

Acute effects of light and darkness on sleep in the pigeon (*Columba livia*)[☆]

Niels C. Rattenborg, William H. Obermeyer, Erika Vacha, Ruth M. Benca*

Department of Psychiatry, University of Wisconsin-Madison, 6001 Research Park Blvd. Madison, WI 53719, USA

Received 13 September 2004; received in revised form 12 January 2005; accepted 10 February 2005

Abstract

In addition to entraining circadian rhythms, light has acute effects on sleep and wakefulness in mammals. To determine whether light and darkness have similar effects in birds, the only non-mammalian group that displays sleep patterns comparable to mammals, we examined the effects of lighting changes on sleep and wakefulness in the pigeon. We quantified sleep behavior (i.e., bilateral or unilateral eye closure) in pigeons maintained under a 12:12 LD cycle, and immediately following a change from a 12:12 to a 3:3 LD cycle. During both LD cycles, sleep was most prevalent during dark periods. During the 3:3 LD cycle, darkness had the greatest sleep promoting effect during the hours corresponding to the subjective night of the preceding 12:12 LD cycle, whereas light suppressed sleep across circadian phases. As previously suggested, the light-induced decrease in sleep in the subjective night might be partly mediated by the suppression of melatonin by light. Although the sleep promoting effect of darkness was modulated by the circadian rhythm, sleep in darkness occurred during all circadian phases, suggesting that darkness per se may play a direct role in inducing sleep. In addition to the effects of lighting on behavioral state, we observed an overall bias toward more right eye closure under all lighting conditions, possibly reflecting a response to the novel testing environment.

© 2005 Elsevier Inc. All rights reserved.

Keywords: Sleep; Light; Darkness; Bird; Pigeon; Laterality; Eye closure

1. Introduction

Light plays a critical role in organizing the timing of behavior in various animals. In addition to entraining endogenous circadian rhythms, light and darkness have acute effects on sleep and wakefulness. In nocturnal mammals such as rats, light promotes sleep whereas darkness promotes wakefulness [1,2]. Light and darkness exert the opposite effect on behavioral state in diurnal mammals, including humans [3,4]. These acute responses to changes in lighting occur immediately after lighting transitions and during all phases of the circadian cycle [1,2,5], although they are modulated by the circadian

rhythm; changes in lighting have a greater effect on shifting behavioral state during the subjective night than during the subjective day [1,5].

The investigation of acute effects of light on behavioral state and the underlying neural mechanisms has been largely restricted to nocturnal mammals. Consequently, the extent to which these findings reflect a fundamental aspect of sleep–wakefulness regulation remains unclear. In contrast to mammals, the acute effects of light and darkness on sleep and wakefulness have undergone relatively little examination in birds. From a comparative standpoint, birds are of particular interest because they are the only non-mammalian taxonomic group to show sleep patterns similar to mammals, including both slow-wave sleep and rapid eye-movement (REM) sleep [6–8]. Moreover, birds possess retino-recipient subcortical brain regions homologous to those implicated in mediating the effects of light on behavioral state in mammals, such as the pretectum [9–

[☆] Financial disclosure: supported by R01 MH52226.

* Corresponding author. Tel.: +1 608 263 6162; fax: +1 608 263 0265.

E-mail address: rmbenca@wisc.edu (R.M. Benca).

12]. Finally, birds are of interest because unlike most mammals, they can engage in unihemispheric slow-wave sleep [13], thereby providing an opportunity to examine the effects of lighting conditions on regional sleep regulation.

The effects of light on sleep and wakefulness have been examined in diurnal pigeons (*Columba livia*). A 93% reduction in sleep was reported in pigeons during the first 24 h after being switched from a 12:12 LD cycle to constant bright light (LL) [14], an effect that seemed to persist in constant LL for up to 74 days. The researchers suggested that LL-induced sleep suppression is mediated via the dampening of melatonin release from the pineal gland [15], since sleep could be restored in LL by infusing physiological levels of melatonin [16,17]. Although these data suggest that melatonin may be involved in the induction of sleep during the normal dark period, darkness per se may also exert an acute sleep-promoting effect in diurnal birds independent of that mediated by melatonin release, or other circadian outputs.

To determine whether light and darkness have effects on behavioral state independent of those mediated by the circadian rhythm, lighting changes need to be dissociated from the circadian rhythm. Reductions in locomotor activity have been reported in captive diurnal birds exposed to acute darkness during the subjective day [18,19], suggesting that darkness per se can induce sleep. However, this darkness-induced reduction in activity could simply reflect a shift from a state of active wakefulness to quiet wakefulness. Since the direct behavioral observations and/or electrophysiological recordings required to confirm sleep have not been performed, it remains unclear whether changes in lighting affect behavioral state during the subjective day in birds. We examined the acute effects of a short light dark cycle (3:3 LD) on sleep behavior in pigeons previously maintained under a 12:12 LD cycle.

2. Methods

2.1. Animals and apparatus

Six pigeons (three female and three male) at least 6 months old were purchased from a local breeder. The pigeons were housed in individual home cages under a 12:12 LD cycle (lights on at 09:00 hours and off at 21:00 hours) for at least 1 month prior to the start of the experiment. A mixed-grain pigeon feed, water and grit were provided ad libitum. Prior to testing, each bird was acclimated to the behavioral observation chamber. Throughout acclimation the LD cycle was maintained on the same 12:12 LD cycle as in the home cage room.

The chamber consisted of a hexagonal glass enclosure (35.0 cm wide × 46.0 cm high) placed in the center of a sound-attenuating testing box (Med Associates Inc., 70.0 cm long × 35.5 wide × 56.0 cm high) (Fig. 1). A fan provided ventilation (1.3 m³/min) and masked environ-

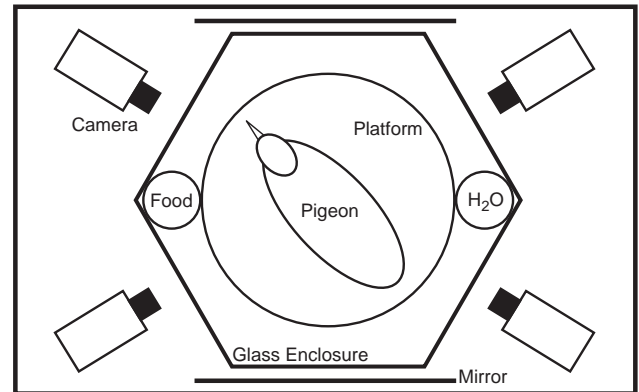


Fig. 1. Overhead view of observation chamber used to videotape the behavioral state of pigeons during the 12:12 and 3:3 LD sessions.

mental noise (32 dBA). The chamber was located in a dark, empty animal housing room to further isolate the pigeon from external stimuli. Each bird was recorded on videotape via four infrared sensitive cameras positioned around the glass enclosure. Two fluorescent lights suspended over the glass enclosure provided light during the light phase (200 lx), and an infrared light source provided luminance for the infrared cameras during the dark phase. A circular platform (23.0 cm in diameter × 7.5 cm high) was positioned in the center of the glass enclosure to encourage the birds to stay centered within the field of view of the cameras. Since birds exhibit more consolidated sleep when surrounded by other birds [20,21], mirrors (30.0 cm × 30.0 cm) were positioned on two sides of the enclosure. Food and water were available ad libitum within the enclosure.

2.2. Experimental protocol

To determine the effects of acute lighting changes on sleep and wakefulness behavior, we videotaped each bird in the observation chamber for 24 h under a 3:3 and 12:12 LD cycle. Each bird experienced both lighting conditions with at least 1 week separating the 3:3 and 12:12 LD sessions. All birds were maintained in their home cage under a 12:12 LD cycle prior to each session. For the 3:3 LD session, pigeons were placed in the chamber at 18:00 hours with the lights on, as in their home cage. At 21:00 hours the lights turned off, also in synchrony with their normal home cage schedule. However, at 00:00 the lights turned on again, and alternated between off and on every 3 h until the birds were removed from the chamber the following day at 18:00 hours. For the 12:12 LD session, pigeons were also placed in the chamber at 18:00 hours but the light schedule remained the same as in their home cage.

2.3. Behavioral state scoring

The behavioral state of the bird was determined by examining a still image from the videotape at the start of each minute across the 24 h sessions. Because eye closure is

Table 1
Mean percent time spent in each eye state as a function of LD schedule and lighting condition

| Eye state | Overall | | Light | | Dark | |
|---------------------|---------|-------|-------|-------|-------|-------|
| | 12:12 | 3:3 | 12:12 | 3:3 | 12:12 | 3:3 |
| Both closed | 41.2% | 26.1% | 4.2% | 2.6% | 78.9% | 50.1% |
| Only one closed | 9.6% | 13.4% | 9.6% | 11.0% | 9.6% | 15.9% |
| Left | 1.1% | 2.1% | 1.2% | 0.6% | 0.9% | 3.6% |
| Right | 8.3% | 11.3% | 7.9% | 10.4% | 8.6% | 12.3% |
| Both or one closed* | 52.3% | 40.1% | 14.2% | 13.5% | 89.0% | 66.5% |

* Sum of all other eye closure states, including instances where only one eye was visible on the video image and that eye was closed.

associated with electrophysiologically defined sleep in every bird examined [8,13], sleep was scored if one or both eyes were closed. An eye was scored as closed if the eyelid occluded more than two-thirds of the eye [22]. Given

previous reports of a bias for closing one particular eye during sleep in young chickens (*Gallus gallus domesticus*) [23–25], we recorded whether the right or left eye was closed during unilateral eye closure.

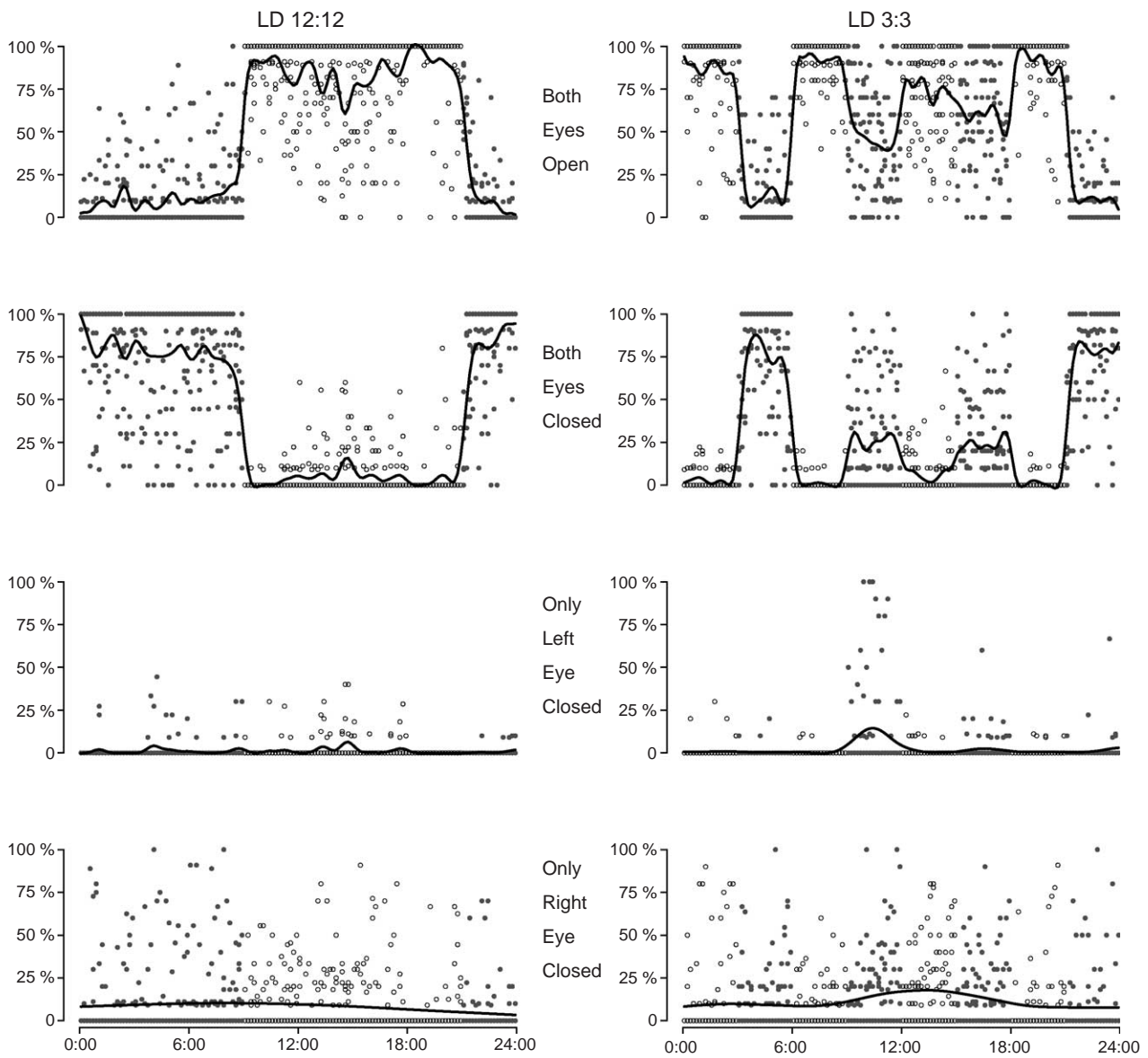


Fig. 2. Percent time spent with both eyes open, both eyes closed, only the left eye closed or only the right eye closed, as a function of time and lighting condition during the 12:12 (left column) and 3:3 (right column) LD sessions. Each data point reflects a 10 m period during light (open circles) and dark (closed circles) periods for individual birds ($n=6$); note that several data points overlap at 0% or 100%. The line is a spline fit of the data averaged across all birds. For both lighting schedules, subjective day is the period between 09:00–21:00 hours and subjective night is the period between 21:00–09:00 hours.

2.4. Data analysis and statistics

Comparisons of conditions were done using within subjects results from repeated measures ANOVA of the 10 m averages of state. Between subjects comparisons were done using averages by bird. The probability of closing the left eye only with that of closing the right eye only was compared with *t*-tests. All computations were done using R (<http://www.r-project.org>).

3. Results

Pigeons recorded under the 12:12 LD cycle exhibited sleep behavior (i.e., bilateral and unilateral eye closure) 52.3% of the time (Table 1). Sleep was largely restricted to the dark period of the 12:12 LD cycle; overall, sleep comprised 89.0% of the dark phase and only 14.2% of the light phase ($F(1143)=2619, p<0.01$). The birds spent less time sleeping during the 3:3 LD cycle (40.1%) than during the 12:12 LD cycle (52.3%) ($F(1287)=112, p<0.01$). Sleep in the 3:3 LD cycle was more prevalent in the dark (66.5%) than in the light (13.5%) ($F(1143)=1072, p<0.01$). The expression of sleep was also significantly ($F(1143)=92, p<0.01$) different between the subjective day (32.2%) and the subjective night (47.8%) without regard to lighting condition. This was attributable to an interaction ($F(1143)=177, p<0.01$) between the effect of darkness and the effect of time of day on sleep such that there was less sleep in the dark periods that occurred during the subjective day (50%) than during the dark periods that occurred during the subjective night (85%) (Fig. 2). The amount of sleep in light periods was low (16% during the daytime and 10% during the nighttime) similar to that during the 12 h light period in the 12:12 LD cycle. Fig. 2 shows that the effects

of lighting changes on sleep in the 3:3 LD cycle were largely due to changes in bilateral eye closure.

In addition to the effects of light and dark on sleep and wakefulness, we observed lateralization of unilateral eye closure. There was a bias for closing the right eye more than the left overall ($t_{11}=3.8, p<0.01$; Fig. 3), as well as under both the 12:12 ($t_5=2.6, p=0.05$) and 3:3 LD cycles ($t_5=2.6, p<0.05$). Neither light-dark nor subjective day-night shifted this bias.

4. Discussion

Our results demonstrate acute effects of light and darkness on sleep and wakefulness behavior in pigeons. Pigeons previously maintained under a 12:12 LD cycle showed acute behavioral responses to lighting changes when switched to a 3:3 LD cycle. In comparison to the corresponding hours of the 12:12 LD cycle, where sleep behavior (i.e., eye closure) occurred primarily at night, sleep behavior was markedly reduced during the 3 h light periods in the subjective night and elevated during the 3 h dark periods in the subjective day. In contrast, sleep during light periods in the subjective day and dark periods in the subjective night did not differ significantly from that observed during the corresponding hours of the 12:12 LD cycle.

The amount of sleep during dark periods in the 3:3 LD cycle varied as a function of circadian time, with sleep in darkness being greatest during the subjective night. The uniform response to 3 h light periods across the day, however, suggests that light is capable of masking potential circadian changes in sleep propensity during the subjective night, and possibly even during the subjective day, as revealed by the increase in sleep during darkness in the

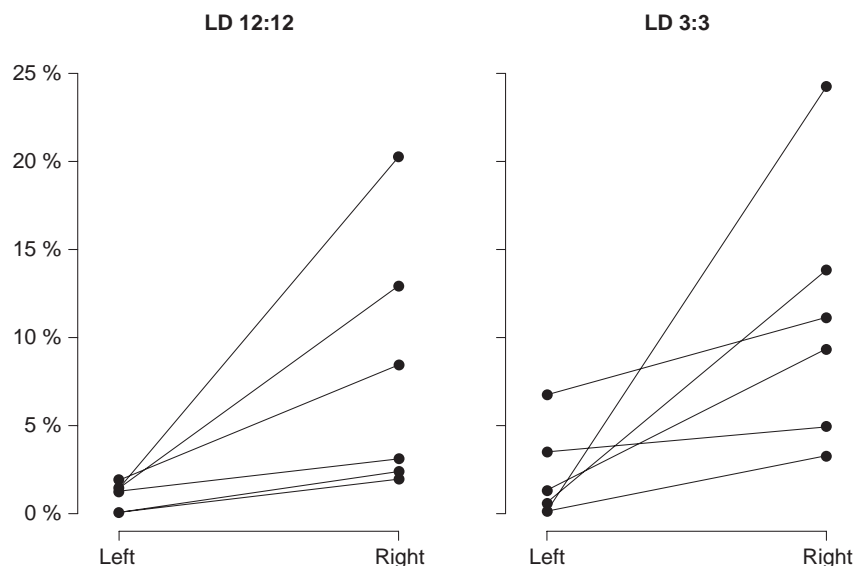


Fig. 3. Percent time spent with only the left or only the right eye closed for the entire 12:12 and 3:3 LD sessions plotted for individual birds.

subjective day. This alerting effect of light is similar to a previous report of sleep suppression by LL in pigeons [14], and might partly involve the suppression of nocturnal melatonin release from the pineal gland [15–17,26,27,34] and retina [28,29], as well as direct alerting effects.

The induction of sleep by darkness during the subjective day does not appear to be mediated by the release of melatonin from the pineal gland or retina. In pigeons switched from a 12:12 LD photoperiod to constant dim (0.1 lx) lighting, the circadian rhythm of melatonin release persists in the pineal gland [26] and retina [30], with low levels during the subjective day and high levels during the subjective night. Similarly, in chickens and rats maintained under a 12:12 LD photoperiod, levels of *N*-acetyltransferase (the rate limiting enzyme involved in the biosynthesis of melatonin from serotonin [31]) and melatonin in the pineal gland are low and do not increase in response to acute darkness during the subjective day of the circadian rhythm [32,33]. As with the biosynthesis of pineal melatonin in chickens and rats, darkness during the subjective day only induces melatonin synthesis in the rat retina if presented late in the day; darkness in the early part of the subjective day does not cause an increase in retinal melatonin, indicating that the circadian rhythm also gates the biosynthesis of retinal melatonin [27]. Although, the corpus of evidence suggests that the 3 h dark periods occurring during the subjective day probably did not cause melatonin to increase in our pigeons, measurements of melatonin levels are needed to determine whether increased levels might have induced sleep during these periods.

Lighting changes during the subjective night have the greatest effects on behavioral state, in both diurnal pigeons and nocturnal rats [1,5], albeit in opposite directions. In both cases, light during the subjective night appears to suppress nocturnal behavior; i.e., sleep in pigeons and wakefulness in rats. Both effects may be partly mediated by the suppression of nocturnal melatonin by light, and are consistent with the idea that nocturnal melatonin acts as a neuromodulator that facilitates nighttime behavior, rather than as a direct sleep-inducing agent [35,36]. Nevertheless, the fact that lighting changes induce changes in behavioral state in pigeons and rats during the subjective day, when the levels of melatonin are low and refractory to changes in lighting, indicates that other mechanisms may also mediate lighting-induced changes in behavioral state. In rats, the retino-recipient, subcortical visual system appears to be involved in orchestrating some of the acute effects of lighting on sleep [11,37]; similar subcortical structures may be involved in the acute effects of lighting in pigeons as well. Alternatively, photoreceptors in the lateral septum of pigeons [38] may mediate the effects of lighting on behavior [39]. Finally, the increase in sleep during darkness may be secondary to darkness-induced immobility, rather than a direct effect of darkness on sleep.

Although darkness had an overall sleep-promoting effect, sleep behavior included both bilateral and unilateral eye

closure, a more vigilant form of sleep. In birds, including pigeons [22], unilateral eye closure is associated with an interhemispheric asymmetry in slow-wave sleep-related electroencephalographic slow-wave activity (2–4 Hz), with the hemisphere contralateral to the closed eye showing greater slow-wave activity when compared to the ipsilateral hemisphere (i.e., unihemispheric slow-wave sleep); bilateral eye closure is associated with bihemispheric slow-wave sleep or REM sleep [13]. The association between unilateral eye closure and an interhemispheric asymmetry in SWS has been shown in six bird species recorded under a variety of experimental conditions (reviewed in Ref. [13]). Birds engage in unilateral eye closure to monitor their environment visually during sleep, and the amount of unilateral eye closure may change in response to alterations in a bird's sleeping environment [20–22].

Unlike a previous study of pigeons [22], we observed an overall bias for closing the right eye more than the left during episodes of unilateral eye closure. The bias for right eye closure may be related to lateralization of cognitive function in the avian brain [40]. Results from young chickens suggest that the pigeons' perception of the testing environment may explain the bias for right eye closure. When presented with a novel item, young chickens show a shift towards more right eye closure [23], a response consistent with the tendency to view novel items with the left eye/right hemisphere during wakefulness [41,42]. Consequently, the bias for right eye closure in our pigeons may reflect a response to the novel testing environment, both in the 12:12 and 3:3 LD cycle. The lack of an overall bias for right eye closure in the earlier study may indicate that the testing environment was more familiar to those pigeons. Indeed, unlike the current study, the pigeons in the earlier study were continuously housed in their testing chamber for at least 2 weeks under a stable 12:12 LD cycle before sleep and wakefulness were measured.

In summary, light and darkness have acute effects on sleep behavior in pigeons that are both independent of and modulated by the circadian rhythm. Although light during the subjective night might induce wakefulness by suppressing melatonin, the induction of sleep by darkness in the subjective day is unlikely to involve melatonin. As in nocturnal rats, the acute effects of light on behavioral state in pigeons may also involve subcortical visual structures. Future studies aimed at comparing the neural mechanisms that mediate the dichotomous behavioral responses to light and darkness in nocturnal rats and diurnal pigeons may influence our understanding of acute light effects in humans.

Acknowledgements

We would like to thank Adrienne Barth, Dolores Martinez-Gonzalez, Roxanne Prichard, Rachel Uttech and Annette Vee for their invaluable assistance with this project. This research was supported by R01 MH52226 to RMB.

References

- [1] Borbely AA. Circadian rhythm of vigilance in rats: modulation by short light–dark cycles. *Neurosci Lett* 1975;1:67–71.
- [2] Borbely AA. Sleep and motor activity of the rat during ultra-short light–dark cycles. *Brain Res* 1976;114:305–17.
- [3] Campbell SS, Dijk D-J, Boulos Z, Eastman CI, Lewy AJ, Terman M. Light treatment for sleep disorders: consensus report: III. Alerting and activating effects. *J Biol Rhythms* 1995;10(2):129–32.
- [4] Cajochen C, Zeitzer JM, Czeisler CA, Dijk DJ. Dose–response relationship for light intensity and ocular and electroencephalographic correlates of human alertness. *Behav Brain Res* 2000;115(1):75–83.
- [5] Benca RM, Gilliland MA, Obermeyer WH. Effects of lighting conditions on sleep and wakefulness in albino Lewis and pigmented Brown Norway rats. *Sleep* 1998;21(5):451–60.
- [6] Klein M, Michel F, Jouvet M. Etude polygraphique du sommeil chez les oiseaux. *CR Soc Biol* 1964;158:90–103.
- [7] Ookawa T, Gotoh J. Electroencephalographic study of chickens: periodic recurrence of low voltage and fast waves during behavioral sleep. *Poultry Sci* 1964;43:1603–4.
- [8] Rattenborg N, Amlaner C. Phylogeny of sleep. In: Lee-Chiong T, Sateia M, Carskadon M, editors. *Sleep Medicine*. Philadelphia: Hanley & Belfus Inc; 2002. p. 7–22.
- [9] McKenna OC, Wallman J. Accessory optic system and pretectum of birds: comparisons with those of other vertebrates. *Brain Behav Evol* 1985;26(2):91–116.
- [10] Miller AM, Obermeyer WH, Behan M, Benca RM. The superior colliculus–pretectum mediates the direct effects of light on sleep. *Proc Natl Acad Sci USA* 1998;95(15):8957–62.
- [11] Miller AM, Miller RB, Obermeyer WH, Behan M, Benca RM. The pretectum mediates rapid eye movement (REM) sleep regulation by light. *Behav Neurosci* 1999;113(4):755–65.
- [12] Prichard JR, Stoffel RT, Quimby DL, Obermeyer WH, Benca RM, Behan M. Fos immunoreactivity in rat subcortical visual shell in response to illuminance changes. *Neuroscience* 2002;114(3):781–93.
- [13] Rattenborg NC, Amlaner CJ, Lima SL. Behavioral, neurophysiological and evolutionary perspectives on unihemispheric sleep. *Neurosci Biobehav Rev* 2000;24(8):817–42.
- [14] Berger RJ, Phillips NH. Constant light suppresses sleep and circadian rhythms in pigeons without consequent sleep rebound in darkness. *Am J Physiol* 1994;267(4Pt2):R945–52.
- [15] Yamada H, Oshima I, Sato K, Ebihara S. Loss of the circadian rhythms of locomotor activity, food intake, and plasma melatonin concentration induced by constant bright light in the pigeon (*Columba livia*). *J Comp Physiol, A Sens Neural Behav Physiol* 1988;163(4):459–63.
- [16] Phillips NH, Berger RJ. Melatonin infusions restore sleep suppressed by continuous bright light in pigeons. *Neurosci Lett* 1992;145(2):217–20.
- [17] Mintz EM, Phillips NH, Berger RJ. Daytime melatonin infusions induce sleep in pigeons without altering subsequent amounts of nocturnal sleep. *Neurosci Lett* 1998;258(2):61–4.
- [18] Aschoff J, von Goetz C. Masking of circadian activity rhythms in canaries by light and dark. *J Biol Rhythms* 1989;4(1):29–38.
- [19] Binkley S, Mosher K. Direct and circadian control of sparrow behavior by light and dark. *Physiol Behav* 1985;35(5):785–97.
- [20] Rattenborg NC, Lima SL, Amlaner CJ. Facultative control of avian unihemispheric sleep under the risk of predation. *Behav Brain Res* 1999;105(2):163–72.
- [21] Rattenborg N, Lima S, Amlaner C. Half-awake to the risk of predation. *Nature* 1999;397:397–8.
- [22] Rattenborg NC, Amlaner CJ, Lima SL. Unilateral eye closure and interhemispheric EEG asymmetry during sleep in the pigeon (*Columba livia*). *Brain Behav Evol* 2001;58(6):323–32.
- [23] Mascetti GG, Rugger M, Vallortigara G. Visual lateralization and monocular sleep in the domestic chick. *Brain Res Cogn Brain Res* 1999;7(4):451–63.
- [24] Mascetti GG, Vallortigara G. Why do birds sleep with one eye open? Light exposure of the chick embryo as a determinant of monocular sleep. *Curr Biol* 2001;11(12):971–4.
- [25] Bobbo D, Galvani F, Mascetti GG, Vallortigara G. Light exposure of the chick embryo influences monocular sleep. *Behav Brain Res* 2002;134(1-2):447–66.
- [26] Hasegawa M, Ebihara S. Circadian rhythms of pineal melatonin release in the pigeon measured by in vivo microdialysis. *Neurosci Lett* 1992;148(1-2):89–92.
- [27] Fukuhara C, Liu C, Ivanova TN, Chan GC, Storm DR, Iuvone PM, Tosini G. Gating of the cAMP signaling cascade and melatonin synthesis by the circadian clock in mammalian retina. *J Neurosci* 2004;24(8):1803–11.
- [28] Hamm HE, Takahashi JS, Menaker M. Light-induced decrease of serotonin *N*-acetyltransferase activity and melatonin in the chicken pineal gland and retina. *Brain Res* 1983;266(2):287–93.
- [29] Fukuhara C, Dirden JC, Tosini G. Photic regulation of melatonin in rat retina and the role of proteasomal proteolysis. *Neuroreport* 2001;12(17):3833–7.
- [30] Adachi A, Nogi T, Ebihara S. Phase-relationship and mutual effects between circadian rhythms of ocular melatonin and dopamine in the pigeon. *Brain Res* 1998;792(2):361–9.
- [31] Klein DC, Coon SL, Roseboom PH, Weller JL, Bernard M, Gastel JA, et al. The melatonin rhythm-generating enzyme: molecular regulation of serotonin *N*-acetyltransferase in the pineal gland. *Recent Prog Horm Res* 1997;52:307–57 [discussion 357–358].
- [32] Binkley S, Macbride SE, Klein DC, Ralph CL. Regulation of pineal rhythms in chickens: refractory period and nonvisual light perception. *Endocrinology* 1975;96(4):848–53.
- [33] Deguchi T, Axelrod J. Control of circadian change of serotonin *N*-acetyltransferase activity in the pineal organ by the beta-adrenergic receptor. *Proc Natl Acad Sci USA* 1972;69(9):2547–50.
- [34] Fukuhara C. Effect of dark exposure in the middle of the day on period1, period2, and arylalkylamine *N*-acetyltransferase mRNA levels in the rat suprachiasmatic nucleus and pineal gland. *Brain Res Mol Brain Res* 2004;130(1-2):109–14.
- [35] Mendelson WB, Gillin JC, Dawson S, Lewy AJ, Wyatt RJ. Effects of melatonin and propranolol on sleep of the rat. *Brain Res* 1980;201:240–4.
- [36] Huber R, Deboer T, Schwierin B, Tobler I. Effect of melatonin on sleep and brain temperature in the Djungarian hamster and the rat. *Physiol Behav* 1998;65(1):77–82.
- [37] Prichard J, RT S, WH O, RM B, Behan M. Alterations in anatomy and function of sleep and circadian centers in dark-reared rats. *Sleep Abstract Supplement*, vol. 25. Abstract Supplement.
- [38] Wada Y, Okano T, Fukada Y. Phototransduction molecules in the pigeon deep brain. *J Comp Neurol* 2000;428(1):138–44.
- [39] Kuenzel WJ. The search for deep encephalic photoreceptors within the avian brain, using gonadal development as a primary indicator. *Poult Sci* 1993;72(5):959–67.
- [40] Vallortigara G. Comparative neuropsychology of the dual brain: a stroll through animals' left and right perceptual worlds. *Brain Lang* 2000;73(2):189–219.
- [41] Andrew RJ. The nature of behavioural lateralization in the chick. In: Andrew RJ, editor. *Neural and Behavioural Plasticity: The Use of the Domestic Chick as a Model*. Oxford: Oxford University Press; 1991. p. 536–54.
- [42] Vallortigara G, Andrew RJ. Lateralization of response to change in a model partner by chicks. *Anim Behav* 1991;41:187–94.