Effects of social interaction on monocular/unihemispheric sleep in male and female domestic chicks

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Abstract
The monocular/unihemispheric sleep was studied in male and female domestic chicks reared socially. In first week post-hatching, chicks were reared in couples whilst during the second week, for half of the chicks the conspecific was maintained (Conspec-chicks) and for the other half the conspecific was removed (No-Conspec-chicks). During the first week, female chicks showed a bias for more left-eye closure/right unihemispheric sleep, whilst male chicks did not show any eye-closure bias. In the second week, both female and male Conspec-chicks showed a bias for right eye-closure/left unihemispheric sleep. Female No-Conspec-chicks did not show any eye-closure bias whilst male No-Conspec-chicks showed a bias for more left eye-closure/right unihemispheric sleep. Based on the role of the avian brain lateralization, a bias for more right or left eye-closure could be associated with a prevalent activation of left or right hemisphere during wakefulness. Eye-opening during sleep might be connected with the hemisphere that was not or was less activated during wakefulness or with lateralization of the environment monitoring against predation.

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1. Introduction
Several studies pointed out that domestic chicks (Gallus gallus) show remarkable lateralization of brain functions (reviews: Rogers and Andrew, 2002; Vallortigara, 2000). Overall, the left hemisphere seems to be mainly involved in visual learning and stimulus categorization whilst the right hemisphere seems to be mainly involved in spatial analysis and response to novelty (Rogers and Andrew, 2002; Vallortigara and Rogers, 2005a,b). Together with some marine mammals (Mukhametov, 1985) and other bird species (Ball et al., 1988), domestic chicks also exhibit a particular behavioural and electrophysiological state dubbed monocular-unihemispheric sleep (Spooner, 1964; Bobbo et al., 2002; Mascetti et al., 1999; Mascetti et al., 2004). During sleep, chicks exhibit brief and transient periods in which one eye is opened while the other remains shut. Electrophysiological recordings have shown that the hemisphere contra-lateral to the open eye exhibits an EEG with the fast waves typical of wakefulness whilst the hemisphere contra-lateral to the closed eye shows an EEG typical of slow wave sleep (Ookawa and Takagi, 1968; Ookawa, 1971; Bobbo et al., 2002). A period of slow-wave sleep in one hemisphere (unihemispheric sleep) is associated with the closure of the contra-lateral eye, whilst closure of both eyes is associated with bihemispheric slow-wave sleep or with REM sleep (Ball et al., 1988; Bobbo et al., 2002).

Mascetti et al. (1999, 2004) reported that chicks show an age-dependent pattern of monocular sleep, which seems to be associated with brain lateralization and strongly affected by the rearing conditions and gender of birds. During the first week post-hatching, female chicks reared with an imprinting object (a red ball) showed a pattern of monocular/unihemispheric sleep with either right or left eye-closure occurring with approximately the same frequency, except on day 5 in which right eye-closure was prevalent. During the second week, there was a clear bias towards more left eye-closure/right unihemispheric sleep (Mascetti et al., 1999). By contrast, female chicks reared without the imprinting object showed predominant left eye-closure/right unihemispheric sleep in both weeks, except on day 8 in which there was an equal amount of right and left eye-closure (Mascetti et al., 1999). Comparing the two rearing
conditions, it was apparent that during the first week imprinted female chicks showed more right-eye closure/left unihemispheric sleep than females reared without of the imprinting object. This effect was tentatively associated with consolidation of imprinting memories in the left hemisphere (review, Horn, 2004). Changes of the imprinting object such as a change of colour or its removal on day 8, caused a striking shift towards a predominant right eye-closure/left hemispheric sleep (Mascetti et al., 1999). This was tentatively associated with right hemisphere involvement (left eye opening during sleep) in response to novelty (Vallortigara and Andrew, 1991). Male chicks showed, however, a different pattern of eye-closure (Mascetti et al., 2004). During the first week post-hatching both imprinted and non-imprinted male chicks showed no significant bias towards predominant left or right eye-closure. During the second week, imprinted male chicks showed a tendency towards a predominant left eye-closure/right unihemispheric sleep, whilst male chicks reared without an imprinting object showed a tendency for more right-eye closure/left unihemispheric sleep. The removal of the imprinting object on day 8 did not cause any significant change in the pattern of eye-closure in male chicks (Mascetti et al., 2004).

There are other well-known sex differences in brain lateralization of domestic chicks. Anatomically, the crossed thalamofugal pathway (dorsal supraoptic decussation) is larger towards the right hyperstriatum than towards the left one (Boxer and Stanford, 1985; Deng and Rogers, 2000), but this asymmetry is more pronounced in males than in females (Deng and Rogers, 2000; Rogers and Erlich, 1983; Rogers and Sink, 1988). As a result of the asymmetry in the thalamofugal pathway, the right hemisphere receives a larger amount of binocular input than the left hemisphere and this difference is larger in males than in females. Rogers and Erlich (1983) claimed that age-dependent shifts in standing bias of behavioural control by one or other hemisphere are different and this difference is more pronounced in males than in females (Mascetti et al., 1999; Vallortigara, 1992) as well as response to novelty (Vallortigara et al., 1990; Vallortigara et al., 1999). This was tentatively associated with right hemisphere involvement (left eye opening during sleep) in response to novelty (Vallortigara and Andrew, 1991). Male chicks showed, however, a different pattern of eye-closure (Mascetti et al., 2004). During the first week post-hatching both imprinted and non-imprinted male chicks showed no significant bias towards predominant left or right eye-closure. During the second week, imprinted male chicks showed a tendency towards a predominant left eye-closure/right unihemispheric sleep, whilst male chicks reared without an imprinting object showed a tendency for more right-eye closure/left unihemispheric sleep. The removal of the imprinting object on day 8 did not cause any significant change in the pattern of eye-closure in male chicks (Mascetti et al., 2004).

2. Experimental

The pattern of monocular/unihemispheric and binocular/bihemispheric sleep of chicks was investigated in two rearing conditions: (a) the presence of social interaction and mutual imprinting with a conspecific; (b) after the removal of the cage-companion at the beginning of second week post-hatching.

2.1. Materials and methods

2.1.1. Subjects

The subjects were 16 males and 16 females Hybro (a local hybrid variety derived from the White Leghorn breed) domestic chicks (Gallus gallus). Chicks arrived in the laboratory from a commercial hatchery in the early morning of day 1 post-hatching.

2.1.2. Apparatus

Chicks were immediately housed in pairs of the same sex into glass cages (40 cm x 40 cm x 30 cm) with semi-transparent cloths on walls that produced a one-way screen effect. Each cage was illuminated continuously from above and contained two identical small transparent glass containers (5 cm in diameter, 5.5 cm in height), one for food and the other for water, both available ad libitum throughout the period of observation. Room temperature was maintained at 28 ± 1 °C.

2.1.3. Procedure

Pairs of chicks of the same sex were studied; this is because male chicks usually tended to be aggressive with opposite sex partners. There were two rearing conditions both for male and female chicks. (A) In the control condition, pairs of chicks of the same sex remained together throughout the overall period of the 2 weeks of experiment (Conspec-chicks). (B) In the experimental condition, the chicks in the pairs remained together during the first week, but during the second week one chick was left alone (No-Conspec-chicks) because the conspecific was removed in the early morning, just before the beginning of first sleep recording session of day 8. Behavioural sleep was recorded for 6 h daily during the 2 weeks in both rearing conditions. On day 1, one chick was marked on the head with red ink. In the experimental condition, the unmarked chick was removed on day 8.

For scoring chicks’ sleep, two experimenters alternated every hour in directly observing two pairs of chicks located in two cages within a single room. The room was completely darkened, but the cages were illuminated singly from above (bulb of 60 W). The experimenters could move all around the cages to find the best position for observing eye closure on the basis of the posture of the animal. Small mirrors mounted on rods allowed the experimenters to see the animal and to check for eye closure without disturbing it when the posture of the animal made the observation difficult. For each day, at least two different experimenters alternated in the task of observing the animals. The experimenters, who could not know the results obtained by each other, recorded the number and the duration of the episodes of binocular and monocular sleep. As in previous studies (Mascetti et al., 1999, 2004) the observations were carried out from days 1 to 12 inclusive, with the exception of days 6 and 7.

2.1.4. Data analyses

The percentage of time spent and percentage of the number of episodes of binocular sleep were analysed by ANOVA with “sex” and “rearing” as between-subjects factors, and “age” as a within-subjects factor. For monocular sleep, a “laterality index” was calculated for time spent and for the number of episodes of right or left monocular sleep using the formula:

\[
\text{Laterality index} = \frac{-\frac{\text{Time (number of episodes) spent with the left eye closed}}{\text{Time (number of episodes) spent with the right eye closed}} + \frac{\text{Time (number of episodes) spent with the left eye closed}}{\text{Time (number of episodes) spent with the right eye closed}}}{100}
\]

Laterality index was analyzed by ANOVA with “sex” and “rearing” as between-subjects factors and “age” as a within-subjects factor. Significant departures from chance level (0%) (significant bias towards right-or left-eye closure) were estimated by one-sample two-tailed t-tests.
2.2. Results

2.2.1. Binocular sleep

The percentage of time spent in binocular sleep during the first week is shown in Fig. 1A. The ANOVA revealed a significant effect of age ($F_{(4,120)} = 3.987, p = 0.0045$) indicating a decrease of binocular sleep in both male and female chicks during the first week post-hatching. There were no other statistically significant effects.

The mean number of events of binocular sleep during the first week is shown in Fig. 1B. The ANOVA revealed a statistically significant effect of age ($F_{(4,120)} = 2.872, p = 0.0259$); the effect of sex was not significant ($F_{(1,30)} = 4.030, p = 0.0538$). There was a general decrease of the number of episodes, but on day 2 such a decrease was higher in female than in male chicks.

The percentage of time spent in binocular sleep during the second week is shown in Fig. 2A and in Fig. 2B, for females and males, respectively. The ANOVA revealed a significant main effect of the rearing condition ($F_{(1,28)} = 23.884, p = 0.0001$). There were no other statistically significant effects. No-Conspec chicks of both sexes (conspecific removed) spent significantly less time in binocular sleep than chicks of Conspec-chicks (with conspecific).

The percentage of events of binocular sleep during the second week is shown in Fig. 3A and in Fig. 3B for females and males, respectively. The ANOVA revealed significant effects of rearing ($F_{(1,28)} = 65.712, p = 0.0001$), age ($F_{(1,112)} = 3.080, p = 0.019$) and age $\times$ sex ($F_{(4,112)} = 2.818, p = 0.0038$) and sex $\times$ rearing interactions ($F_{(1,120)} = 8.784, p = 0.0061$). The number of events of binocular sleep of males and females No-Conspec-chicks (with conspecific removal) was lower than in Conspec-chicks (with conspecific). This difference was more pronounced in males than in females.

2.2.2. Monocular sleep

The laterality indices for the time spent with either the right or the left eye closed during the first week are shown in Fig. 4A. The ANOVA revealed that the interaction age $\times$ sex was significant ($F_{(4,120)} = 4.297, p = 0.0028$). There were no other statistically significant effects. In females, there was prevalent left eye closure on days 1 and 2 ($t_{(15)} = 5.824, p = 0.0001$ and $t_{(15)} = 2.537, p = 0.023$, respectively) that subsequently tended to disappear. Males did not show any significant eye-closure bias during the first week.

The laterality index for the number of episodes of right or left eye closure during the first week is shown in Fig. 4B. The ANOVA revealed that the interaction age $\times$ sex ($F_{(4,120)} = 3.507, p = 0.0096$) was significant. There were no other statistically significant effects. Again, $t$-tests revealed that there was a bias for more left eye-closure on days 1 and 2, ($t_{(15)} = 5.519, p = 0.0001$ and $t_{(15)} = 2.619, p = 0.019$, respectively) in female chicks, whilst no significant biases were observed in male chicks.

The laterality index for the time spent with either the right or the left eye closed during the second week is shown in Fig. 5A and B for females and males, respectively. The ANOVA revealed a significant effect of rearing ($F_{(1,28)} = 47.895, p = 0.0001$), while the interaction age $\times$ rearing ($F_{(4,120)} = 2.301, p = 0.063$) was only close to significance. There were no other statistically significant effects. $t$-tests revealed that there was a bias towards more left eye-closure in Conspec-chicks ($t_{(15)} = 6.994, p = 0.0001$) whilst in No-Conspec-chicks the bias was towards a more right eye closure ($t_{(15)} = 3.601, p = 0.003$).

Fig. 1. (A) Mean percentages of time spent in binocular/bihemispheric sleep in male and females chicks during the first week post-hatching. (B) Mean percentages of number of events of binocular/bihemispheric sleep in male and females chicks during the first week post-hatching.

Fig. 2. Mean percentage of time spent in binocular/bihemispheric sleep during the second week post-hatching: No-Conspec-chicks: after the removal of conspecific. Conspec-chicks: with the conspecific. (A) Female chicks. (B) Male chicks.
The laterality index for the number of events of right or left eye-closure during the second week is shown in Fig. 6A and B for females and males, respectively. The ANOVA revealed that the main effect of rearing condition \((F(4,120) = 34.790, p = 0.0001)\) and the interaction age \(\times\) rearing \((F(4,112) = 2.506, p = 0.0461)\) were both statistically significant.

In Conspec-chicks, \(t\)-tests revealed that there was significant departures from chance level with a bias towards more left eye-closure in Conspec-chicks \((t(15) = 5.165, p = 0.0001)\) whilst in No-Conspec-chicks there was a bias towards more right eye closure \((t(15) = 3.261, p = 0.005)\).

3. Discussion

In agreement with previous studies (Mascetti et al., 1999, 2004) binocular sleep of male and female chicks (time spent and number of events) decreased during the first week post-hatching whilst during the second week, binocular sleep decreased more in No-Cospec-chicks (chicks that remained alone in the cage) than in Cospec-chicks (chicks that remained in pairs).

Regarding monocular/unihemispheric sleep, three statements should be formulated in advance: (1) lateralization of brain functions is remarkable in the domestic chicks and it is influenced by rearing conditions, age and sex (Rogers and Andrew, 2002; Vallortigara, 2000); (2) the closure of one eye is associated with EEG patterns of sleep only in the contralateral hemisphere (Ookawa and Takagi, 1968; Ookawa, 1971; Ball et al., 1988; Bobbo et al., 2002); (3) the pattern of eye-closure/eye-opening (monocular/unihemispheric sleep) could be associated with two concurrent behavioral processes: an extension of sleep in the hemisphere that assumed the control of behavior during wakefulness and the recurrent necessity of monitoring the environment during sleep: i.e. the presence or absence of the conspecific.

A significant bias towards a more left-eye closure/right unihemispheric sleep was recorded in female chicks during the first week, and particularly during the first 3 days. That bias could be associated with the process of imprinting, reinforced by the marked affiliative tendencies and social motivation shown by female chicks (Vallortigara et al., 1990; Vallortigara, 1992). In other terms, female chicks imprinted with each other during the first days post-hatching (Cipolla-Neto et al., 1982) showing an associated high level of social and emotional interaction. Therefore, the increase of right unihemispheric sleep would be connected with a prevalent activation of right hemisphere during wakefulness (Andrew and Brennan, 1983) and the consolidation of imprinting memories during sleep. Solodkin et al. (1985) reported that after imprinting there was an increase of REM sleep. Therefore, imprinting in female chicks should be connected with two effects: a bias for more right unihemispheric sleep and perhaps an increase of REM sleep.
sleep (Solodkin et al., 1985). Male chicks did not show any eye-
closure bias during the first week, which is in agreement with a
previous study on monocular sleep of male chicks reared with
an artificial imprinting object (Mascetti et al., 2004). Perhaps,
the imprinting process with the conspecific did not affect the
pattern of eye-closure because males showed a more reduced
social interaction and emotional motivation. It has been
reported that male chicks have low tendencies for social
interaction and social reinstatement (Vallortigara et al., 1990;
Vallortigara, 1992). Probably, male chicks also showed an
increase of REM sleep (Solodkin et al., 1985) associated with
imprinting but not with a unihemispheric sleep bias.
Unfortunately, the sex of their chicks was not indicated in
Solodkin et al. study (1985); they reported recording sleep in
chicks of “unknown sex”.

During the second week, both male and female Conspec-
chicks showed a bias towards more right eye-closure/left
unihemispheric sleep. By contrast, male No-Conspec-chicks
showed an overall bias for more left eye-closure/right
unihemispheric sleep whilst female No-Conspec-chicks did
not show any eye-closure bias, they rather showed a symmetric
unihemispheric sleep pattern. In other terms, the presence of the
conspecific up to the second week post-hatching, seems to be
associated with a marked increase of left unihemispheric sleep
in both female and male chicks, whilst the removal of the
conspecific seems to be associated with an increase in right
unihemispheric sleep in males but with an absence of bias in
females. On one hand, the interest in social partners of female
and male Conspec-chicks would tend to decrease with age
because other stimuli become more interesting such as objects
that are not social companions and features of environment. It
has been reported that chicks on the second week post-hatching
start to move about and to abandon the strict physical contact
with groom partners (hen and siblings) (Andrew, 1991). On the
other hand, the kind of social interaction changed and the
features of conspecific would be analysed and assigned into
categories thus requiring the dominant control of the left
hemisphere (Vallortigara, 2000). In males No-Conspec chicks,
there was an increase in right unihemispheric sleep after the
removal of conspecific that could be associated with two
aspects of chicks’ behaviour for both of which the right
hemisphere seems to be involved (Vallortigara, 2000): the
response to a novel condition, caused by the removal of the
conspecific and the analysis of topographic features associated
with exploratory behaviour. It is known that male chicks show a
marked exploratory behaviour (Vallortigara and Regolin, 2002)
and it may be that such behaviour was facilitated by the removal
of the conspecific. The absence eye-closure bias of females

Fig. 5. Mean percentage of time spent in monocular/unihemispheric sleep patterns of female and male chicks during the second week post-hatching: No-Conspec-chicks: after the removal of conspecific. Conspec-chicks: with the conspecific. (A) Female chicks. (B) Male chicks. (*) Indicates significant
departures from chance level (0).

Fig. 6. Mean percentage of events of monocular/unihemispheric sleep patterns of female and male chicks during the second week post-hatching: No-Conspec-chicks: after the removal of conspecific. Conspec-chicks: with the conspecific. (A) Female chicks. (B) Male chicks. (*) Indicates significant departures from chance level (0).
after the removal of the conspecific would be connected with an absence of hemispheric dominance during wakefulness. However, the interpretation of this phenomenon is difficult. A possible hypothesis could be provided by a comparison between the eye-closure patterns of females: No-conspec-chicks had relatively more left eye-closure/right unihemispheric sleep than Conspec-chicks. This would suggest that the removal of the conspecific caused a certain degree of right hemisphere activation in No-Conspec-chicks. Finally, it may be stressed that the removal of conspecific would have different outcomes (and neural consequences) in males and females.

A further interesting aspect of a typical event of monocular/unihemispheric sleep is that one eye remains shut but the other eye is opened and contra-lateral hemisphere shows a typical EEG pattern of wakefulness composed by fast and low amplitude waves (Ookawa and Takagi, 1968; Ball et al., 1988; Bobbo et al., 2002). The social interaction with conspecific and its change may also influenced the pattern of eye-openings during subsequent sleep. It has been suggested that eye-opening could be a response associated with the necessity of monitoring the surroundings or checking for the presence of a predator (Rattenborg et al., 1999) or the imprinting object (Mascetti et al., 1999). The presence/removal of a conspecific would modulate the patterns of eye-openings and chicks would open more frequently the eye connected with the hemisphere that was not in control of behaviour during wakefulness. When there was no hemispheric dominance, one or the other eye was opened with equal frequency during sleep.

Since, the overall amount of monocular/unihemispheric sleep was about 2% of total time spent sleeping, a final important issue concerning its biological function merits to be considered. There is no reason why should a highly significant left-right difference be less relevant because the behaviour only occurs in a portion of time of total sleep. First, several important behavioural patterns do occur with reduced frequency in animals (i.e. anti-predatory responses) but are nonetheless of enormous relevance from a biological point of view. Second, the consolidation of memories acquired during wakefulness is one of the current hypothesis about the sleep function (see: Graves et al., 2001; Smith, 1995, 1996). Likely, monocular/unihemispheric sleep in chicks would be involved in processes of local cerebral recovery and particularly in the hemispheric recovery (Horne, 1988; Bennington and Heller, 1995; Vyazovskiy et al., 2000) and with consolidation of imprinting memory. Third, the unilateral closure of right or left eye during sleep does not occur randomly but it is closely correlated with the shifts of hemispheric dominance during chick’s development (Mascetti et al., 1999, 2004), it is modulated by specific experiences during wakefulness such as presence, absence and changes of imprinting object (Mascetti et al., 1999, 2004), the light stimulation in “ovo” (Bobbo et al., 2002; Mascetti and Vallortigara, 2001) and visual learning experiences during wakefulness (Mascetti, unpublished data). Therefore, monocular/unihemispheric sleep seems to be a function correlated with chick’s behavioural experiences and with the hemisphere that was in control of behaviour during the previous wakefulness. Finally, it has been reported that one eye-opening during sleep in birds would have a vigilance and anti-predatory functions (Rattenborg et al., 1999, 2000). Then, 2% of Mo-Un sleep should be enough time for accomplishing vigilance functions.

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