biology
letters

Daytime micro-naps in a nocturnal migrant: an EEG analysis

T Fuchs, D Maury, F.R Moore and V.P Bingman

Biol. Lett. 2009 **5**, 77-80
doi: 10.1098/rsbl.2008.0405

biology
letters

Biol. Lett. (2009) **5**, 77–80
doi:10.1098/rsbl.2008.0405
Published online 5 November 2008

Neurobiology

Daytime micro-naps in a nocturnal migrant: an EEG analysis

T. Fuchs[1,*], **D. Maury**[2], **F. R. Moore**[3] **and V. P. Bingman**[2]

[1]*Department of Biology, University of Pittsburgh at Johnstown, Johnstown, PA 15904, USA*
[2]*J. P. Scott Center for Neuroscience Mind and Behaviour and Department of Psychology, Bowling Green State University, Bowling Green, OH 43403, USA*
[3]*University of Southern Mississippi, Hattiesburg, MS 39406, USA*
**Author for correspondence (tfuchs@pitt.edu).*

Many species of typically diurnal songbirds experience sleep loss during the migratory seasons owing to their nocturnal migrations. However, despite substantial loss of sleep, nocturnally migrating songbirds continue to function normally with no observable effect on their behaviour. It is unclear if and how avian migrants compensate for sleep loss. Recent behavioural evidence suggests that some species may compensate for lost night-time sleep with short, uni- and bilateral 'micro-naps' during the day. We provide electrophysiological evidence that short episodes of sleep-like daytime behaviour (approx. 12 s) are accompanied by sleep-like changes in brain activity in an avian migrant. Furthermore, we present evidence that part of this physiological brain response manifests itself as unihemispheric sleep, a state during which one brain hemisphere is asleep while the other hemisphere remains essentially awake. Episodes of daytime sleep may represent a potent adaptation to the challenges of avian migration and offer a plausible explanation for the resilience to sleep loss in nocturnal migrants.

Keywords: unihemispheric sleep; migratory birds; naps

1. INTRODUCTION

Every year, millions of songbirds lose a substantial portion of their night-time sleep when they embark on their predominantly nocturnal journeys. Although the performance degrading effects of sleep deprivation are well documented in mammals (Everson 1995; Durmer & Dinges 2005), avian migrants successfully navigate the complex challenges of migration presumably with only a fraction of their 'normal' sleep. How such resilience to sleep loss comes about remains a mystery. Although birds may be relatively resilient to the detrimental effects of sleep loss (Berger & Phillips 1994) more recent research suggests that they respond to short-term sleep loss with changes in brain activity similar to mammals (Jones *et al.* 2008; Martinez-Gonzalez *et al.* 2008). To date, the only study of sleep in migratory songbirds suggests that sleep deprivation is tolerated during the migratory season only (Rattenborg *et al.* 2004). One possible explanation for the apparent resilience of migrants to sleep loss may be found in behavioural adaptations occurring during the migratory season. Such behaviour is difficult to observe in the field yet it would create opportunities to compensate for curtailed night-time sleep during the day (Schwilch *et al.* 2002; Rattenborg *et al.* 2004; Fuchs *et al.* 2006). For instance, in the migratory Swainson's thrush (*Catharus ustulatus*), 'daytime rest' is composed of frequent, short 'micro-naps', i.e. episodes of bilateral and unilateral eye closure, that typically last only several seconds and occur during longer periods of 'drowsiness', an intermediate sleep-like state. In captive Swainson's thrushes the frequency of daytime sleep-like behaviour is dramatically increased during the migratory season (Fuchs *et al.* 2006). Unilateral eye closure is a behavioural indicator of unihemispheric sleep, an ability to selectively sleep with one brain hemisphere, while the other hemisphere remains essentially awake. A near complete decussation of the optic chiasma combined with reduced interconnectivity between the avian brain hemispheres may allow birds to monitor their environment with one eye while 'resting' the brain hemisphere connected to the other eye (for review see Rattenborg *et al.* 2000).

However, the behavioural indicators of sleep alone are not a demonstration that the brain is in a physiological state of sleep. The present study investigates brain activity during sleep-like daytime behaviour in captive, migratory Swainson's thrushes and investigates if the behaviourally observed episodes of unilateral eye closure are also accompanied by hemispheric differences in brain activity.

Much of the electroencephalogram (EEG) analysis of mammalian sleep follows from the assumption that the intensity of Δ-activity (average EEG slow-wave activity typically in the 1–4 Hz frequency range, assessed as 'power' in the 'Δ-band' by power spectrum analysis) accurately reflects sleep quality (i.e. depth of sleep). Consequently, spectral power in the Δ-band was employed as a measure of sleep quality in the present study (also see the electronic supplemental material).

2. MATERIAL AND METHODS

Seven Swainson's thrushes were bilaterally implanted with stainless steel electrodes over the hyperpallium accessorium and the orbital bones to monitor EEG and eye movements (electrooculogram). The presented data are based on daytime EEG and video recordings during the migratory season and night-time recordings in the same birds when non-migratory (see methods in the electronic supplementary material). All procedures were in accordance with BGSU animal care and use regulations.

Video recordings were manually scored for behaviour (daytime sleep, unilateral eye closure, drowsiness, alert wakefulness, night-time sleep) and the corresponding sections of the time stamped EEG were subjected to power spectrum analysis. Average EEG power was computed for frequency values between 1.4 and 4 Hz (Δ-power; see methods in the electronic supplementary material).

Δ-power values for sleep-like behaviour were then standardized and expressed as a percentage of Δ-power during alert wakefulness before they were subjected to statistical analysis. A total of 558 episodes were analysed in this fashion (drowsiness, 192; daytime sleep, 169; unilateral eye closure, 197). The data were then subjected to paired *t*-tests, Wilcoxon signed-rank tests or repeated measures analysis of variance (ANOVA). If significant main effects were found with ANOVAs, paired *t*-tests were used for follow-up comparisons (see methods in the electronic supplementary material).

Electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2008.0405 or via http://journals.royalsociety.org.

Received 21 July 2008
Accepted 17 October 2008

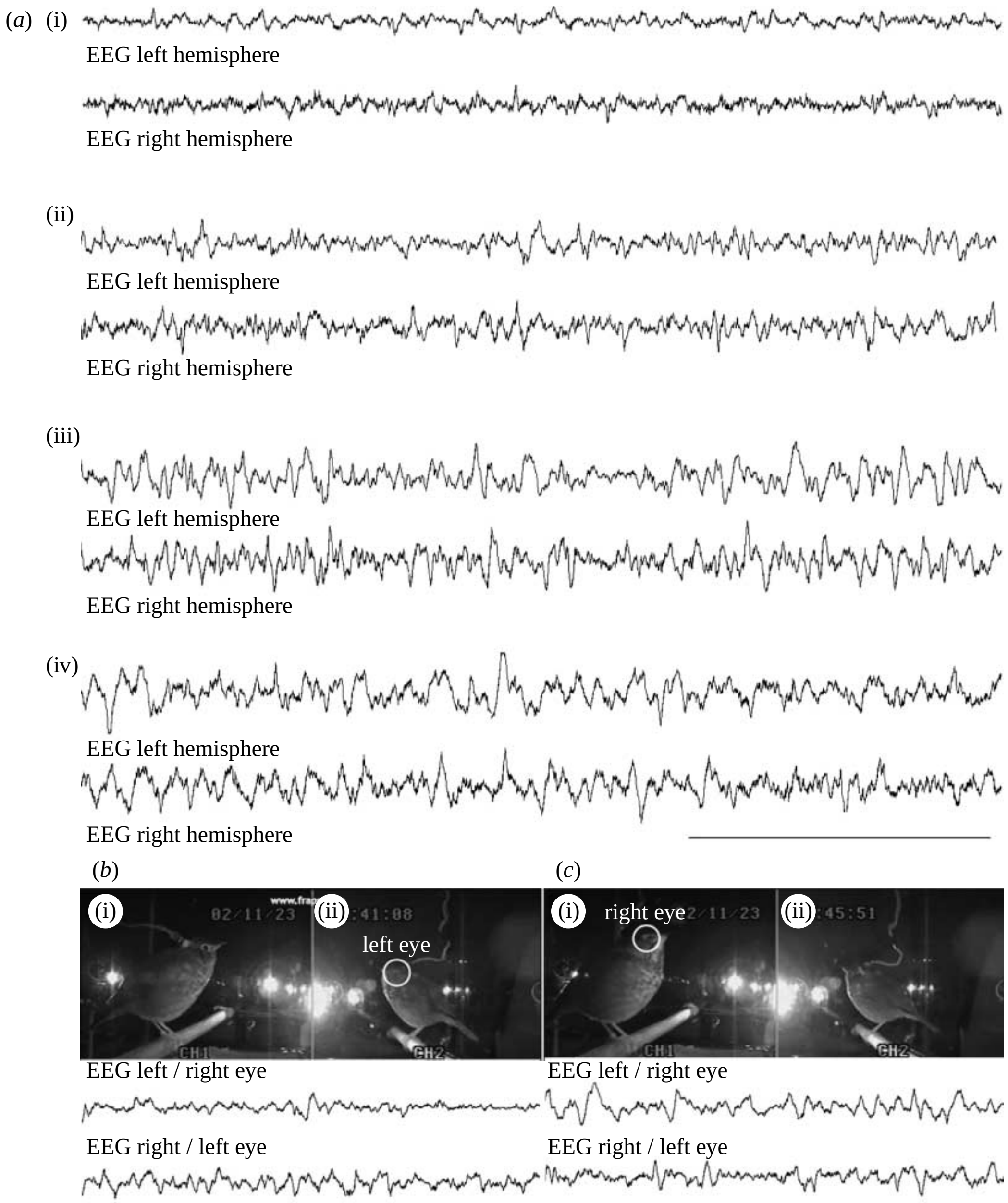

Figure 1. Representative samples of EEG activity. (*a*) EEG-amplitude progressively increases from (i) alert wakefulness to (ii) drowsiness and sleep due to an increase in low-frequency high-amplitude brain activity (slow-wave or Δ-activity). Note that (iii) daytime sleep and (iv) night-time sleep EEG are of similar amplitude. Recordings stem from the same bird and EEG tracks use the same amplitude scale. (*b*,*c*) Episodes of unilateral eye closure are accompanied by interhemispheric EEG asymmetries. (*b*) Closure of the (ii) left eye with sleep-like EEG activity in the contralateral right brain hemisphere (EEG R). (*c*) Closure of the (i) right eye with increased slow-wave activity in the left hemisphere (EEG L; same animal; same recording session).

3. RESULTS

Visual inspection and spectral analysis of EEG records from the analysed episodes of behavioural daytime sleep (duration 13.9±1 s, X±s.e.m.), unilateral eye closure (duration 10.9±0.5 s) and drowsiness revealed that all three types of daytime, sleep-like behaviour are accompanied by reliable changes in brain activity (figure 1). A comparison of average Δ-power (1.4–4 Hz) showed statistically significant differences between alert wakefulness and all three types of daytime sleep-like behaviour (Wilcoxon: drowsiness, $Z=-2.37$, $p<0.05$; daytime sleep, $Z=-2.37$, $p<0.05$; unilateral eye closure, $Z=-2.37$, $p<0.05$). Daytime sleep, unilateral eye closure and drowsiness also differed significantly from each other ($F_{1.08/6.53}=8.87$, $p<0.05$). Follow-up comparisons revealed significant differences between daytime sleep and drowsiness (Paired t-test: $t_6=-3.12$, $p<0.05$), unilateral eye closure and drowsiness (Paired t-test: $t_6=-3.76$, $p<0.05$) and unilateral eye closure and daytime sleep (Paired t-test: $t_6=2.45$, $p<0.05$; figure 2*a*).

(a) *Daytime sleep*

To investigate whether slow-wave activity during daytime sleep approaches the levels of night-time sleep, the average Δ-power during daytime sleep in migratory active birds was compared with an early (2 hours) and a late (10 hours) sample of nocturnal

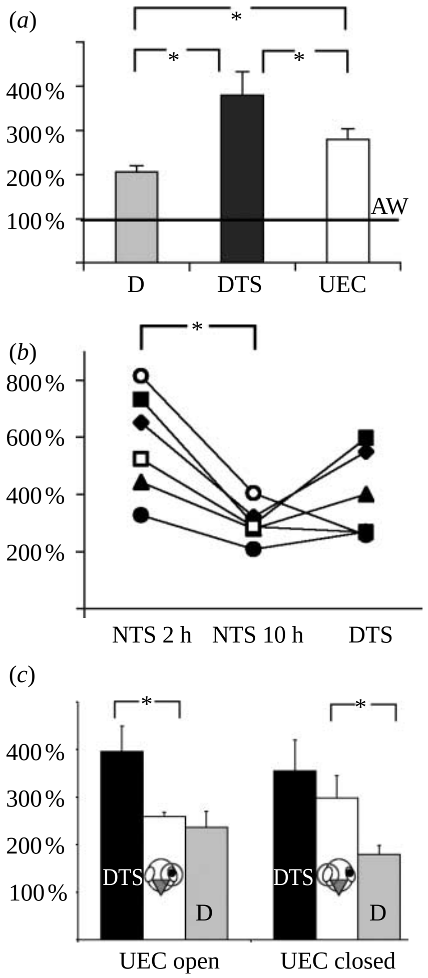

Figure 2. (*a*) Average Δ-power (1.4–4 Hz) during sleep-like daytime behaviour expressed as a percentage of alert wakefulness (AW 100%). Daytime sleep (DTS), drowsiness (D) and unilateral eye closure (UEC) show increased Δ-power compared with AW and also differ significantly from each other ($n = 7$; 100% = AW). (*b*) Comparison of DTS Δ-power with an early (2 hours) and a late (10 hours) sample of NTS ($n = 6$; 100% = AW). (*c*) Intrahemispheric comparison of Δ-power (1.4–4 Hz) during UEC with DTS and D. Δ-power in the brain hemisphere corresponding to the closed eye (UEC closed) is similar to Δ-power during DTS. Δ-power in the brain hemisphere corresponding to the open eye (UEC open) is significantly lower than during DTS. The reverse pattern is observed with D. UEC-closed Δ-power is significantly higher than D while UEC open corresponds to Δ-power values similar to D ($n = 7$; $X \pm$ s.e.m.; 100% = AW).

slow-wave sleep in the same birds when non-migratory. While daytime sleep was characterized by higher average Δ-power than late night-time sleep, it did not exceed the levels of early night-time sleep (figure 2*b*). Within subjects repeated measures analysis yielded a significant main effect for Δ-power ($F_{2/10} = 9.16$, $p < 0.05$). However, follow-up comparisons showed that only early and late night-time sleep differed significantly from each other (Paired *t*-test: $t_5 = 5.278$, $p < 0.05$). In four out of the six animals, daytime sleep Δ-power surpassed the levels of late night-time sleep, yet in no animal did Δ-activity during daytime exceed the activity of early night-time sleep (figure 2*b*).

Similar to mammals, nocturnal slow-wave sleep in birds alternates with episodes of rapid eye movement (REM) sleep (Rattenborg & Amlaner 2002). We did not detect episodes of daytime REM sleep in our experimental animals.

(b) *Unihemispheric sleep*

The visual inspection of EEG recordings during episodes of unilateral eye closure provided evidence of EEG asymmetries indicative of unihemispheric sleep (figure 1*b*,*c*). Even with hemispheric EEG differences present, brain activity in the hemisphere contralateral to the open eye typically resembled an EEG of drowsiness rather than an EEG of alert wakefulness.

When Δ-power during unilateral eye closure and daytime sleep was compared within the same animal and brain hemisphere, the brain hemisphere receiving input from the open eye showed significantly lower Δ-power than the same hemisphere during daytime sleep (Paired *t*-test: $t_6 = 3.25$, $p < 0.05$; figure 2*c*). By contrast, Δ-power in the brain hemisphere receiving input from the closed eye was not significantly different from Δ-power during daytime sleep (Paired *t*-test: $t_6 = 1.48$, $p > 0.05$). Interestingly, when unilateral eye closure was compared with drowsiness the opposite pattern was observed. The brain hemisphere receiving input from the closed eye now showed significantly higher Δ-power than during drowsiness (Paired *t*-test: $t_6 = 3.89$, $p < 0.05$), while brain activity in the hemisphere corresponding to the open eye was no different from what occurred during bilateral drowsiness (Paired *t*-test: $t_6 = 1.46$, $p > 0.05$; figure 2*c*).

4. DISCUSSION

Daytime sleep-like behaviour in captive Swainson's thrushes is observed almost exclusively during the migratory season (Fuchs *et al.* 2006). The electrophysiological evidence reported here supports the conclusion that even short eye closures during the day are true sleep episodes, which not only behaviourally *but also physiologically* resemble night-time sleep and probably provide migrants with recuperative opportunities to compensate for nocturnal sleep loss. Slow-wave activity during bihemispheric daytime micro-naps approaches the levels of night-time sleep, although it does not reach the peak levels observed during the early portion of the night.

The observed decline in Δ-power from the early to the late-night sleep samples suggests that avian and mammalian slow-wave sleep are similarly regulated (e.g. Szymczak *et al.* 1996; Rattenborg *et al.* 2004; Jones *et al.* 2008; Low *et al.* 2008; Martinez-Gonzalez *et al.* 2008) lending additional support to the hypothesis that Δ-power and sleep quality are correlated in birds (see methods in the electronic supplementary material).

Unilateral eye closure is accompanied by slow-wave activity similar to daytime sleep in the hemisphere corresponding to the closed eye and an EEG similar to drowsiness in the hemisphere receiving input from the open eye, indicating that unilateral eye closure in Swainson's thrushes is accompanied by a physiological state similar to mammalian unihemispheric sleep (Rattenborg *et al.* 2000). If the intensity of slow-wave activity accurately reflects sleep quality in birds, it appears that daytime sleep, per unit of time, is the most beneficial form of daytime rest, followed by unilateral eye closure and daytime drowsiness (figure 2*a*).

Behavioural observations revealed that, in the migratory season, captive Swainson's thrushes spend substantially more time of the day in a state of drowsiness than daytime sleep or unilateral eye closure (Fuchs *et al.* 2006). drowsiness combines behavioural signs of wakefulness (open or partially closed eyes) with physiological characteristics of sleep and may therefore allow an animal to monitor its environment while benefiting from sleep-like brain activity. Despite this advantage Swainson's thrushes close their eyes (one or both) during daytime. At least during episodes of unilateral eye closure a bird's ability to respond to visual stimuli is probably not entirely compromised. Unihemispherically sleeping mallard ducks respond quickly to threatening stimuli presented to the open eye (Rattenborg *et al.* 1999) indicating that predator detection is an important feature of this state.

Sleep-like behaviour associated with eye closure corresponds to increased slow-wave activity, indicating that visual activation may constrain the sleep-like benefits of resting behaviours associated with open eyes (Kavanau 2001). Daytime rest in migrants could be viewed as a compromise among the costs, risks and benefits associated with sleep-like behaviour (Lima *et al.* 2005). Episodes of daytime sleep and even unilateral eye closure may render a migrant less vigilant to approaching predators. However, short bi- or unihemispheric micro-naps nested within longer episodes of drowsiness would make it difficult for predators to approach unnoticed while granting a bird the additional benefits of uni- or bilateral eye closure. The behaviour reported here was observed in captivity and it remains to be determined whether Swainson's thrushes display the same behaviour in the wild. However, a series of field observations in other migratory species (Schwilch *et al.* 2002) supports our hypothesis that migrants in the wild may compensate for sleep loss with daytime naps.

As long as the precise functions of sleep or slow-wave activity in birds and mammals remain unexplained, the full range of benefits associated with unilateral eye closure, daytime sleep and drowsiness will necessarily remain speculative. However, given the electrophysiological resemblance to nocturnal slow-wave sleep and a substantial increase in the frequency and duration of sleep-like daytime behaviour during the migratory season, daytime naps provide a plausible explanation for the apparent resilience of avian migrants to the detrimental effects of sleep loss.

All procedures were conducted in accordance with Bowling Green State University animal care and use regulations.

Supported by National Science Foundation grant IBN 0333032.

Berger, R. J. & Phillips, N. H. 1994 Constant light suppresses sleep and circadian rhythms in pigeons without consequent sleep rebound in darkness. *Am. J. Physiol.* **267**, 945–952.

Durmer, J. S. & Dinges, D. F. 2005 Neurocognitive consequences of sleep deprivation. *Semin. Neurol.* **25**, 117–129. (doi:10.1055/s-2005-867080)

Everson, C. A. 1995 Functional consequences of sustained sleep deprivation in the rat. *Behav. Brain Res.* **69**, 43–54. (doi:10.1016/0166-4328(95)00009-I)

Fuchs, T., Haney, A., Jechura, T. J., Moore, F. R. & Bingman, V. P. 2006 Daytime naps in night-migrating birds: behavioural adaptation to seasonal sleep deprivation in the Swainson's thrush (*Catharus ustulatus*). *Anim. Behav.* **72**, 951–958. (doi:10.1016/j.anbehav.2006.03.008)

Jones, S. G., Vyazovskiy, V. V., Cirelli, C., Tononi, G. & Benca, R. M. 2008 Homeostatic regulation of sleep in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). *BMC Neurosci.* **9**, 47. (doi:10.1186/1471-2202-9-47)

Kavanau, J. L. 2001 Brain processing limitations and selective pressures for sleep, fish schooling and avian flocking. *Anim. Behav.* **62**, 1219–1224. (doi:10.1006/anbe.2001.1881)

Lima, S. L., Rattenborg, N. C., Lesku, J. A. & Amlaner Jr, C. J. 2005 Sleeping under the risk of predation. *Anim. Behav.* **70**, 723–736. (doi:10.1016/j.anbehav.2005.01.008)

Low, P. S., Shank, S. S., Sejnowski, T. J. & Margoliash, D. 2008 Mammalian-like features of sleep structure in zebra finches. *Proc. Natl Acad. Sci. USA* **105**, 9081–9086. (doi:10.1073/pnas.0703452105)

Martinez-Gonzalez, D., Lesku, J. A. & Rattenborg, N. C. 2008 Increased EEG spectral power density during sleep following short-term sleep deprivation in pigeons (*Columba livia*): evidence for avian sleep homeostasis. *J. Sleep Res.* **17**, 140–153. (doi:10.1111/j.1365-2869.2008.00636.x)

Rattenborg, N. C. & Amlaner Jr, C. J. 2002 Phylogeny of sleep. In *Sleep medicine* (eds L. T. Lee-Chiong, M. Sateia & M. A. Carskadon), pp. 7–22. Philadelphia, PA: Hanley & Belfus.

Rattenborg, N. C., Lima, S. L. & Amlaner Jr, C. J. 1999 Facultative control of avian unihemispheric sleep under the risk of predation. *Behav. Brain. Res.* **105**, 163–172. (doi:10.1016/S0166-4328(99)00070-4)

Rattenborg, N. C., Amlaner, C. J. & Lima, S. L. 2000 Behavioural, neurophysiological and evolutionary perspectives on unihemispheric sleep. *Neurosci. Biobehav. Rev.* **24**, 817–842. (doi:10.1016/S0149-7634(00)00039-7)

Rattenborg, N. C., Mandt, B. H., Obermeyer, W. H., Winsauer, P. J., Huber, R., Wikelski, M. & Benca, R. M. 2004 Migratory sleeplessness in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). *PLoS Biol.* **2**, 0924–0936. (doi:10.1371/journal.pbio.0020212)

Schwilch, R., Piersma, T., Holmgren, N. & Jenni, L. 2002 Do migratory birds need a nap after a long non-stop flight? *Ardea* **90**, 149–154.

Szymczak, J. T., Kaiser, W., Helb, H. W. & Beszczynska, B. 1996 A study of sleep in the European blackbird. *Physiol. Behav.* **60**, 1115–1120. (doi:10.1016/0031-9384(96)00231-4)