## RESEARCH ARTICLE

# **Monocular learning of a spatial task enhances sleep in the right hemisphere of domestic chicks (Gallus gallus)**

**Cristian Nelini · Daniela Bobbo · Gian G. Mascetti** 

Received: 16 June 2011 / Accepted: 29 January 2012 / Published online: 19 February 2012 © Springer-Verlag 2012

**Abstract** Unihemispheric sleep is an aspect of cerebral lateralization of birds. During sleep, domestic chicks show brief periods during which one eye is open whilst the other remains shut. In this study, time spent in sleeping and in monocular-unihemispheric sleep (Mo-Un sleep) was investigated following the monocular learning of a spatial discrimination task. Two groups of experimental chicks from day 8 to day 11 post-hatching were trained in a spatial paradigm based on geometrical and topographical clues. One group performed the task with left eye open (LE-chicks), whilst another group performed the task with the right eye open (RE-chicks). LE-chick learned the task, whilst REchicks were unable to learn. Time spent in binocular sleep and right Mo-Un sleep (right eye closed and left hemisphere sleeping) was equal in both groups of chicks. Time spent in left Mo-Un sleep (left eye closed and right hemisphere sleeping) was significantly higher in LE-chicks than in RE-chicks. Laterality index reveals that LE-chicks had a significant bias towards more left Mo-Un sleep at any recording day, whilst RE-chicks showed a significant bias towards more right Mo-Un sleep at day 8 and 9 but not at days 10 and 11. RE-chick bias at days 8 and 9 could be attributed to a recovery process in left hemisphere connected to its activation/use effect during trials whilst recovery would be absent at days 10 and 11. LE-chicks bias would be associated with the formation of a spatial memory trace and with a recovery process in right hemisphere.

**Keywords** Sleep · Unihemispheric sleep · Local sleep · Spatial learning · Domestic chick · Lateralization

## **Introduction**

An important aspect of the cerebral lateralization of birds (Ball et al. [1988](#page-7-0)) is the phenomenon of monocular-unihemispheric sleep (Mo-Un sleep). During sleep, birds show brief and transient periods in which one eye is open whilst the other one remains shut (Spooner [1964](#page-7-1); Ball et al. [1988;](#page-7-0) Mascetti et al. [1999:](#page-7-2) Mascetti and Vallortigara [2001\)](#page-7-3). Electrophysiological recordings revealed that the hemisphere contra-lateral to the open eye shows an EEG with fast waves typical of wakefulness, whilst the EEG in hemisphere contra-lateral to the closed eye shows a typical pattern of slow wave sleep. Bilateral eye closure is associated with bihemispheric slow wave and REM sleep as widely reported (Ookawa and Takagi [1968;](#page-7-4) Ookawa [1971](#page-7-5); Ball et al. [1988](#page-7-0); Rattenborg et al. [1999](#page-7-6); Bobbo et al. [2002\)](#page-7-7).

The experience during wakefulness influences subsequent patterns and the homoeostasis of sleep (i.e. Horne and Walmsley [1976;](#page-7-8) Horne and Minard [1985](#page-7-9); Borbely [2001](#page-7-10); Martinez-Gonzalez et al. [2008,](#page-7-11) Rattenborg et al. [2009](#page-7-12); Hanlon et al. [2009](#page-7-13)). In addition, several studies have pointed out that sleep has a regional aspect named local sleep, which is dependent on the specific activation of brain regions during wakefulness (i.e. Kattler et al. [1994](#page-7-14); Huber et al. [2004](#page-7-15)). That is, when one part of the brain is involved in a specific learning process, that part would subsequently have more sleep than other parts less or not at all involved in that learning. The increase in local sleep would be beneficial to the local plastic changes actively involved in the learning task (Huber et al. [2004](#page-7-15)). It has been proposed that Mo-Un sleep of birds may be considered as a kind of local sleep.

Nelini et al. ([2010](#page-7-16)) studied the relationship between the Mo-Un sleep pattern and spatial learning in domestic chicks using a paradigm of geometric modules (Vallortigara et al.

C. Nelini  $\cdot$  D. Bobbo  $\cdot$  G. G. Mascetti ( $\boxtimes$ ) Department of General Psychology, University of Padova, Padova, Italy e-mail: giangastone.mascetti@unipd.it

[1990](#page-7-17)). They reported that experimental chicks were able to learn the spatial task, subsequently showing a significant bias towards more left Mo-Un sleep. That bias was associated with a predominant engagement of the right hemisphere during trials because several studies had reported that chick's right hemisphere has a preferential involvement in topographic orientation behaviour (Rashid and Andrew [1989](#page-7-18); Rogers and Anson [1979;](#page-7-19) Vallortigara [2000](#page-7-20); Vallortigara and Andrew [1991;](#page-7-21) Vallortigara et al. [1996](#page-7-22); Vallortigara and Rogers [2005](#page-7-23)). Control chicks that did not learn the task showed no eye-closure bias at the first 2 days of training and a slight bias for more right eye closure at the latter two. It was assumed that there was an absence of hemispheric dominance in former days and an activation of the left hemisphere in latter ones (Nelini et al. [2010\)](#page-7-16). In Nelini et al. ([2010\)](#page-7-16) study, experimental chicks were trained binocularly, and therefore a right hemisphere dominance during trials was safely inferred from previous behavioural studies (Rashid and Andrew [1989;](#page-7-18) Rogers and Anson [1979](#page-7-19); Vallortigara et al. [1996](#page-7-22)). Nelini et al. ([2010\)](#page-7-16) suggested that the bias for more left Mo-Un sleep of experimental chicks was associated with the consolidation of spatial memory in the right hemisphere, even though an additional process of recovery process after a higher activation (use effect) of right hemisphere was not excluded.

The rationale of present study would rely on two aims: (1) the association between spatial learning and sleep (Mo-Un sleep and Bin-sleep) was more precisely verified because training on the spatial task was performed monocularly thereby lateralized to only one eye-hemisphere system; (2) the training paradigm and subsequent sleep data could clarify the roles of learning and hemispheric activation (use effect) on the pattern of Mo-Un sleep which was only assumed in the Nelini et al. ([2010\)](#page-7-16) previous paper.

### **Materials and methods**

#### Subjects

The subjects were 12 female Hybro domestic chicks (*Gallus gallus*) hatched from eggs obtained from a commercial hatchery ("Agricola Berica", Montegalda, Vicenza, Italia). The eggs were incubated in the laboratory, in an automatically turning incubator FIEM snc, MG 100H  $(45 \times 58 \times 43$  cm), under constant temperature  $(37.7^{\circ}C)$ , humidity (about 50–60%) and in darkness because previous studies showed that light stimulation in ovo affects the pattern of Mo-Un sleep (Bobbo et al. [2002\)](#page-7-7). We used 8-dayold chicks because they show a consistent pattern of sleep behaviour during the second week post-hatching and stable feeding and drinking behaviour. Moreover, at this age, they are already imprinted and their body growth and motor



<span id="page-1-0"></span>**Fig. 1** Apparatus for chicks rearing and sleep recording

activity are suitable for the learning–training used in this experiment.

#### Apparatus

The apparatus used for chick rearing and sleep recording has been described elsewhere (Bobbo et al. [2002](#page-7-7), [2006;](#page-7-24) Mascetti et al. [1999,](#page-7-2) [2004a,](#page-7-25) [b;](#page-7-26) Nelini et al. [2010\)](#page-7-16). Briefly, it consisted of two glass home-cages (30  $\times$  40  $\times$  40 cm) with semi-transparent cloths along the wall serving as one-way screen (Fig. [1](#page-1-0)). Each cage was continuously lit from above by a 60-W electric light bulb. Two transparent glass containers provided water and food for the whole duration of the experiment. The imprinting object was suspended freely in the middle of the cage at about head height for the chick.

The apparatus for spatial training has been described elsewhere (Nelini et al. [2010\)](#page-7-16). Briefly, it consisted of a rectangular-shaped arena which walls were 120 cm (longer walls) and 60 cm (shorter walls) length and 40 cm height (Fig. [2\)](#page-2-0). Transparent glass containers (diameter 5 cm, height 6 cm) were positioned at the four corners and filled with food and having a thin plastic net glued over the top opening. Only one container also had a small hole (diameter 2 cm) cut on top of the net, to allow chicks the access to food. The top of the arena was covered by a veil and three light bulbs (25 W each), positioned at the top homogeneously illuminated the arena.

## Procedure

The experimental paradigm used for spatial learning phase was the paradigm of the geometric module (rectangular arena), which allows the evaluation of the re-orienteering abilities of animals based exclusively on geometrical and topographical clues (Vallortigara et al. [1990](#page-7-17)). The procedure



<span id="page-2-0"></span>**Fig. 2** Apparatus used for spatial training

was similar to that reported in the study of Nelini et al. [\(2010](#page-7-16)) for the experimental animals, but in present study, chicks were trained monocularly. Immediately after hatching, chicks were placed singly into the glass home-cages and kept there from day 1 to day 8 post-hatching. At day 7, chicks were placed singly into the training arena for 30– 40 min, allowing to explore and peaking for food at the corners. Thereafter, chicks were deprived of food for 13 h in order to induce the necessary level of motivation.

Training sessions were carried out at days 8, 9, 10 and 11 post-hatching. Each session consisted of three blocks of 10 trials, each one separated by a 3-min interval. A trial lasted 2 min maximum. At the beginning of each trial, chick was taken from a cardboard box with one hand, after being disoriented, taking care to cover its eyes with the other hand for entire duration of displacement; the animal was placed in the middle of the arena in a random orientation with respect to the sagittal axis of the body. During the inter-trial interval, the chick was placed back into the cardboard box and was slowly rotated for 5–10 s, in order to exclude the use of compass or inertial information. Meanwhile, the floor of the arena was accurately cleaned from any trace of food and any other debris.

Six chicks were trained with the right eye occluded and the left eye open (LE-chicks) and six chicks were trained with the left eye occluded and the right eye open (REchicks). Eye occlusion was performed with an easy-removable sticky black patch made of canvas (Fig. [3](#page-2-1)).

All chicks were trained singly in the spatial task in which only one container, positioned in the corner A of the arena (Fig. [4a](#page-2-2)), having a hole on the top thus making the food available. A trial ended either when the animal chose the reinforced container (A) and eat some food (few pecks were allowed) or when the chick failed to chose it. The first corner the chick selected and approached was scored. Given the shape of the arena, two pairs of positions can be identified: (1) the "correct corner" includes both the reinforced corner and its rotational equivalent (corners A and C in Fig. [4a](#page-2-2)) (the long wall of the arena was at the left side of chick's body); a correct trial was scored either the chick first approached corner A or corner C.  $(2)$  the "incorrect corner" includes the other two corners (corners B and D in





**Fig. 3** Chick with the sticky patch made of canvas that covers one eye and the object of imprinting

<span id="page-2-1"></span>

<span id="page-2-2"></span>**Fig. 4** Arenas used in: **a** training paradigm for spatial learning. **b** test session paradigm

Fig. [4a](#page-2-2)) (the long wall was at the right side of chick's body) and when they were approached, an incorrect trial was scored. The choice of reinforcing only one of the two correct corners was made in order to be sure that both were really indistinguishable for the chicks. The learning criterion was achieved when the animals chose the correct corners in 24 or more trials out of 30. The animals that not reached that criterion at any of the training days were discarded  $(20\%)$ . At day 11, both groups of chicks were first submitted monocularly to 20 training trials and thereafter to



<span id="page-3-0"></span>**Fig. 5** The experimental scheme

two test blocks of 7 trials each. In the "test condition," the procedure was the same of training but food was not accessible at any of the four containers (Fig. [4b](#page-2-2)), so that test was conduced in an extinction paradigm. Criterion was attained when experimental chicks chose the corners A or C in at least the 80% or more of test trials that was reached by all experimental chicks.

At the end of each one of the training session and after the test session, chicks were returned singly in their homecage and sleep behaviour (eye closure and body positions) was scored for 3 h hours consecutively by direct observation. Small mirrors mounted on rods allowed the experimenters to approach the animal and to check for the eye state (open or closed) when the chick's position or posture hindered observation from outside. The experimenter recorded the number and duration of episodes of Bin-sleep (both eye closed) and Mo-Un sleep (one eye was open whilst the other remained shut). The experimental scheme is shown in Fig. [5](#page-3-0).

#### Data analysis

For learning, the mean percentages of correct choices (corner A or corner C) on the total choices showed by chicks during training and test sections were calculated. Data were analysed by ANOVA repeated measures with Group (LEchicks and RE-chicks) as a between-subjects factor and Day  $(8, 9, 10,$  and test day 11) as a within-subjects factor. Moreover, we calculated one-sample two-tailed t tests. Significant departures from chance level  $(50\%)$  in mean percentages of corrects choices indicated significant choice for the correct position.

For sleep, the time (calculated in seconds) of total sleep (binocular plus monocular), Bin-sleep, Mo-Un sleep (right plus left), left and right Mo-Un sleep were analysed by ANOVA repeated measures (after checking for homogeneity and normality of data distributions) with Group as between-subjects factors and Day (days 8, 9, 10 and 11) as within-subjects factors.

In order to evaluate the Mo-Un sleep biases, we used a proportional measure of the time spent exactly, because we wanted to check for left–right differences irrespective of the absolute amount of Mo-Un sleep. The "laterality index" was calculated for time spent in right or left monocular sleep using the following formula: {[time (number of episodes) spent with the left eye closed $-$  [time (number of episodes) spent with the right eye closed]/[time (number of episodes) spent with the left eye closed] + [time (number of episodes) spent with the right eye closed] $\} \times 100$ . Laterality index was analysed by ANOVA repeated measure (after checking for homogeneity and normality of data distributions) with Group as between-subjects factors and Day  $(days 8, 9, 10 and 11)$  as within-subjects factors. Significant departures (biases) from chance level (0%) in the "laterality index", which indicated significant bias towards more right or left eye closure, were estimated by one-sample *twotailed t test*.

#### **Results**

#### Learning

The results of spatial learning are reported in Fig. [6.](#page-4-0) They represent the percentage of the first choice in each position (correct position: corners A or C; and wrong position: corners B or D) during 3 successive days of training and a short training session at day 11 before the test. ANOVA showed a main effect of condition  $(F_{(1,10)} = 71,359,$ *P* < .001) and a main effect of day (session)  $(F_{(4,40)} = 3,413,$  $P < .020$ ) whilst the interaction condition  $\times$  session was not significant  $(F_{(4,40)} = 4,452, P = \text{ns})$ . The data indicated a systematic improvement in searching behaviour at corner A or C (correct position) for LE-chicks, whilst the performance of RE-chicks remained at chance level. One-sample two-tailed t tests calculated for LE-chicks at each day revealed: day 8,  $t_{(5)} = 1,709$ ,  $P = ns$ ; day 9,  $t_{(5)} = 7.427$ , *P* = .002; day 10,  $t_{(5)} = 8,226$ , *P* = .001; day 11,  $t_{(5)} = 6,345$ , *P* = .003; test at day 11,  $t_{(5)} = 26,245, P < .001$ ). LE-chicks learning performance was above chance level at all days: below criterium level at day 8 and above that level at days 9, 10 and 11. RE-chicks performance remained around chance level. Overall, LE-chicks learned the task, whilst RE-chicks did not.

Time spent sleeping in Bin-sleep

ANOVA repeated measures reveals that time spent in Binsleep was not different between LE-chicks and RE-chicks (Fig. [7\)](#page-4-1) (Day: *F*(3,30) 2,486, *P* = n.s.; Group: *F*(1,10) 1,079, *P* = n.s.; interaction Day  $\times$  Group,  $F_{(3,30)}$  2,486, *P* = n.s.). Both groups of animals showed the same time spent in Binsleep.



<span id="page-4-0"></span>**Fig. 6** Learning curves of LE-chicks and RE-chicks



<span id="page-4-1"></span>**Fig. 7** Total time spent in binocular sleeping (in seconds). *Bars* represent standard errors of means

#### Monocular/unihemispheric sleep

Total time spent in Mo-Un sleep and time spent in Mo-Un are shown in (Figs. [8](#page-4-2) and [9](#page-4-3)a, b). ANOVA repeated measures on the total time spent in Mo-Un sleep (right and left together) revealed no significant effects (Day:  $F_{(3,30)}$  0,655,  $P =$  n.s.; Group  $F_{(1,10)}$ ,  $P =$  n.s. and interaction Day  $\times$ Group  $F_{(3,30)}$  0,737,  $P =$  n.s.) (Fig. [8\)](#page-4-2). ANOVA revealed no significant effects of time spent in right Mo-Un sleep (right eye closed/left eye open): Day  $_{(3,30)}$  1,243, *P* = n.s.; Group  $_{(1,10)}$ 3,198,  $P =$  n.s.; interaction Day  $\times$  Group  $F_{(3,30)}$  0,737,  $P =$ n.s.) (Fig. [9](#page-4-3)a). ANOVA on the time spent in left Mo-Un sleep (left eye closed/right eye open) revealed no significant effects of Day ( $F_{(3,30)}$  0,203,  $P =$  n.s. and interaction Day  $\times$  Group  $F_{(3,30)}$  1,717,  $P =$  n.s.) but there was a significant effect of Group ( $F_{(1,10)} = 20,596$  $F_{(1,10)} = 20,596$  $F_{(1,10)} = 20,596$ ,  $P = .001$ ) (Fig. 9b). Overall, total time spent in Mo-Un sleep and time spent in right Mo-Un sleep were similar in both groups of animals,



<span id="page-4-2"></span>**Fig. 8** Total time spent sleeping in monocular sleep (in seconds). *Bars* represent standard errors of means



<span id="page-4-3"></span>**Fig. 9 a** Time spent in right monocular sleep (seconds). **b** time spent in left monocular sleep (seconds). *Bars* represent standard errors of means

whilst time spent in left Mo-Un sleep was significantly higher in LE-chicks than in RE-ones.

# Laterality index of Mo-Un sleep

Laterality index of the percentage of time spent in Mo-Un sleep is shown in Fig. [10.](#page-5-0) ANOVA repeated measures revealed a significant main effects only on Group  $(F_{(1,10)} = 20,596, P < .001)$  but Day  $(F_{(3,30)} 1,435 P = n.s.)$ and interaction Group  $\times$  Day ( $F_{(3,30)}$  1,764,  $P =$  n.s.) were both not significant. LE-chicks showed a preference of left Mo-Un, whilst RE-chicks chicks showed a reverse pattern.



<span id="page-5-0"></span>**Fig. 10** Laterality index of monocular sleep. *Bars* represent standard errors of means

This effect was consistent during all training and test sessions. ANOVA data indicate that post hoc analysis was not allowed. But, laterality biases were evaluated with *t tests* (one-sample two-tailed) comparing laterality score (%) of each group-per-day with chance level  $(0\%)$ . Significant departures towards more left Mo-Un sleep for LE-chicks after all training sessions were found: (day 8,  $t_{(5)} = 3,936$ , *P* = .011; day 9,  $t_{(5)} = 5,795$ , *P* = .002; day 10,  $t_{(5)} = 4,235$ , *P* = .008 and day 11(test sessions) ( $t_{(5)}$  = 4,427, *P* = .007). The *t tests* on RE-chicks revealed significant departures from chance level  $(0\%)$  with a significant bias towards for more right Mo-Un sleep only after training sessions of days 8 and 9 (day 8,  $t_{(5)} = -4,387, P = .007$ ; day 9,  $t_{(5)} = 5,431$ ,  $P = .003$ , but there was no significant departures at days 10 and 11 (day 10,  $t_{(5)} = -1,379$ ,  $P =$  n.s.; day 11 (test sessions),  $(t_{(5)} = -1,289, P = n.s.).$ 

## **Discussion**

It is known that sleep plays a role in memory consolidation (i.e. Ambrosini et al. [1988](#page-6-0); Smith and Butler [1982;](#page-7-27) Winson [1993](#page-7-28); Smith [1996;](#page-7-29) Graves et al. [2001;](#page-7-30) Maquet, [2001](#page-7-31); Walker and Stickgold [2004](#page-7-32), [2006;](#page-7-33) Orban et al. [2006\)](#page-7-34). In fact, waking experiences (i.e. learning) influence subsequent duration, pattern and homoeostasis of sleep (Horne and Walmsley [1976](#page-7-8); Horne and Minard [1985;](#page-7-9) Borbely [2001](#page-7-10); Martinez-Gonzalez et al. [2008;](#page-7-11) Rattenborg et al. [2009](#page-7-12); Hanlon et al. [2009](#page-7-13)). In present study, the total duration of both Bin-sleep and Mo-Un sleep was similar in both groups of chicks, indicating that monocular training was not followed by changes in the duration of sleep irrespective that there was learning (LE-chicks) or there was not (RE-chicks). In other words, the functional involvement of one hemisphere during training was not followed by an increase in time spent sleeping. In a previous study of Nelini et al. ([2010\)](#page-7-16), chicks of experimental group were trained binocularly, thereby both hemispheres were simultaneously involved during trials. Subsequently, those experimental chicks showed an increase in the duration of Bin-sleep, whilst that increase was not found in the control chicks that were not submitted to the learning procedure. A reasonable question could be formulated: would a significant increase in time spent in sleeping takes place only when the whole brain is activated during trials but it would not when half brain is directly involved in a task whilst the other half remains quiescent? Data from present study would provide a positive answer but previous studies on unilateral brain stimulation and sleep do not give clear cues so that issue would remain open. In humans, Kattler et al. [\(1994\)](#page-7-14) showed that unilateral stimulation of left somatosensory cortex during wakefulness resulted in a small but significant increase in NREM sleep in the central EEG derivation relative to baseline which meant a shift of power towards the left hemisphere. But, there were no significant differences between the NREM and REM sleep baseline values and latencies, and the same sleep measures recorded after unilateral somatosensory stimulation. Vyazovskiy et al. [\(2000](#page-7-35)) submitted rats to unilateral whiskers stimulation, whilst whiskers of the other side were previously cut. Besides an increase in sleep on the hemisphere contra-lateral to the intact whiskers, they also reported an increase in NREM and REM sleep relative to corresponding baseline values. Sleep recordings were performed after a 6-h sleep deprivation during dark period, and consequently, the increase in both sleep stages would be associated with both deprivation and/or to unilateral whiskers stimulation. In humans, Huber et al. ([2004](#page-7-15) and [2006](#page-7-36)) submitted subjects to motor learning, which involved a specific brain region of one hemisphere whilst one arm was immobilized. They reported regional increase in SWS in the hemisphere that controlled the arm used for learning and a regional decrease in SWS in the hemisphere connected with immobilized arm, but values of NREM and REM were not significantly different between experimental subjects and control ones. In a study on human subjects, Cajohem et al. ([2008\)](#page-7-37) found that a  $2 h$  of light stimulation of a left visual hemifield caused an attenuation of the waking alfa EEG activity and a decrease in EEG delta activity during subsequent sleep in the right visual cortex, but no effect was recorded on the left visual cortex after right visual hemifield. However, total sleep and sleep efficiency did not change in experimental subjects as compared with non-light stimulated controls (Cajohem et al. [2008\)](#page-7-37).

LE-chick learned the task whilst RE-chicks did not and both groups of chicks differed in the pattern of Mo-Un sleep. Time spent in right Mo-Un sleep was similar in both groups of chicks, whilst time spent in left Mo-Un sleep was significantly higher in LE-chicks than in RE-chicks. In addition, *t tests* on laterality index scores revealed that LE-chicks showed a significant bias for more left Mo-Un sleep after every training session (days), which should be associated with the competence of right hemisphere on the control of spatial behaviour which allowed LE-chicks to learn the task. Right hemisphere preferential involvement in topographic orientation tasks has been reported by several authors (Rashid and Andrew [1989;](#page-7-18) Rogers and Anson [1979](#page-7-19); Vallortigara [2000;](#page-7-20) Vallortigara and Andrew [1991](#page-7-21); Vallortigara et al. [1996;](#page-7-22) Vallortigara and Rogers [2005](#page-7-23)). LE-chicks bias was similar to the bias recorded in experimental chicks in Nelini et al. ([2010\)](#page-7-16) study. Three points should be discussed regarding the correlation between learning performance and left Mo-Un sleep. Learning performance of LE-chicks improved gradually from day 8 to day 11. The amount of time spent in left Mo-Un sleep was similar at all days, which would not correlate with gradual increase in learning level. But laterality index (a behavioural measure that allows to check for left–right differences irrespective of the absolute amount of Mo-Un sleep) showed that the amount of bias towards more left Mo-Un sleep in LE-chicks increased gradually from day 8 to day 11 correlating closely with the gradual increase in the level of learning performance. Several studies indicate that duration, pattern and homoeostasis of sleep correlated with waking experiences (i.e. learning) (Horne and Walmsley [1976](#page-7-8); Horne and Minard [1985](#page-7-9); Borbely [2001,](#page-7-10) Martinez-Gonzalez et al. [2008](#page-7-11); Rattenborg et al. [2009;](#page-7-12) Hanlon et al. [2009\)](#page-7-13). In adult pigeon, Lesku et al. [\(2011\)](#page-7-38) stimulated one left eye (right hemisphere) for 8 h and found that SWA during subsequent sleep was asymmetrical and higher in the right visual hyperpallium but not in the non-visual mesopallium (Lesku et al. [2011\)](#page-7-38). If passive left eye stimulation was followed by an increase in SWS in the contra-lateral visual hyperpallium, it is reasonable to assume that an active behaviour such as monocular learning should be able to elicit a significant bias towards more left Mo-Un sleep, which is in close correlation with the level of leaning performance and causing an extension of sleep time in the right hemisphere.

RE-chicks were unable to learn because left hemisphere should be incompetent for solving the spatial topographic task. The time spent in right Mo-Un sleep of RE-chicks was similar to that recorded in LE-chicks. Laterality index revealed a significant bias for more right Mo-Un sleep at days 8 and 9 and a bias absence at days 10 and 11. The bias at days 8 and 9 could be associated with a high activation or use effect of left hemisphere (i.e. Lesku et al. [2011\)](#page-7-38) likely caused by the initial submission to the training procedure (novelty effect) along with an intense motivation for searching the only container in which food was available (chicks were food-deprived). Left hemisphere activation would decrease at days 10 and 11 probably because novelty effect faded away and searching the proper food container became easier.

The issue that should be discussed is whether the Mo-Un bias of LE-chicks could be associated with the establishment of a spatial memory trace and/or to a process of recovery after right hemisphere activation (use effect). LE-chicks learned the task and it is reasonable to assume that a memory trace should be formed in the right hemisphere. In a recent study in adult pigeon, Lesku et al. ([2011\)](#page-7-38) stimulated the left eye (the right one was covered) for 8 h and found that SWA during subsequent sleep was asymmetrical and higher in the right hyperpallium but symmetrical in the non-visual mesopallium. In addition, the slope of SWSrelater slow waves was steeper in the right stimulated hyperpallium, which indicate a sort of synaptic potentiation in that structure (Lesku et al. [2011\)](#page-7-38). If a passive visual stimulation was able to cause plastic changes in right hyperpallium, it seems reasonable to suggest a presence of plastic changes after an active and highly motivated behaviour such as spatial learning of topographic cues in right hemisphere of LE-chicks. The more left Mo-Un sleep (time and bias) would cause an slight extension of sleep time in the right hemisphere (Bin-sleep plus Mo-Un sleep), which could be in favour to the establishment of a memory trace. It is known that sleep plays a role in memory consolidation (i.e. Ambrosini et al. [1988;](#page-6-0) Smith and Butler [1982;](#page-7-27) Winson [1993](#page-7-28); Smith, [1996](#page-7-29); Graves et al. [2001](#page-7-30); Maquet [2001;](#page-7-31) Walker and Stickgold [2004,](#page-7-32) [2006;](#page-7-33) Orban et al. [2006](#page-7-34)). However, a recovery process after a right hemisphere activation (use effect) during trials would have also a role in causing the more time spent/bias for more left Mo-Un sleep. A support comes from RE-chicks that did not learn but their use of right eye-left hemisphere during trial was able to trigger a significant bias for more right Mo-Un sleep at day 8 and 9 but not at days 10 and 11 (although not significant there was a tendency at latter days).

Finally, this study further confirms that sleep, whilst being a global process in birds as in mammals, also shows a regional aspect called local sleep (Huber et al. [2004](#page-7-15); Lesku et al. [2011\)](#page-7-38). That is, when one part of the brain is strongly stimulated (Cajohem et al. [2008;](#page-7-37) Lesku et al. [2011](#page-7-38)) or involved in a specific learning process (Huber et al. [2004\)](#page-7-15) that part would subsequently have more sleep than other parts less or not at all involved in learning.

**Acknowledgments** This study has been supported by Grant–PRIN-COFIN No. 200073JY8HY4\_001 of the Italian Ministry of University and Scientific Research (MIUR). The authors state that they have adhered to the "Principles of laboratory animal care (NIH publication No. 86-23, revised 1985)" and to legal requirements of our country (Authorization of Italian Ministry of Health, DM No. 156/2006-C).

#### **References**

<span id="page-6-0"></span>Ambrosini MV, Sadile AG, Gironi Carnevale UA, Mattiaccio M, Giuditta A (1988) The sequential hypothesis on sleep function. I. Evidence that the structure of sleep depends on nature of previous waking experience. Physiol Behav 143:325–337

- <span id="page-7-0"></span>Ball NJ, Amlaner CD, Shaffery JP, Opp MR (1988) Asynchronous eyeclosure and unihemispheric sleep in birds. In: Koella WP, Schultz H, Obal F, Visser P (eds) Sleep'86. Gustav Fischer Verlag, Stuttgart, pp 151–153
- <span id="page-7-7"></span>Bobbo D, Galvani F, Mascetti GG, Vallortigara G (2002) Light exposure of chick embryo influences monocular sleep. Behav Brain Res 134:447–466
- <span id="page-7-24"></span>Bobbo D, Vallortigara G, Mascetti GG (2006) The effects of early posthatching changes of imprinting object on the pattern of monocular/unihemispheric sleep of domestic chicks. Behav Brain Res 170:23–28
- <span id="page-7-10"></span>Borbely AA (2001) From slow waves to sleep homeostasis: new perspectives. Arch Ital Biol 139:53–61
- <span id="page-7-37"></span>Cajohem C, Di Biase R, Imai M (2008) Interhemispheric EEG asymmetries durino unilateral bright-light exposure and subsequent sleep in humans. Am J Physiol Regul Integr Comp Physiol 294:R1053–R1060
- <span id="page-7-30"></span>Graves L, Pack A, Abel T (2001) Sleep and memory: a molecular perspective. Trends Neurosci 24:237–243
- <span id="page-7-13"></span>Hanlon EC, Farraguna U, Vyazovskij V, Tononi G, Cirelli C (2009) Effects of skilled training on sleep slow wave activity and cortical gene expression in the rat. Sleep 32:719–729
- <span id="page-7-9"></span>Horne JA, Minard A (1985) Sleep and sleepiness following a behaviourally active day. Ergonomics 28:567–575
- <span id="page-7-8"></span>Horne JA, Walmsley B (1976) Daytime visual load and the effects upon human sleep. Psychophysiol 13:115–120
- <span id="page-7-15"></span>Huber R, Ghilardi MF, Massimini M, Tononi G (2004) Local sleep and learning. Nature 430:78–81
- <span id="page-7-36"></span>Huber R, Ghilardi MF, Massimini M, Ferrarelli F, Riedner BA, Peterson MJ, Tononi G (2006) Arm immobilization causes cortical plastic changes and locally decrease sleep slow wave activity. Nat Neurosci 9:1169–1176
- <span id="page-7-14"></span>Kattler H, Dijk DJ, Boberly A (1994) Effects of unilateral somatosensory stimulation prior to sleep to the sleep EEG in humans. J Sleep Res 3:159–164
- <span id="page-7-38"></span>Lesku JA, Vyssotski AL, Martinez-Gonzalez D, Wilzeck C, Rattemborg NC (2011) Local sleep homeostasis in the avian brain: convergence of sleep function in mammals and birds? Proc R Soc B 278:2419–2428
- <span id="page-7-31"></span>Maquet P (2001) The role of sleep in learning and memory. Science 294:1048
- <span id="page-7-11"></span>Martinez-Gonzalez D, Lesku JA, Rattenborg NC (2008) Increased EEG spectral power density during sleep following short-term sleep in pigeons Columbia livia: evidence for avian sleep omestasis. J Sleep Res 17:140–153
- <span id="page-7-3"></span>Mascetti GG, Vallortigara G (2001) Why do birds sleep with one eye open? Light exposure of chick embryo as a determinant of monocular sleep. Curr Biol 11:971–974
- <span id="page-7-2"></span>Mascetti GG, Rugger M, Vallortigara G (1999) Visual lateralization and monocular sleep in the domestic chick. Cogn Brain Res 7:451–463
- <span id="page-7-25"></span>Mascetti GG, Bobbo D, Rugger M, Vallortigara G (2004a) Monocular sleep in male domestic chick. Behav Brain Res 153:447–452
- <span id="page-7-26"></span>Mascetti GG, Rugger M, Vallortigara G, Menesatti S (2004b) Unihemispheric sleep and visual learning in domestic chicks. J Sleep Res 13(Sup. 1):482
- <span id="page-7-16"></span>Nelini C, Bobbo D, Mascetti GG (2010) Local sleep: a spatial learning task enhances sleep in the right hemisphere of domestic chicks (Gallus gallus). Exp Brain Res 205:195–204
- <span id="page-7-5"></span>Ookawa T (1971) Electroencephalograms recorded from the telencephalon of blinded chickens during behavioural sleep and wakefulness. Poultry Sci 50:731–736
- <span id="page-7-4"></span>Ookawa T, Takagi K (1968) Electroencephalograms of free behavioral chicks at various developmental ages. Jap J Physiol 18:87–99
- <span id="page-7-34"></span>Orban P, Rauchs G, Balteau E, Degueldre C, Luxen A, Maquet P, Peigneux P (2006) Sleep after spatial learning promotes covert reorganization of brain activity. PNAS 103:7124–7129
- <span id="page-7-18"></span>Rashid N, Andrew RJ (1989) Right hemisphere advantages for topographical orientation in the domestic chick. Neuropsychologia 27:937–948
- <span id="page-7-6"></span>Rattenborg NC, Lima SL, Amlaner CJ (1999) Half-awake to the risk of predation. Nature 397:397–398
- <span id="page-7-12"></span>Rattenborg NC, Martinez-Gonzalez D, Lesku JA (2009) Avian sleep homeostasis: convergent evolution of complex brains, cognition and sleep function in mammals and birds. Neurosci Behav Rev 33:253–270
- <span id="page-7-19"></span>Rogers LJ, Anson JM (1979) Lateralization of function in the chicken forebrain. Pharmacol Biochem Behav 10:679–686
- <span id="page-7-29"></span>Smith C (1996) Sleep states, memory processes and synaptic plasticity. Behav Brain Res 78:49–56
- <span id="page-7-27"></span>Smith C, Butler S (1982) Paradoxical sleep at selective times following training is necessary for learning. Physiol Behav 29:469–473
- <span id="page-7-1"></span>Spooner C (1964) Observations on the use of the chick in the pharmacological investigation of the central nervous system. PhD Dissertation, UCLA
- <span id="page-7-20"></span>Vallortigara G (2000) Comparative neuropsychology of the dual brain: a stroll through left and right animals' perceptual worlds. Brain Lang 73:189–219
- <span id="page-7-21"></span>Vallortigara G, Andrew RJ (1991) Lateralization of response to change in a model partner by chicks. Anim Behav 41:187–194
- <span id="page-7-23"></span>Vallortigara G, Rogers LJ (2005) Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. Behav Brain Sci 28:575–589
- <span id="page-7-17"></span>Vallortigara G, Zanforlin M, Pasti G (1990) Geometric modules in animal spatial representations: a test with chicks (Gallus gallus). J Comp Psychol 104:248–254
- <span id="page-7-22"></span>Vallortigara G, Regolin L, Bortolomiol G, Tommasi L (1996) Lateral asymmetries due to preference in eye use during visual discrimination learning in chicks. Behav Brain Res 74:135–143
- <span id="page-7-35"></span>Vyazovskiy V, Borbely A, Tobler I (2000) Unilateral vibrissae stimulation during waking induces interhemispheric asymmetry during subsequent sleep in the rat. J Sleep Res 9:367–371
- <span id="page-7-32"></span>Walker MP, Stickgold R (2004) Sleep dependent learning and memory consolidation. Neuron 44:121–133
- <span id="page-7-33"></span>Walker MP, Stickgold R (2006) Sleep, memory and plasticity. Ann Rev Psychol 57:139–166
- <span id="page-7-28"></span>Winson J (1993) The biology and function of rapid eye movement sleep. Curr Opin Neurobiol 3:243–248