

# Mammalian-like features of sleep structure in zebra finches

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**A suite of complex electroencephalographic patterns of sleep occurs in mammals. In sleeping zebra finches, we observed slow wave sleep (SWS), rapid eye movement (REM) sleep, an intermediate sleep (IS) stage commonly occurring in, but not limited to, transitions between other stages, and high amplitude transients reminiscent of K-complexes. SWS density decreased whereas REM density increased throughout the night, with late-night characterized by substantially more REM than SWS, and relatively long bouts of REM. Birds share many features of sleep in common with mammals, but this collective suite of characteristics had not been known in any one species outside of mammals. We hypothesize that shared, ancestral characteristics of sleep in amniotes evolved under selective pressures common to songbirds and mammals, resulting in convergent characteristics of sleep.**

birds | EEG | evolution | mammals | automation

In mammals, a typical night of sleep is composed by successive episodes of slow wave sleep (SWS), intermediate sleep (IS), and rapid eye movement (REM) sleep. In humans, IS and SWS are further subdivided into stages I and II and into stages III and IV, respectively. REM sleep is also strongly associated with vivid dreaming in humans. IS tends to act as a transition state between SWS and REM. Throughout the night, there is typically a progression toward less SWS and more REM sleep. Electroencephalograms (EEGs) associated with these sleep stages follow a 1/f distribution, i.e., higher frequencies in the EEG have smaller raw amplitudes and thus less spectral power. SWS is characterized by a high amplitude and low frequency EEG signal whereas REM sleep corresponds to a more “awake-like” raw signal with lower amplitudes and higher frequencies (1, 2). Brief EEG landmarks known as spindles and K-complexes are often seen in non-REM sleep (NREM) (1, 3, 4). Because this suite of characteristics has never been observed outside of mammals, it has been proposed that the cortex was necessary for its generation (5, 6).

It is now well established that avian and mammalian forebrain organization share far more commonalities than has traditionally been recognized (7). These similarities are observed at molecular, cellular, and systems levels (8). A new terminology has been created to correct misconceptions especially regarding the avian forebrain, and which recognizes forebrain homologies comparing birds and mammals (8, 9). Of relevance to this report, direct reciprocal thalamocortical projections have been implicated in generation of sleep rhythms in mammals (6). These projections are not known in birds, but recent studies have identified descending recurrent projections of sensory pathways in birds that might serve similar functional roles, for example in the auditory system (10, 11).

Both REM and NREM are known for birds, with sleep in most species being dominated by NREM with brief REM episodes (12), although passerine birds exhibit greater amounts of REM (13, 14). Circadian patterns in REM and NREM are commonly known in birds (15), and there is also fragmentary evidence regarding other characteristics (16). From these bases, and given

our interest in sleep-dependent mechanisms of birdsong learning, we explored the organization of sleep states in zebra finches.

## Results

We chronically implanted five birds with EEG electrodes, three with bilateral electrode pairs. From the recordings made after birds acclimated to the recording environment (including a cable leading to an overhead commutator), one full-night record was selected for each bird. These records were characterized by good quality EEG signals with relatively few movement-related or other artifacts and video monitoring of eye movements throughout the night (see *Experimental Procedures*). Sleep is associated with species-specific postures. Zebra finches commonly adopt a head-forward position and occasionally a head-backward position during sleep. Our birds adopted both positions. Although we did not assess the relative frequency of these two behaviors compared with controls, this observation suggests that the birds experienced relatively undisturbed sleep in our experimental conditions.

The EEG data from these recordings were scored both manually and automatically. Manual scoring relied on visual inspection of EEGs in parallel with scoring of overt behaviors such as eye, head, and body movements. Sleep stages were scored in 3-s epochs to achieve sufficient temporal resolution for the rapid stage transitions commonly observed. Manual scoring classified each epoch as either REM, NREM, or awake. REM occurred reliably in conjunction with eye and low-amplitude head movements, as seen in other species (3, 17). The eye movements were on the order of one saccade per second. The head movements were not as reliable, but tended to follow the directional movement of the eyes when present. As well as visible differences in EEG waveforms, during NREM birds breathed slowly and regularly; eye and head movements were slow and infrequent, did not follow a stereotypical pattern, and were quite distinct from those in REM [[supporting information \(SI\) Movies S1 and S2](#)].

Manual scoring was applied to 3-s contiguous epochs and produced three different designations: REM, NREM, and AWAKE. Automated scoring complemented manual scoring insofar as it relied on manual scoring for wakefulness and allowed for the identification of an IS category that was observed

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but not systematically recorded by the human scorer. The automated scoring was applied to EEG power spectra from 3-s epochs with a 1-s sliding window, computed by using two orthogonal tapers following a standard multitaper estimation technique (18) on sleep data devoid of artifacts. Every third score produced by the algorithm was compared against the manual score, because the algorithm and the manual score had a 1-s and a 3-s resolution, respectively. The algorithm produced a SWS, REM, and IS designation and used the manual scorer's classification of Wakefulness. Thus, for the algorithm, NREM is further subdivided into SWS and the much shorter IS. The automated scoring initially subdivided the sleep data into REM, NREM, SWS, and non-SWS (NSWS). Epochs that were scored neither as REM nor as SWS were labeled as IS. Epochs that were automatically labeled as both REM and SWS were relabeled as outliers. There were very few outliers in the data (SI Table S1). Disagreement between the human and automated scores would occur only if the human scorer or the automated algorithm would classify the same epoch as REM (the human scorer would call the epoch NREM or the algorithm would classify it as SWS or IS). The overall agreement rate was  $84.30 \pm 3.81\%$  (mean  $\pm$  SEM) (Table S1 and Figs. S1 and S4). Ultradian distributions for SWS and REM were apparent from the automated and manual scores alike.

Full night spectrograms of the EEG signals identified temporal variations in power in the 1- to 4-Hz (delta) and 30- to 55-Hz (gamma) frequency bands, which were selected for automated classification of sleep stages. The interdigitation of power in delta and gamma observed in the birds was similar to interdigitation of low and high frequencies reported for cat cortical local field potentials (LFPs) (19) and was highly apparent in two birds (Fig. 1 *a* and *b*). The power in delta was used to separate SWS from NSWS. Because REM was not linearly separable from NREM in gamma, the power ratio gamma/delta was used as a more robust parameter to extract REM. This separation of epochs into different stages was accomplished by using a k-means clustering algorithm. Three additional variables were included for both separations: the standard deviation of the 3-s waveform and the absolute values of the differences in delta power and gamma/delta between successive and preceding epochs. REM epochs formed segments that punctured the sleep data in the latter variable at a 1-s temporal resolution (Fig. S1).

As expected from K-means clustering, a multivariate ANOVA on the five-dimensional clustering space separated REM, SWS, and IS ( $P < 0.001$ ) in each bird. When plotting delta, gamma/delta, and the differences in gamma/delta, SWS would form a spear along delta and the differences in gamma/delta, because, during SWS epochs, the gamma/delta ratio was not only low but also stable across successive epochs as well (Fig. 1*c*). Conversely, when the differences in gamma/delta were replaced by the differences in delta, REM sleep would now collapse into a spear (Fig. 1*d*) as variations in delta tended to be small in REM sleep. The intermediate state can here be thought of as the only sleep state that does not collapse into either spear in the two aforementioned parameter spaces. IS has previously been reported only in mammals (3, 4, 20, 21).

The REM, SWS, and IS epochs could also be visualized in a 3D space defined by a principal component analysis (PCA) of the five-dimensional space spanned by delta, gamma, the standard deviation of each waveform, and the temporal variations in delta and delta/gamma. The three sleep stages occupied separate regions in the 3D space (Fig. 1*e*). SWS and REM formed orthogonal planes in this space, with IS corresponding to a warped transitional region linking the two planes (Fig. 1*f*). A similar 3D structure was observed when PCA was applied to data from each of the five birds (Fig. S2).

Each sleep stage was associated with specific EEG characteristics. SWS had a high amplitude EEG signal with significant

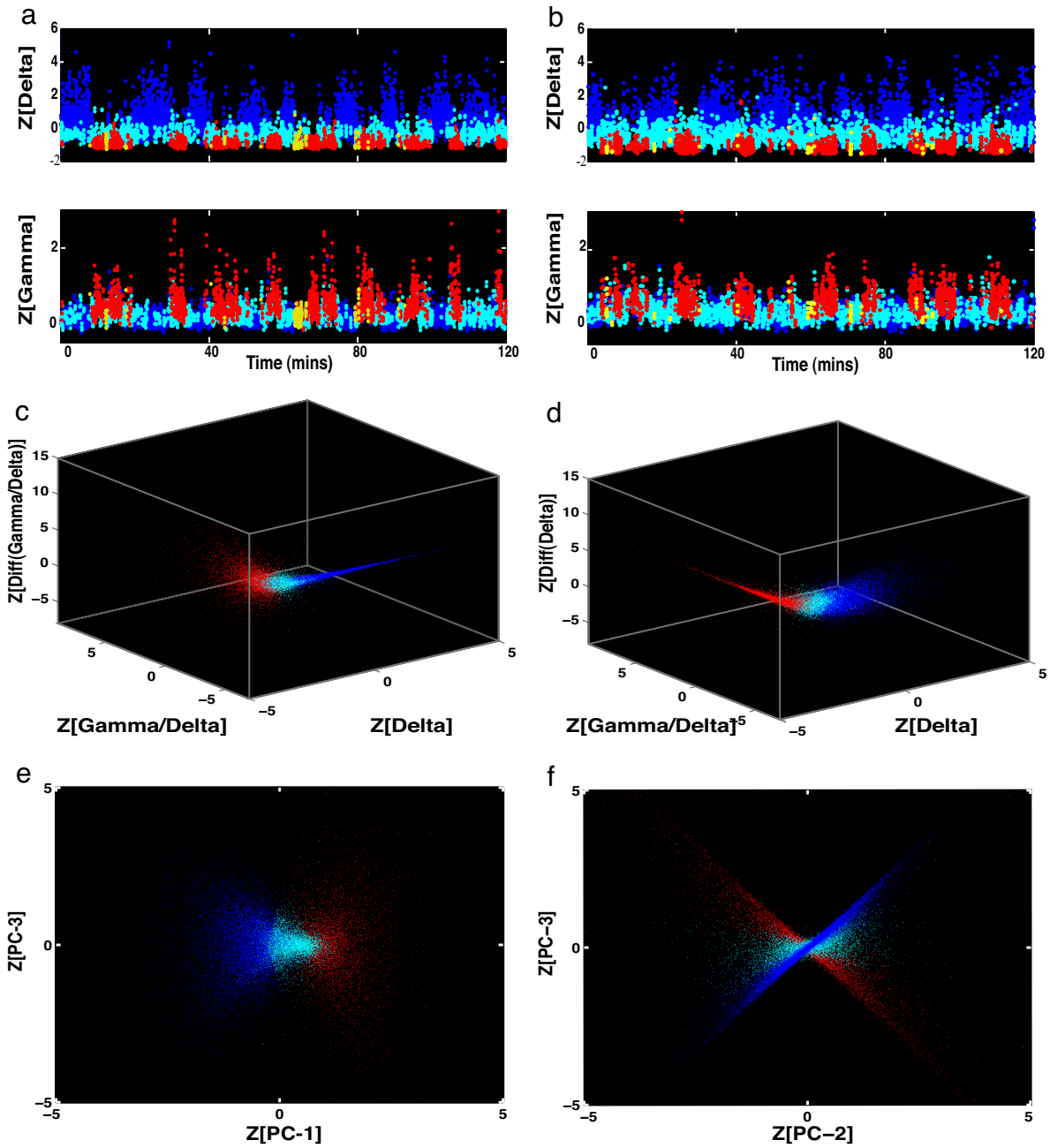
power in the delta range (Figs. 1 *a–d* and 2*a*), as has been observed in mammals. REM was characterized by a very low amplitude “awake-like” EEG signal (Fig. 2 *b* and *e*), typically approximately  $\pm 30 \mu\text{V}$  with higher power in gamma (Fig. 1 *a* and *b*) than NREM, also consistent with REM in mammals (1, 2, 22). Birds with relatively little power increase in the 30- to 55-Hz range for REM had a greater power increase in the 70- to 100-Hz range. IS had highly variable amplitude, typically centered approximately  $\pm 50 \mu\text{V}$  and did not have significant power in either the delta or gamma ranges (Figs. 1 *a–d* and 2*c*). Large, brief amplitude transients observed in NREM sleep, with biphasic waveforms, were observed in two birds (Fig. 2*d* and Table S2). These transients are reminiscent of mammalian K-complexes (1). Mammalian-like spindles were not reliably observed in NREM (higher frequency and shorter spindle-like landmarks were very occasionally but not reliably observed). As in mammals, all birds exhibited a 1/f type pattern, i.e., higher frequencies had lower power (Fig. 3).

We also observed instances when one eye was open and the other was closed. The hemisphere contralateral to the open eye displayed a low amplitude and high frequency EEG whereas the hemisphere contralateral to the closed eye displayed SWS oscillations (Fig. 2*f*). These instances of unihemispheric sleep were almost exclusively restricted to the light phase, and were especially frequent toward the end of the subjective day when birds had a greater tendency to nap (Table S1). Unihemispheric sleep is broadly observed in birds, cetaceans, and other marine mammals (23, 24).

SWS and REM sleep were associated with specific circadian patterns, whose structure was not constrained by our classification procedure for the epochs. There was an overall decrease in SWS density throughout the night (Fig. 4*a*, Fig. S3*a*, and Table S1). REM episodes were typically brief early in the night and became longer throughout the night (Fig. 4*c*, Fig. S3*c*, and Table S1) as the REM density increased (Fig. 4*b*, Fig. S3*b*, and Table S1) and the inter-REM intervals decreased (Fig. 4*d*, Fig. S3*d*, and Table S1). These features are similar to patterns of sleep staging in mammals (25, 26). The total amount of REM sleep averaged  $22.99 \pm 3.83\%$  (mean  $\pm$  SEM) (Table S1) of the dark period, greater than reported in most avian sleep studies, including the few studies of oscines (13, 14). The intermediate epochs were brief and numerous (Fig. S3 *e* and *g* and Table S1) and were usually more stable throughout the night than REM and SWS in terms of density, average episode duration and average number of episodes per hour. As is the case in mammals (3, 4, 20, 21), the intermediate stage consistently acted as, but was not limited to, a transition phase between SWS and REM (Fig. S3*f* and Table S1). Therefore, whereas there seem to be structural differences between IS in birds and mammals, IS in birds can be thought of as a short transitional period during which neither delta waves nor eye movements were reliably detected at a high temporal resolution. This observation is important because eye movements had to be present in a given 3-s window to be visually scored as REM. Therefore, not allowing for IS computationally, by imposing two clusters on the sleep data, could have resulted into large portions of the data being scored as REM by the algorithm and NREM by the visual scorer.

## Discussion

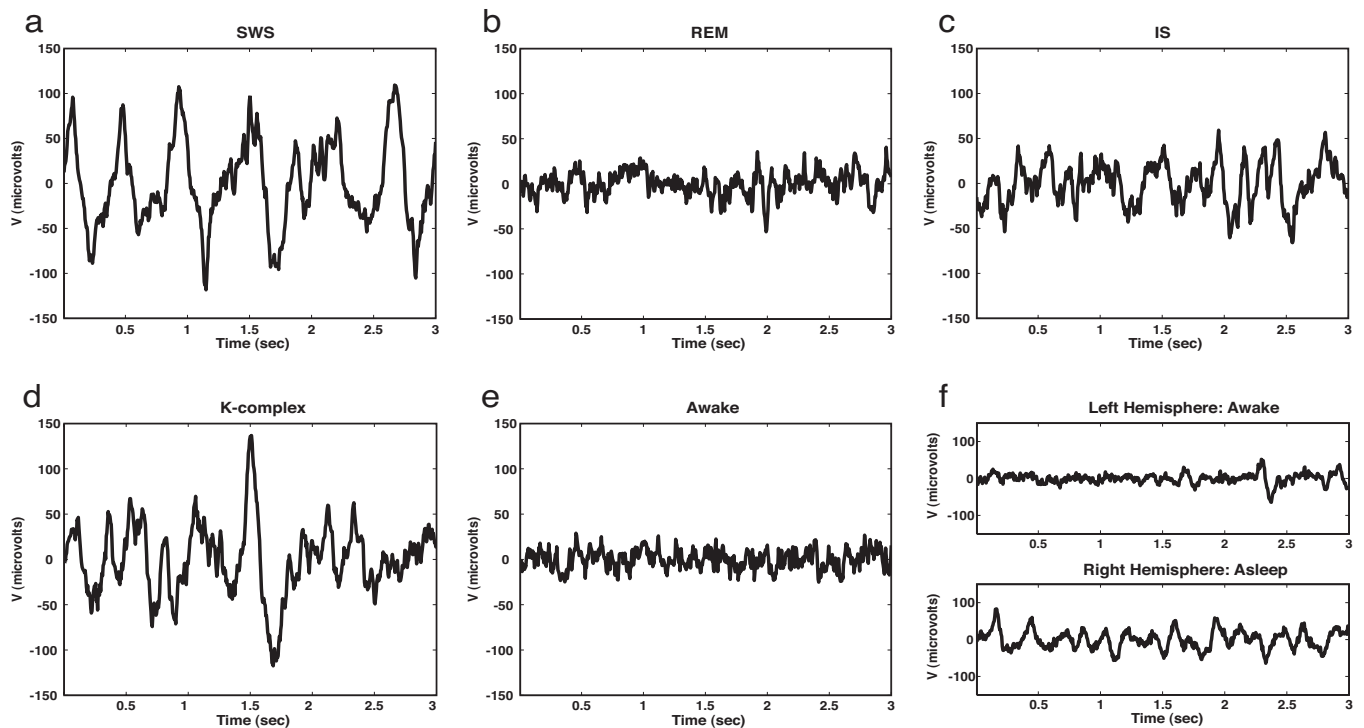
Sleep patterning is thought to differ between birds and mammals. NREM and REM are known broadly among birds. The observation of REM sleep is by itself an insufficient basis to equate avian and mammalian sleep patterns, except to distinguish them from reptilian sleep (27), where REM is poorly established (28), but other similarities of sleep architecture in birds and mammals have not been well established. Avian REM periods are reported to be extremely brief and infrequent in most



**Fig. 1. Multidimensional visualization of stages.** (a and b) Delta power (upper trace) and gamma power (lower trace) for 2 h, represented in units of standard deviations from the mean which has been set to 0 (i.e., the whole delta power time series and gamma power time series have been normalized). The dots correspond to 3-s epochs, separated over 1-s increments. Z[x] indicates that the variable x has been z-scored. Delta and gamma power activation interdigitates with SWS (blue) occurring in the Up states of delta and Down states of gamma whereas REM (red) occurs during the Down states of delta and Up states of gamma. The intermediate and awake states are in cyan and yellow, respectively. The awake state had amplitudes in the gamma range that were not always comparable with those of REM. Artifacts are not shown. (b) Another example of the information shown in a, computed for a second bird (B133). a and c–f are from the same recording (W147). (c) One night of sleep is represented in a 3D space spanned by delta, gamma/delta, and the power differences in gamma/delta. In this space, SWS (blue) forms a spear. IS and REM are shown in cyan and red, respectively. (d) When the differences in gamma/delta in c are replaced with the differences in delta, REM sleep collapses into a spear. (e and f) Separation of states in a reduced parameter space. A five-dimensional space is reduced to three dimensions with PCA for the purpose of visualization. (e) REM (red), IS (cyan), and SWS (blue) are spatially localized. (f) REM and SWS form orthogonal planes, and IS (cyan) corresponds to the warped region linking the two planes.

species hence “rudimentary” (12) with the exception that oscine passerines have more REM (13, 14, 23, 29). Mammalian sleep has a circadian distribution, is triphasic and is associated with precise electroencephalographic and spectral patterns. Whereas birds exhibit a pattern of sleep closer to mammals than reptiles

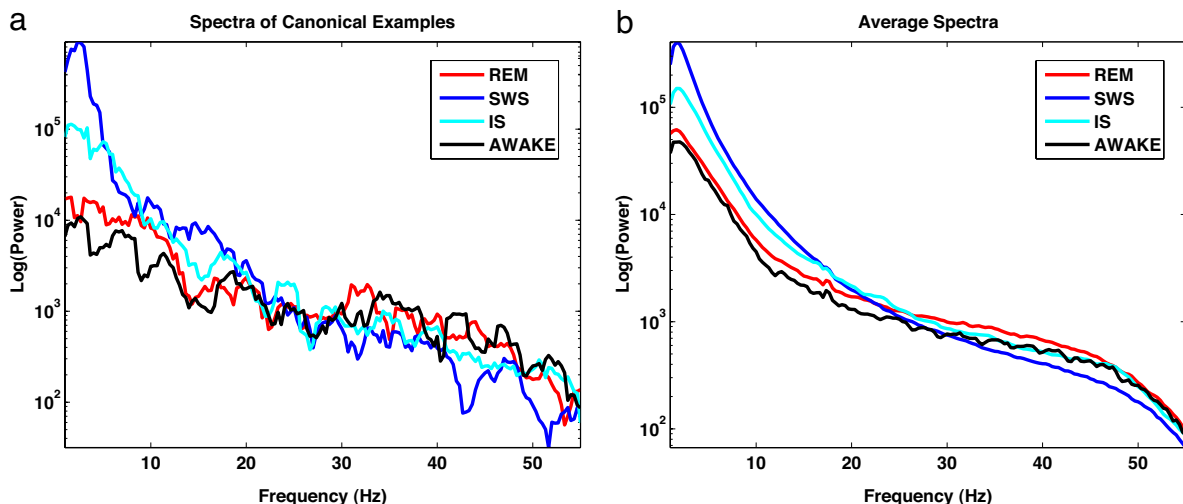
insofar as they both have SWS and REM, and circadian rhythms of SWS and REM, mammalian sleep also entails other features such as intermediate sleep, gamma oscillations during REM sleep, K-complexes, and up and down states that have set them apart from birds.



**Fig. 2.** Representative EEG samples for SWS (*a*), REM (*b*), IS (*c*), a K-complex like transient (*d*), the awake state (*e*), and unihemispheric sleep (*f*). *a*–*c* and *e* were automatically generated by using the MATLAB “silhouette” function on the scatter plot in Fig. 1 *e* and *f*. *a*–*e* were chosen from W 147; *f* was chosen from B 133, which exhibited the most unihemispheric epochs (Table S1).

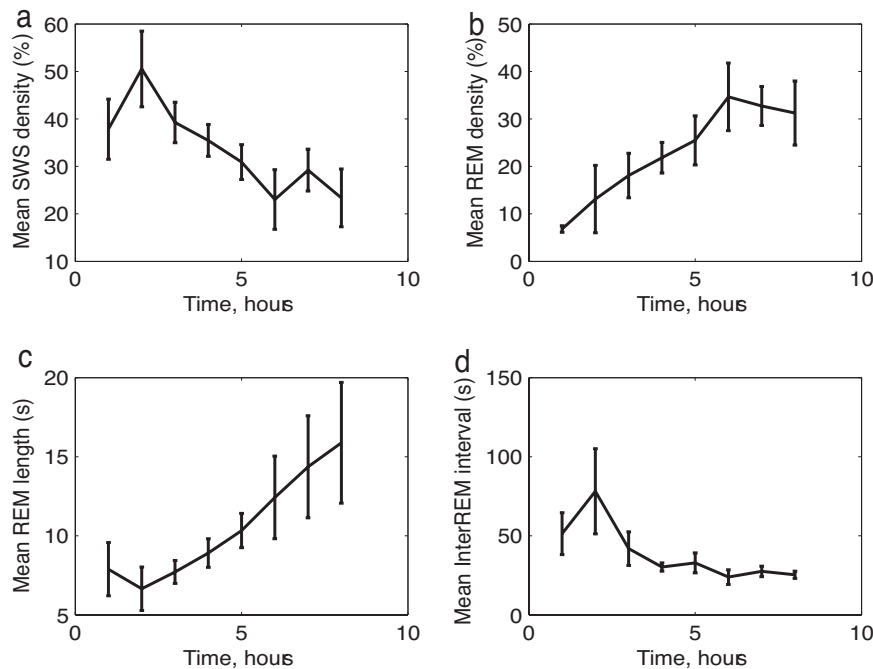
In contrast, the present study helps to bridge the gap between birds and mammals by highlighting a broad suite of characteristics of sleep that mammals were not known to share with birds. These characteristics include the existence of similar spectral signatures, delta (30) and gamma interdigitations, overnight increases in REM associated with an elongation of REM episodes, IS [a transition state between SWS and REM, distinct from the drowsy state taking place during transitions from Waking to NREM (14)], K-complexes, and other similarities. Moreover, the interdigitation between delta and gamma power activation described here (Fig. 1 *a* and *b*) and K-complexes (Fig.

2*d* and Table S2) during sleep have been observed in (and sometimes specifically attributed to) the mammalian cortex (5, 6, 19, 31). In mammals, these patterns have been associated with Up and Down states (19, 32), raising the question as to whether these patterns are also generated in the avian brain. Birds have a well developed thalamus but are devoid of a neocortex. Therefore, a neocortex is not necessary for the development of complex sleep stages as defined by the systematic variation in EEG signals that we have observed. Our observation of K-complexes leaves open the possibility that these signals are not of cortical origin in mammals as has been suggested (5). Our



**Fig. 3.** Power Spectra. (*a*) The log of the power ( $\mu V^2$ ) vs. frequency (0.33 Hz bins) for samples shown in Fig. 2 *a*–*c* and *e*. (*b*) The log of the average of the power in all 3-s windows scored as REM, SWS, IS, and awake is shown across frequency.





**Fig. 4.** A mammalian-like distribution. Average stage statistics are plotted for each hour of the dark period for all birds. Birds exhibited a significant decrease in SWS density (a), a significant increase in REM sleep density (b), and average REM episode length (c) and a significant decrease in inter-REM intervals (d) throughout the night. Bars correspond to the standard error of the mean. Individual data for each bird are plotted in Fig. S3.

results are therefore consistent with previous studies of K-complexes in reptiles (33) and nonlaminar networks from multiple species displaying increased power in a given frequency range because of network synchronization (34–40).

Additional neurophysiological work, with even broader band-pass filters, as well as neuroanatomical studies will be necessary to fully characterize these signals and their neural substrates in birds. It is, however, interesting to note that, in mammals, the slow oscillation seems linked to K-complexes as well as to the grouping of spindles. If the slow oscillation is responsible for the K-complexes in birds, one would think that spindles, if present, could be grouped as well, which is not the case. Because our birds have a large thalamus and no neocortex, one would, *a priori*, have expected them to produce spindles and not K-complexes, which is the opposite of what we report.

Recent observations of REM-like sleep in basal mammals (17) are consistent with the hypothesis that the characteristics of sleep in the amniotes leading to birds and mammals may have been more complex than has been generally assumed. One hypothesis is that REM is associated with greater connectivity in avian and mammalian forebrain as compared with reptiles that apparently lack REM (28). However, the complex sleep architecture we have observed in zebra finches has not been reported in the numerous non-oscine (non-songbird) species that have been examined (23) but is likely to be broadly shared across songbirds (13, 14). Thus, this remarkable similarity of characteristics may have resulted from a convergent evolution in mammals and songbirds. It has been hypothesized that birds possess a mammalian cortex homolog (8, 9). A specific form of this hypothesis homologizes regions of the avian forebrain with cortical layers (41). If so, then the patterns of cortical activation, interactions between thalamus and cortex, and the change in those patterns in response to changes in behavioral state, may be similarly expressed in the avian forebrain. The developmental molecular basis conserving forebrain homologies, and potential homologies of sleep rhythms, between birds and mammals is not yet known.

The selective pressures that resulted in these features of sleep developing so prominently in songbirds but apparently not generally among birds remains unresolved. Juvenile song learning and adult territorial and mating behaviors involving song are complex sensorimotor skills and social behaviors proving strong selective pressures on songbirds. A causal link between song learning and associated behaviors and the complex sleep architecture we have described here remains speculative, and a viable alternate hypothesis is that there exists greater complexity to sleep structure broadly expressed across bird species than has commonly been recognized. The independent development of vocal learning in parrots and some hummingbirds (42) and application broadly across birds of the analysis procedures described herein provide good material to test this hypothesis.

## Materials and Methods

**Experimental Procedures.** Experimental procedures were approved by the Institutional Animal Care and Use Committee at the University of Chicago. In preliminary acute experiments in urethane-anesthetized animals, coordinates for the positioning of platinum electrodes were determined relative to the midsagittal sinus (in mm): (1.5R, 3L), (3R, 2L) and a ground electrode at (0.5C, 0L). The electrode impedance was 90 k $\Omega$  measured in saline.

For chronic recordings, birds were briefly anesthetized (Equithesin), and L-shaped platinum electrodes were epidurally implanted, secured, and attached to a head connector. In subsequent days, during recordings, a cable was attached linking the bird's head to an overhead mercury commutator (Dragonfly, Ridgeley, WV), allowing for free movement in the cage during data acquisition. Video recording was accomplished by an infrared (IR) light and an IR camera (Ikegama, Tokyo, Japan). Strategically placed mirrors facilitated detection of eye, head, and body movements. In one case the animal's eyes were obscured from view for  $\approx$ 1 h, but nevertheless the EEG signal was easy to score manually. EEGs were amplified by a factor of 1K, sampled at 1 kHz, and filtered at 1–100 Hz (with a 60-Hz notch filter, except for B133). In two birds (B133 and E1), which exhibited low frequency artifacts, the data were filtered at 2–100 Hz. For these birds, delta was set at 2–4 Hz for the automated analysis.

**Algorithm for Automated Sleep Analysis.** As part of the automated analysis, EEGs were downsampled to 200 Hz and DC filtered. Spectral power was

computed in  $\mu\text{V}^2/\text{Hz}$  using 0.33-Hz bins. For each epoch, the power differences in delta power and in gamma/delta were computed over the preceding and successive epochs, by using the Matlab "gradient" function. All clustering variables were normalized by z-scoring before the sleep stage classification. After initial REM/NREM and SWS/NSWS classification, the score of each epoch was smoothed by using a 5-s window to minimize the score contamination by brief artifacts that might not have been isolated by manual scoring. When artifacts occurring during sleep were manually labeled, the algorithm would score such an artifact according to the state of the following epoch unless the latter was awake, in which case the algorithm would assign the sleep artifact the score of the preceding epoch.

For bilateral recordings during the dark phase, the automated scoring algorithm filtered out epochs inconsistent with unihemispheric sleep. The small number of remaining epochs, in conjunction with simultaneous video recordings, were subsequently examined manually to assess whether they constituted instances of unihemispheric sleep.

The data analysis technique developed enabled us to resolve changes in power over a broad spectral range and a high temporal resolution, which were a key differentiating factor for automated REM sleep detection. This analysis was further corroborated by extensive manual scoring (Fig. S2), which was restricted to identification of REM, NREM, awake and artifacts, distinctions and signals observable by inspection of the EEG and video. Moreover, the

automated EEG scoring relied on whole-night statistics (21) rather than on arbitrarily defined thresholds, maximum likelihood methods, or supervised nonlinear classifiers, all of which tend to reflect and impose a human bias on the data analysis.

The double separation used in the automated separation allows for a minimum of two categories (REM and SWS) and a maximum of four categories (REM, SWS, IS, and the outliers, which are unclustered). Therefore, the algorithm does not assume a fixed number of states. In that respect, running the algorithm on data without REM (and wakefulness) or SWS greatly shortened the length of the respective REM and SWS spears whereas removing IS from the data caused the algorithm to detect insignificant levels of IS.

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