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Sleep and wakefulness in the green iguanid lizard (*Iguana iguana*) ☆

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Abstract

The reptile *Iguana iguana* exhibits four states of vigilance: active wakefulness (AW), quiet wakefulness (QW), quiet sleep (QS) and active sleep (AS). Cerebral activity decreases in amplitude and frequency when passing from wakefulness to QS. Both parameters show a slight increase during AS. Heart rate is at a maximum during AW (43.8±7.9 beats/min), decreases to a minimum in QS (25.3±3.2 beats/min) and increases in AS (36.1±5.7 beats/min). Tonical and phasical muscular activity is present in wakefulness, decreases or disappears in QS and reappears in AS. Single or conjugate ocular movements are observed during wakefulness, then disappear in QS and abruptly reappear in AS. Although these reptiles are polyphasic, their sleep shows a tendency to concentrate between 20:00 and 8:00 h. Quiet sleep occupies the greater percentage of the total sleep time. Active sleep episodes are of very short duration, showing an average of 21.5±4.9 (mean±SD). Compensatory increment of sleep following its total deprivation was significant only for QS. Reaction to stimuli decreased significantly when passing from wakefulness to sleep. It is suggested that the lizard *I. iguana* displays two sleep phases behaviorally and somatovegetatively similar to slow wave sleep and paradoxical sleep in birds and mammals.
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Keywords: Active sleep; *Iguana iguana*; Quiet sleep; Reptiles

1. Introduction

Mammals (Ruckebusch, 1963; Jouvet, 1967; Allison and Van Twyver, 1970; Freemon et al., 1971; Brebbia and Pyne, 1972; Prudom and Klemm, 1973; Mukhametov, 1990; Zepelin, 1994) and birds (Susic and Kovacevic, 1973; Schlehuber et al., 1974; Vasconcelos-Dueñas and Ayala-Guerrero, 1983; Mexicano et al., 1992) present two sleep phases. The first, called slow wave sleep (SWS), is characterized by brain activity of high amplitude slow waves. The second, known as paradoxical sleep (PS) or rapid eye movement sleep (REM), exhibits a low voltage fast frequency electroencephalographic pattern. This sleep phase is usually further distinguished by the presence of eye movements, myoclonic twitches of the extremities, reduced muscle tone and autonomic variability.

Most sleep studies have been performed in endothermic vertebrates. However, in recent years, the comparative approach towards an understanding of the brain has provided significant new insights. Reptiles appear to be most useful in this approach because of their ancestral relationship to mammals and birds. Sleep in these ectothermic vertebrates remains as a matter of controversy (Walker et al., 1973), since it has been determined almost exclusively by considering the electrical activity of mammalian brain as a prototype for comparative sleep studies. However, the absence of electroencephalographic signs of SWS or PS might imply only the absence of the appropriate neurophysiological generators of such activity but not necessarily of sleep. In contrast, it has been suggested that a number of common behavioral characteristics can be used to delineate sleep for any class of animals. These characteristics include: 1) the spontaneous assumption of a stereotypic specific posture, 2) the maintenance of behavioral immobility, 3) an elevated behavioral response threshold which may be reflected in the intensity of an arousing stimulus and/or in the frequency,

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latency, or duration of a behavioral response, and 4) rapid behavioral state reversibility with stimulation (Flanigan, 1974).

It has been reported that several reptile species belonging to chelonians (Vasilescu, 1970; Karmanova and Churnosov, 1972; Flanigan, 1974; Ayala-Guerrero, 1987), crocodilians (Peyrethon and Dusan–Peyrethon, 1969; Flanigan et al., 1973; Warner and Huggings, 1978) and lizards (Tauber et al., 1966, 1968a; Karmanova et al., 1971; Flanigan, 1972; Romo et al., 1978; Huntley, 1987; Ayala-Guerrero and Mexicano, in press) exhibit behavioral sleep. In the particular case of iguanid lizards two phases of sleep have been described in *Ctenosaura pectinata* (Tauber et al., 1966, 1968a; Ayala-Guerrero and Huitrón-Reséndiz, 1991), and *Ctenosaura similis* (Ayala- Guerrero and Vargas-Reyna, 1987; Huitrón-Reséndiz et al., 1992). However in *Iguana iguana* only one phase has been observed (Flanigan, 1973). Since genetic factors exist in expressing certain sleep characteristics (Liknowski et al., 1991), and *I. iguana* is, from the phylogenetic point of view, closely related to the other two lizards, it is probable that it also presents two similar sleep phases.

2. Materials and methods

2.1. Surgical and recording procedures

Ten adult specimens of the lizard *I. iguana* of both sexes were used in this study. Stainless steel, electrodes insulated except for the tip were used.

Electrodes were implanted, after a period of habituation in our laboratory, under Nembutal anesthesia (35 mg/kg i.p). After removing the superficial scales, the muscle mass overlying the parietal bones on each side was separated through a midline skin incision. Drill holes were made in the skull and the electrodes for chronic bipolar recordings of cerebral activity (EEG) were implanted bilaterally on the anterior and posterior telencephalon. Two electrodes were placed in the skull at the external and internal canthi of each eye for ocular activity recording (EOG). Muscular activity (EMG) and heart rate were obtained from the same pair of electrodes placed in the neck muscles. One screw (ground electrode) was placed in the skull approximately 2.5 cm anterior to the parietal eye. All electrode leads were soldered to a small connector fixed to the skull with acrylic cement. Seven days after postoperative recovery the lizards were placed in a shielded sound attenuated chamber constantly illuminated by a 60 W light bulb, in order to facilitate the observation through a one-way glass window. Chamber temperature during recording sessions varied between 25 and 30 °C.

A po1ygraphical recording by animal, under constant visual observations, was taken continuously during 24 h on an 8 channel Grass model III-D electroencephalograph.

2.2. Data analysis

Polygraphic recordings were visually analyzed. The total time spent by animals in each state of vigilance during the 24-h period was measured, and the percentage within the period was calculated. The mean duration and the total number of active sleep episodes over the 24-h period were obtained as well as their nycterohemeral distribution. Muscular activity measurements of each state of vigilance were made in reference to activity exhibited during active wakefulness, which was considered as 100%. Heart rate and frequency of ocular activity were extrapolated to 1 min.

Values of states of vigilance obtained during the astronomical day (from 8:00 to 20:00 h) were compared to those of the astronomical night (from 20:00 to 8:00 h) through the Student's *t*-test.

2.3. Arousal reactions

Behavioral response latencies during behavioral waking and behavioral sleep were measured in three additional specimens. Electrical stimulation consisting in dipolar pulses of 50 ms duration at 60 c/s was delivered to pairs of EMG electrodes. The voltage used was 2 V which was randomly applied during AW, QW, QS and AS. Behavioral responses consisted of a head movement accompanied by eyelid, limb and body movements. Experimental trials were conducted during 24 h/day for three consecutive periods or until 30 stimulus presentations during behavioral waking and 50 during behavioral sleep (30 in QS and 20 in AS) had been made.

2.4. Enforced waking

These three specimens were also kept behaviorally awake for 48 continuous hours, and baseline recordings were compared with post-stimulation recovery recordings of 24 h. Enforced wakefulness was maintained by lifting, stroking and handling.

3. Results

The lizard *I. iguana* (Fig. 1) displayed the following states of vigilance during the nycterohemeral cycle: active wakefulness (AW), quiet wakefulness (QW), quiet sleep (QS) and active sleep (AS). Each sate showed its own behavioral and electrophysiological features.

3.1. Behavioral and electrophysiological data during AW

The iguanid stood on their four legs. The body was raised from the chamber floor, head and neck were elevated, and eyes

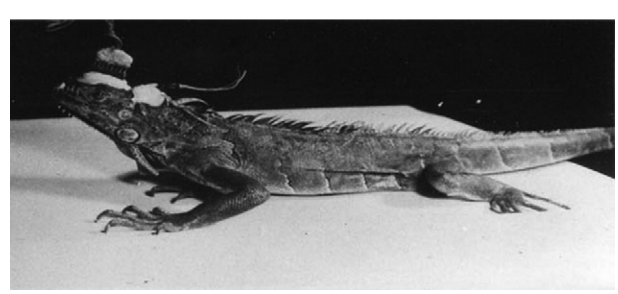

Fig. 1. An *Iguana iguana* during active wakefulness.

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