical spindles during slow-wave sleep. *Neuron*. 1998; 21: 1123–1128. [https://doi.org/10.1016/S0896-6273\(00\)80629-7](https://doi.org/10.1016/S0896-6273(00)80629-7).
- [88] Ochoterena H, Vrijdaghs A, Smets E, Claßen-Bockhoff R. The Search for Common Origin: Homology Revisited. *Systematic Biology*. 2019; 68: 767–780. <https://doi.org/10.1093/sysbio/syz013>.
- [89] Woych J, Ortega Gurrola A, Deryckere A, Jaeger ECB, Gumnit E, Merello G, *et al*. Cell-type profiling in salamanders identifies innovations in vertebrate forebrain evolution. *Science* (New York, N.Y.). 2022; 377: eabp9186. <https://doi.org/10.1126/science.abp9186>.
- [90] Naumann RK, Ondracek JM, Reiter S, Shein-Idelson M, Tosches MA, Yamawaki TM, *et al*. The reptilian brain. *Current Biology: CB*. 2015; 25: R317–R321. <https://doi.org/10.1016/j.cub.2015.02.049>.
- [91] Puelles L. Thoughts on the development, structure and evolution of the mammalian and avian telencephalic pallium. *Philosophical Transactions of the Royal Society of London. Series B,*

- Biological Sciences. 2001; 356: 1583–1598. <https://doi.org/10.1098/rstb.2001.0973>.
- [92] Striedter GF. Evolution of the hippocampus in reptiles and birds. *The Journal of Comparative Neurology*. 2016; 524: 496–517. <https://doi.org/10.1002/cne.23803>.
- [93] Herold C, Schlömer P, Mafoppa-Fomat I, Mehlhorn J, Amunts K, Axer M. The hippocampus of birds in a view of evolutionary connectomics. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*. 2019; 118: 165–187. <https://doi.org/10.1016/j.cortex.2018.09.025>.
- [94] Ulinski PS. *Dorsal ventricular ridge: a treatise on forebrain organization in reptiles and birds*. J. Wiley: New York. 1983.
- [95] Garcia-Calero E, Puelles L. Development of the mouse anterior amygdalar radial unit marked by Lhx9-expression. *Brain Structure & Function*. 2021; 226: 575–600. <https://doi.org/10.1007/s00429-020-02201-8>.
- [96] Briscoe SD, Albertin CB, Rowell JJ, Ragsdale CW. Neocortical Association Cell Types in the Forebrain of Birds and Alligators. *Current Biology: CB*. 2018; 28: 686–696.e6. <https://doi.org/10.1016/j.cub.2018.01.036>.
- [97] Tosches MA, Yamawaki TM, Naumann RK, Jacobi AA, Tushkev G, Laurent G. Evolution of pallium, hippocampus, and cortical cell types revealed by single-cell transcriptomics in reptiles. *Science (New York, N.Y.)*. 2018; 360: 881–888. <https://doi.org/10.1126/science.aar4237>.
- [98] Stacho M, Herold C, Rook N, Wagner H, Axer M, Amunts K, *et al.* A cortex-like canonical circuit in the avian forebrain. *Science (New York, N.Y.)*. 2020; 369: eabc5534. <https://doi.org/10.1126/science.abc5534>.
- [99] Colquitt BM, Merullo DP, Konopka G, Roberts TF, Brainard MS. Cellular transcriptomics reveals evolutionary identities of songbird vocal circuits. *Science (New York, N.Y.)*. 2021; 371: eabd9704. <https://doi.org/10.1126/science.abd9704>.
- [100] Spool JA, Macedo-Lima M, Scarpa G, Morohashi Y, Yazaki-Sugiyama Y, Ramage-Healey L. Genetically identified neurons in avian auditory pallium mirror core principles of their mammalian counterparts. *Current Biology: CB*. 2021; 31: 2831–2843.e6. <https://doi.org/10.1016/j.cub.2021.04.039>.
- [101] Tosches MA. Different origins for similar brain circuits. *Science (New York, N.Y.)*. 2021; 371: 676–677. <https://doi.org/10.1126/science.abf9551>.
- [102] Güntürkün O. The avian ‘prefrontal cortex’ and cognition. *Current Opinion in Neurobiology*. 2005; 15: 686–693. <https://doi.org/10.1016/j.conb.2005.10.003>.
- [103] Nieder A. Inside the corvid brain—probing the physiology of cognition in crows. *Current Opinion in Behavioral Sciences*. 2017; 16: 8–14. <https://doi.org/10.1016/j.cobeha.2017.02.005>.
- [104] Ditz HM, Nieder A. Format-dependent and format-independent representation of sequential and simultaneous numerosity in the crow endbrain. *Nature Communications*. 2020; 11: 686. <https://doi.org/10.1038/s41467-020-14519-2>.
- [105] Veit L, Nieder A. Abstract rule neurons in the endbrain support intelligent behaviour in corvid songbirds. *Nature Communications*. 2013; 4: 2878. <https://doi.org/10.1038/ncomms3878>.
- [106] Nieder A, Wagnen L, Rinnert P. A neural correlate of sensory consciousness in a corvid bird. *Science (New York, N.Y.)*. 2020; 369: 1626–1629. <https://doi.org/10.1126/science.abb1447>.
- [107] Bolhuis JJ, Zijlstra GG, den Boer-Visser AM, Van Der Zee EA. Localized neuronal activation in the zebra finch brain is related to the strength of song learning. *Proceedings of the National Academy of Sciences of the United States of America*. 2000; 97: 2282–2285. <https://doi.org/10.1073/pnas.030539097>.
- [108] Gobes SMH, Zandbergen MA, Bolhuis JJ. Memory in the making: localized brain activation related to song learning in young songbirds. *Proceedings. Biological Sciences*. 2010; 277: 3343–3351. <https://doi.org/10.1098/rspb.2010.0870>.
- [109] Chew SJ, Vicario DS, Nottebohm F. A large-capacity memory system that recognizes the calls and songs of individual birds. *Proceedings of the National Academy of Sciences of the United States of America*. 1996; 93: 1950–1955. <https://doi.org/10.1073/pnas.93.5.1950>.
- [110] Yanagihara S, Yazaki-Sugiyama Y. Auditory experience-dependent cortical circuit shaping for memory formation in bird song learning. *Nature Communications*. 2016; 7: 11946. <https://doi.org/10.1038/ncomms11946>.
- [111] Gentner TQ, Margoliash D. Neuronal populations and single cells representing learned auditory objects. *Nature*. 2003; 424: 669–674. <https://doi.org/10.1038/nature01731>.
- [112] Gill P, Woolley SMN, Fremouw T, Theunissen FE. What’s that sound? Auditory area CLM encodes stimulus surprise, not intensity or intensity changes. *Journal of Neurophysiology*. 2008; 99: 2809–2820. <https://doi.org/10.1152/jn.01270.2007>.
- [113] Roberts TF, Hisey E, Tanaka M, Kearney MG, Chattree G, Yang CF, *et al.* Identification of a motor-to-auditory pathway important for vocal learning. *Nature Neuroscience*. 2017; 20: 978–986. <https://doi.org/10.1038/nn.4563>.
- [114] Elmaleh M, Kranz D, Asensio AC, Moll FW, Long MA. Sleep replay reveals premotor circuit structure for a skilled behavior. *Neuron*. 2021; 109: 3851–3861.e4. <https://doi.org/10.1016/j.neuron.2021.09.021>.
- [115] Elmaleh M, Yang Z, Ackert-Smith LA, Long MA. Uncoordinated sleep replay across hemispheres in the zebra finch. *Current Biology: CB*. 2023; 33: 4704–4712.e3. <https://doi.org/10.1016/j.cub.2023.09.005>.
- [116] Shank SS, Margoliash D. Sleep and sensorimotor integration during early vocal learning in a songbird. *Nature*. 2009; 458: 73–77. <https://doi.org/10.1038/nature07615>.
- [117] Horn G. Pathways of the past: the imprint of memory. *Nature Reviews. Neuroscience*. 2004; 5: 108–120. <https://doi.org/10.1038/nrn1324>.
- [118] Jackson C, McCabe BJ, Nicol AU, Grout AS, Brown MW, Horn G. Dynamics of a memory trace: effects of sleep on consolidation. *Current Biology: CB*. 2008; 18: 393–400. <https://doi.org/10.1016/j.cub.2008.01.062>.
- [119] McCabe BJ, Horn G, Bateson PP. Effects of restricted lesions of the chick forebrain on the acquisition of filial preferences during imprinting. *Brain Research*. 1981; 205: 29–37. [https://doi.org/10.1016/0006-8993\(81\)90717-4](https://doi.org/10.1016/0006-8993(81)90717-4).
- [120] Horn G, McCabe BJ. Predispositions and preferences. Effects on imprinting of lesions to the chick brain. *Animal Behaviour*. 1984; 32: 288–292. [https://doi.org/10.1016/S0003-3472\(84\)80349-8](https://doi.org/10.1016/S0003-3472(84)80349-8).
- [121] McCabe BJ, Cipolla-Neto J, Horn G, Bateson P. Amnesic effects of bilateral lesions placed in the hyperstriatum ventrale of the chick after imprinting. *Experimental Brain Research*. 1982; 48: 13–21. <https://doi.org/10.1007/BF00239568>.
- [122] Patel SN, Clayton NS, Krebs JR. Hippocampal tissue transplants reverse lesion-induced spatial memory deficits in zebra finches (*Taeniopygia guttata*). *The Journal of Neuroscience: the Official Journal of the Society for Neuroscience*. 1997; 17: 3861–3869. <https://doi.org/10.1523/JNEUROSCI.17-10-03861.1997>.
- [123] Lormant F, Cornilleau F, Constantin P, Meurisse M, Lansade L, Leterrier C, *et al.* A trait for a high emotionality favors spatial memory to the detriment of cue-based memory in Japanese quail. *Behavioural Processes*. 2018; 157: 256–262. <https://doi.org/10.1016/j.beproc.2018.10.006>.
- [124] Lormant F, Cornilleau F, Constantin P, Meurisse M, Lansade L, Leterrier C, *et al.* Research Note: Role of the hippocampus in spatial memory in Japanese quail. *Poultry Science*. 2020; 99: 61–66. <https://doi.org/10.3382/ps/pez507>.
- [125] Bingman VP, Ioalé P, Casini G, Bagnoli P. Unimpaired

- acquisition of spatial reference memory, but impaired homing performance in hippocampal-ablated pigeons. *Behavioural Brain Research*. 1988; 27: 179–187. [https://doi.org/10.1016/0166-4328\(88\)90043-5](https://doi.org/10.1016/0166-4328(88)90043-5).
- [126] Bingman VP, Ioalé P, Casini G, Bagnoli P. The avian hippocampus: evidence for a role in the development of the homing pigeon navigational map. *Behavioral Neuroscience*. 1990; 104: 906–911. <https://doi.org/10.1037//0735-7044.104.6.906>.
- [127] Hampton RR, Shettleworth SJ. Hippocampal lesions impair memory for location but not color in passerine birds. *Behavioral Neuroscience*. 1996; 110: 831–835. <https://doi.org/10.1037//0735-7044.110.4.831>.
- [128] Shiflett MW, Smulders TV, Benedict L, DeVoogd TJ. Reversible inactivation of the hippocampal formation in food-storing black-capped chickadees (*Poecile atricapillus*). *Hippocampus*. 2003; 13: 437–444. <https://doi.org/10.1002/hipo.10065>.
- [129] Shiflett MW, Tomaszycski ML, Rankin AZ, DeVoogd TJ. Long-term memory for spatial locations in a food-storing bird (*Poecile atricapilla*) requires activation of NMDA receptors in the hippocampal formation during learning. *Behavioral Neuroscience*. 2004; 118: 121–130. <https://doi.org/10.1037//0735-7044.118.1.121>.
- [130] Clayton NS, Yu KS, Dickinson A. Interacting Cache memories: evidence for flexible memory use by Western Scrub-Jays (*Aphelocoma californica*). *Journal of Experimental Psychology. Animal Behavior Processes*. 2003; 29: 14–22.
- [131] Clayton NS, Dickinson A. Episodic-like memory during cache recovery by scrub jays. *Nature*. 1998; 395: 272–274. <https://doi.org/10.1038/26216>.
- [132] Clayton NS, Dally J, Gilbert J, Dickinson A. Food caching by western scrub-jays (*Aphelocoma californica*) is sensitive to the conditions at recovery. *Journal of Experimental Psychology. Animal Behavior Processes*. 2005; 31: 115–124. <https://doi.org/10.1037//0097-7403.31.2.115>.
- [133] Chettih SN, Mackevicius EL, Hale S, Aronov D. Barcoding of episodic memories in the hippocampus of a food-caching bird. *Cell*. 2024; 187: 1922–1935.e20. <https://doi.org/10.1016/j.cell.2024.02.032>.
- [134] Davies JR, Keuneke LS, Clayton NS, Davidson GL. Episodic-like memory in wild free-living blue tits and great tits. *Current Biology: CB*. 2024; 34: 3593–3602.e5. <https://doi.org/10.1016/j.cub.2024.06.029>.
- [135] Brawn TP, Nusbaum HC, Margoliash D. Sleep-dependent consolidation of auditory discrimination learning in adult starlings. *The Journal of Neuroscience: the Official Journal of the Society for Neuroscience*. 2010; 30: 609–613. <https://doi.org/10.1523/JNEUROSCI.4237-09.2010>.
- [136] Brawn TP, Nusbaum HC, Margoliash D. Sleep consolidation of interfering auditory memories in starlings. *Psychological Science*. 2013; 24: 439–447. <https://doi.org/10.1177/0956797612457391>.
- [137] Davies JR, Garcia-Pelegrin E, Clayton NS. Eurasian jays (*Garulus glandarius*) show episodic-like memory through the incidental encoding of information. *PloS One*. 2024; 19: e0301298. <https://doi.org/10.1371/journal.pone.0301298>.
- [138] Adret P. Operant conditioning, song learning and imprinting to taped song in the zebra finch. *Animal Behaviour*. 1993; 46: 149–159. <https://doi.org/10.1006/anbe.1993.1170>.
- [139] Derégnaucourt S, Poirier C, Kant AVD, Linden AVD, Gahr M. Comparisons of different methods to train a young zebra finch (*Taeniopygia guttata*) to learn a song. *Journal of Physiology, Paris*. 2013; 107: 210–218. <https://doi.org/10.1016/j.jphysparis.2012.08.003>.
- [140] Brainard MS, Doupe AJ. What songbirds teach us about learning. *Nature*. 2002; 417: 351–358. <https://doi.org/10.1038/417351a>.
- [141] Konishi M. The role of auditory feedback in the control of vocalization in the white-crowned sparrow. *Zeitschrift Fur Tierpsychologie*. 1965; 22: 770–783.
- [142] Konishi M. The role of auditory feedback in birdsong. *Annals of the New York Academy of Sciences*. 2004; 1016: 463–475. <https://doi.org/10.1196/annals.1298.010>.
- [143] Margoliash D, Schmidt MF. Sleep, off-line processing, and vocal learning. *Brain and Language*. 2010; 115: 45–58. <https://doi.org/10.1016/j.bandl.2009.09.005>.
- [144] Jarvis ED. Learned birdsong and the neurobiology of human language. *Annals of the New York Academy of Sciences*. 2004; 1016: 749–777. <https://doi.org/10.1196/annals.1298.038>.
- [145] Cipolla-Neto J, Horn G, McCabe BJ. Hemispheric asymmetry and imprinting: the effect of sequential lesions to the hyperstriatum ventrale. *Experimental Brain Research*. 1982; 48: 22–27. <https://doi.org/10.1007/BF00239569>.
- [146] Burgess N, Maguire EA, O'Keefe J. The human hippocampus and spatial and episodic memory. *Neuron*. 2002; 35: 625–641. [https://doi.org/10.1016/s0896-6273\(02\)00830-9](https://doi.org/10.1016/s0896-6273(02)00830-9).
- [147] Healy SD, Hurly TA, Godard J, Tello-Ramos M. The function of episodic memory in animals. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*. 2024; 379: 20230403. <https://doi.org/10.1098/rstb.2023.0403>.
- [148] Clayton NS, Griffiths DP, Emery NJ, Dickinson A. Elements of episodic-like memory in animals. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*. 2001; 356: 1483–1491. <https://doi.org/10.1098/rstb.2001.0947>.
- [149] Jelbert SA, Hurly TA, Marshall RES, Healy SD. Wild, free-living hummingbirds can learn what happened, where and in which context. *Animal Behaviour*. 2014; 89: 185–189. <https://doi.org/10.1016/j.anbehav.2013.12.028>.
- [150] Margoliash D, Brawn TP. Sleep and Learning in Birds: Rats! There's More to Sleep. *Sleep and Brain Activity*. 2012; 53: 109–146. <https://doi.org/10.1016/B978-0-12-384995-3.00006-X>.
- [151] Derégnaucourt S, Mitra PP, Fehér O, Pytte C, Tchernichovski O. How sleep affects the developmental learning of bird song. *Nature*. 2005; 433: 710–716. <https://doi.org/10.1038/nature03275>.
- [152] Phan ML, Pytte CL, Vicario DS. Early auditory experience generates long-lasting memories that may subserve vocal learning in songbirds. *Proceedings of the National Academy of Sciences of the United States of America*. 2006; 103: 1088–1093. <https://doi.org/10.1073/pnas.0510136103>.
- [153] Dave AS, Margoliash D. Song replay during sleep and computational rules for sensorimotor vocal learning. *Science (New York, N.Y.)*. 2000; 290: 812–816. <https://doi.org/10.1126/science.290.5492.812>.
- [154] Rausche PL, Chi Z, Dave AS, Margoliash D. Neuronal stability and drift across periods of sleep: premotor activity patterns in a vocal control nucleus of adult zebra finches. *The Journal of Neuroscience: the Official Journal of the Society for Neuroscience*. 2010; 30: 2783–2794. <https://doi.org/10.1523/JNEUROSCI.3112-09.2010>.
- [155] Young BK, Mindlin GB, Arneodo E, Goller F. Adult zebra finches rehearse highly variable song patterns during sleep. *PeerJ*. 2017; 5: e4052. <https://doi.org/10.7717/peerj.4052>.
- [156] McCoy JG, Christie MA, Kim Y, Brennan R, Poeta DL, McCarley RW, *et al*. Chronic sleep restriction impairs spatial memory in rats. *Neuroreport*. 2013; 24: 91–95. <https://doi.org/10.1097/WNR.0b013e32835cd97a>.
- [157] Orban P, Rauchs G, Balteau E, Degueldre C, Luxen A, Maquet P, *et al*. Sleep after spatial learning promotes covert reorganization of brain activity. *Proceedings of the National Academy of Sciences of the United States of America*. 2006; 103: 7124–7129. <https://doi.org/10.1073/pnas.0510198103>.

- [158] Nelini C, Bobbo D, Mascetti GG. Local sleep: a spatial learning task enhances sleep in the right hemisphere of domestic chicks (*Gallus gallus*). *Experimental Brain Research*. 2010; 205: 195–204. <https://doi.org/10.1007/s00221-010-2352-x>.
- [159] Nelini C, Bobbo D, Mascetti GG. Monocular learning of a spatial task enhances sleep in the right hemisphere of domestic chicks (*Gallus gallus*). *Experimental Brain Research*. 2012; 218: 381–388. <https://doi.org/10.1007/s00221-012-3023-x>.
- [160] Poo MM, Pignatelli M, Ryan TJ, Tonegawa S, Bonhoeffer T, Martin KC, *et al.* What is memory? The present state of the engram. *BMC Biology*. 2016; 14: 40. <https://doi.org/10.1186/s12915-016-0261-6>.
- [161] Yeganegi H, Luksch H, Ondracek JM. Hippocampal-like network dynamics underlie avian sharp wave-ripples. *bioRxiv*. 2019; 825075. <https://doi.org/10.1101/825075>. (preprint)
- [162] Payne HL, Lynch GF, Aronov D. Neural representations of space in the hippocampus of a food-caching bird. *Science*. 2021; 373: 343–348. <https://doi.org/10.1126/science.abg2009>.
- [163] Csicsvari J, Hirase H, Czurko A, Buzsáki G. Reliability and state dependence of pyramidal cell-interneuron synapses in the hippocampus: an ensemble approach in the behaving rat. *Neuron*. 1998; 21: 179–189. [https://doi.org/10.1016/s0896-6273\(00\)80525-5](https://doi.org/10.1016/s0896-6273(00)80525-5).
- [164] Yeganegi H, Ondracek JM. Local sleep in songbirds: different simultaneous sleep states across the avian pallium. *Journal of Sleep Research*. 2025; 34: e14344. <https://doi.org/10.1111/jsr.14344>.
- [165] Rasch B, Born J. About sleep's role in memory. *Physiological Reviews*. 2013; 93: 681–766. <https://doi.org/10.1152/physrev.00032.2012>.
- [166] Sherry DF, Schacter DL. The Evolution of Multiple Memory Systems. *Psychological Review - PSYCHOL REV*. 1987; 94: 439–454. <https://doi.org/10.1037//0033-295X.94.4.439>.
- [167] Yartsev MM. The emperor's new wardrobe: Rebalancing diversity of animal models in neuroscience research. *Science (New York, N.Y.)*. 2017; 358: 466–469. <https://doi.org/10.1126/science.aan8865>.