25 Rotin, D., Feyereisen, R., Koener, J., and Tobe, S.S., Haemolymph juvenile hormone esterase activity during the reproductive cycle of the viviparous cockroach *Diploptera punctata*. Insect Biochem. *12* (1982) 263–268.

26 Rotin, D., and Tobe, S.S., The possible role of juvenile hormone esterase in the regulation of juvenile hormone titre in the female cockroach *Diploptera punctata*. Can. J. Biochem. Cell Biol. *61* (1983) 811–817.

27 Sanburg, L.L., Kramer, K.J., Kezdy, F.J., Law, J.H., and Oberlander, H., Role of juvenile hormone esterase and carrier proteins in insect development. Nature *253* (1975) 266–267.

28 Schooley, D.A., Baker, F.C., Tsai, L.W., Miller, C.A., and Jamieson, G.C., Juvenile hormones 0, I, and II exist only in Lepidoptera, in: Biosynthesis, Metabolism and Mode of Action of Invertebrate Hormones, pp. 373–383. Eds J.A. Hoffmann and M. Porchet. Springer-Verlag, Heidelberg 1984.

29 Shirk, P.D., Dahm, K.H., and Röller, H., The accessory sex glands as the repository for juvenile hormone in male cecropia moths. Z. Naturf. *31c* (1976) 199–200.

30 Stay, B., and Coop, A., Developmental stages and chemical composition in embryos of the cockroach, *Diploptera punctata*, with observations on the effect of diet. J. Insect Physiol. *19* (1973) 147–171.

31 Stay, B., and Tobe, S.S., Control of juvenile hormone biosynthesis during the reproductive cycle of a viviparous cockroach. II. Effects of unilateral allatectomy, implantation of supernumerary corpora allata and ovariectomy. Gen. comp. Endocr. *34* (1978) 276–286.

32 Szibbo, C.M., Rotin, D., Feyereisen, R., and Tobe, S.S., Synthesis and degradation of $C_{16}$ juvenile hormone (JH III) during the final two stadia of the cockroach, *Diploptera punctata*. Gen. comp. Endocr. *48* (1982) 25–32.

33 Tobe, S.S., Regulation of the corpora allata in adult female insects, in: Insect Biology in the Future: VBW 80, pp. 345–367. Eds M. Locke and D.S. Smith. Academic Press, New York (1980).

34 Tobe, S.S., and Pratt, G.E., The influence of substrate concentrations on the rate of insect juvenile hormone biosynthesis by corpora allata of the desert locust in vitro. Biochem. J. *144* (1974) 107–113.

35 Tobe, S.S., and Pratt, G.E., Corpus allatum activity in vitro during ovarian maturation in the desert locust, *Schistocerca gregaria*. J. exp. Biol. *62* (1975) 611–627.

36 Tobe, S.S., and Stay, B., Corpus allatum activity in vitro during the reproductive cycle of the viviparous cockroach, *Diploptera punctata* (Eschscholtz). Gen. comp. Endocr. *31* (1977) 138–147.

37 Tobe, S.S., and Stay, B., Modulation of juvenile hormone synthesis by an analogue in the cockroach. Nature *281* (1979) 481–482.

38 Weaver, R.J., and Pratt, G.E., The effect of enforced virginity and subsequent mating on the activity of the corpus allatum of *Periplaneta americana* measured in vitro, as related to changes in the rate of ovarian maturation. Physiol. Ent. *2* (1977) 59–76.

39 Wigglesworth, V.B., Hormone balance and the control of metamorphosis in *Rhodnius prolixus* (Hemiptera). J. exp. Biol. *29* (1952) 620–631.

40 Wigglesworth, V.B., The hormonal regulation of growth and reproduction in insects. Adv. Insect Physiol. *2* (1964) 247–336.

41 Williams, C.M., The juvenile hormone. II. Its role in the endocrine control of molting, pupation, and adult development in the cecropia silkworm. Biol. Bull. Mar. Biol. Lab., Woods Hole *121* (1961) 572–585.


0014-4754/85/081028-08$1.50 + 0.20/0


# Short Communications

## Interhemispheric asynchrony of the sleep EEG in northern fur seals

L.M. Mukhametov, O.I. Lyamin and I.G. Polyakova

*Severtsov Institute of Evolutionary Morphology and Ecology of Animals, USSR Academy of Sciences, 117 071 Moscow (USSR),*
*30 July 1984*

*Summary*. In northern fur seals the two brain hemispheres can generate the EEG slow waves during sleep not only simultaneously, as in all the terrestrial mammals investigated, but also independently as in dolphins.

*Key words*. Sleep; interhemispheric relations; pinnipeds.

Electrophysiological studies on sleep in the bottlenose dolphin, *Tursiops truncatus*[1,2], and in the porpoise, *Phocoena phocoena*[3], have revealed that the main stage of sleep in both dolphin species is unihemispheric slow wave sleep. This type of sleep was not found in the Caribbean manatee, *Trichechus manatus*[4], but this study was based only on two night-recording sessions on a single animal. No unihemispheric sleep has been recorded in the Caspian seal, *Phoca caspica*[5], or in the harp seal, *Pagophilus groenlandicus*. Two other studies on Phocidae[6,7] provide no information about interhemispheric interrelations during slow wave sleep.

The present investigation is an attempt to test the existence of unihemispheric slow wave sleep in a member of the Otariidae, the other pinniped family; the northern fur seal, *Callorhinus ursinus*. A detailed characterization of the sleep-wakefulness cycle for this species will be given later.

*Methods*. Sleep was studied in 12 fur seals of both sexes (6 males and 6 females) and different ages (from 2 months old to 22 years old). Electrodes were implanted under chloralose anesthesia (30 mg/kg i.m. for cubs and 50 mg/kg i.m. for subadults and adults). The skull dorsal surface was exposed. Epidural electrodes (steel screws, 0.8 mm in diameter) were situated over different cortical areas. Standard for all the animals were bipolar recordings of the electroencephalogram (EEG) from each hemisphere through the electrodes located symmetrically over the frontal and occipital cortical fields. Pairs of nichrome wire electrodes, 0.3 mm in diameter, were implanted in one of the orbits to record the electrooculogram, in the neck muscles to record their electromyogram and in the nasal muscles for the recording of the nostril respiratory motions and whisker twitches during paradoxical sleep. There was always a pair of the implanted electrodes available to record an electrocardiogram. The lead wires from all the electrodes were soldered to a 10-pin socket and embedded in acrylic cement. The skin cut was sewn up. All the seals were allowed to recover from the operation for several days. Thereafter polygraphic recording was started to last 3–6 days continuously. The electrodes were connected to the electroencephalograph input by special artefact-free cables. The experimental cage (3 × 3 m) was housed in a spacious open-air tank. Prior to the operation, the animals were allowed to adapt to the cage for up to two weeks.

The sleep of the fur seals was studied in two experimental situations: on the land and in the water. In the former case the water level was maintained at a minimum to ensure the seals' normal thermoregulation and a platform was set up above the water surface. In this situation the seals slept on the platform only. In the latter case, the platform was removed, and the water level was raised to reach 1.2 m so that the animals could sleep only in the water.

*Results and discussion*. The major EEG patterns in fur seals were not distinctive from those of laboratory mammals. In analyzing the EEG records three stages were distinguished: stage 1, desynchronization; stage 2, intermediate synchronization including sleep spindles, theta- and delta-waves; stage 3, maximal synchronization when delta-waves of maximal amplitude occupied over 50% of each scoring epoch (20 sec).

Wakefulness, slow wave sleep and paradoxical sleep were identified according to the usual polygraphic criteria (fig. 1). Wakefulness and paradoxical sleep were characterized by bilateral desynchronization, and slow wave sleep by synchronization in one or both hemispheres. As an example of the quantitative relationship between the main behavioral stages, data for fur seal No. 1 can be given. In this animal (male, 3.5 years old and 22 kg in weight, 24-h session on the land) wakefulness accounted for 69.7% of the total recording time, slow wave sleep 23.3% and paradoxical sleep 7.0%. The amount and structure of sleep varied, depending on the age of the fur seals and on whether the animal was sleeping on the land or in the water. A complete quantitative characterization of the sleep-wakefulness cycle in fur seals of different ages and sexes sleeping on land and in the water will be published after the accumulation of a body of statistically significant data for every group under consideration.

As in the Caspian seal[5], in the northern fur seal slow wave sleep was not preceded by paradoxical sleep, nor was there the sharp increase in the heart rate during paradoxical sleep that was reported for the grey seal[6].

Total duration of different relationship patterns of EEG stages in the two hemispheres of fur seal No. 1 as a percentage of the recording time. 24-h session out of water

| | EEG stages in left hemisphere | | |
|---|---|---|---|
| in right hemisphere | 1 | 2 | 3 |
| 1 | 76.7* | 3.1 | 1.8 |
| 2 | 2.2 | 4.5 | 1.3 |
| 3 | 1.2 | 4.5 | 4.7 |

*The bilateral desynchronization corresponded to wakefulness during 69.7% of recording time and to paradoxical sleep during 7.0% of the time.

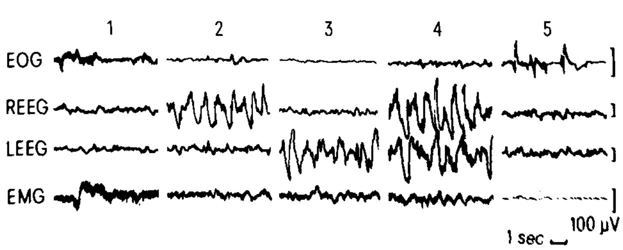


Figure 1. Polygraphic manifestations of different behavioral states in a northern fur seal. *1* wakefulness, *2* right-side delta-sleep, *3* left-side delta-sleep, *4* bilateral delta-sleep, *5* paradoxical sleep. Abbreviations: EOG, electrooculogram; REEG, right electroencephalogram; LEEG, left electroencephalogram; EMG, neck electromyogram.

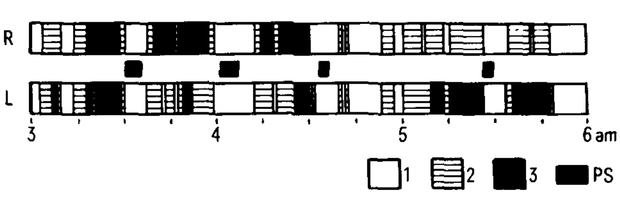


Figure 2. Diagrams of EEG stages 1 (desynchronization), 2 (intermediate synchronization), and 3 (delta synchronization) in right (R) and left (L) brain hemispheres of a northern fur seal sleeping on the land. PS: the paradoxical sleep episodes. Time scale in hours.

The most important finding of our experiments is the interhemispheric asynchrony of the EEG slow waves (figs 1,2). As in dolphins, either hemisphere (right or left in different time periods) exhibited the intermediate or delta-stage of EEG slow wave synchronization as against desynchronization or definitely different synchronization stages in the other hemisphere. All the EEG interhemispherically asynchronous slow wave patterns accounted for 14.1% of the total recording time in fur seal No. 1, i.e. over one half of the entire slow wave sleep amount (table). The incidence of the asynchrony was similar in males and females. It was recorded both in and out of the water, but the relative amount of EEG asynchrony is greater during sleep in the water in the same animal. Interhemispherically asynchronous EEG activity was recorded in the animals of all the age classes including the cubs of two months of age, which sleep only out of the water when in the wild. At the same time, in cubs, asynchrony is expressed to a lesser extent than in subadult and adult animals. Analysis of the slow wave cortical topography has revealed that the EEG asynchrony actually manifests interhemispheric interrelations but is not a function of local synchronization or desynchronization in a particular cortical field only.

The interhemispheric asynchrony of the slow wave EEG in fur seals is similar to the dolphin's unihemispheric slow wave sleep in many respects, but there are also essential differences. The principal difference concerns the delta-sleep. In dolphins the delta-sleep pattern arises in either hemisphere only alternately to manifest reciprocal interrelationships of the hemispheres in the course of delta-sleep development. In fur seals delta-waves of maximal amplitude may, for considerable periods, follow both bilaterally, with normal respiration fully retained, and unilaterally in either hemisphere.

On the basis of some experimental evidence, we assumed that in the dolphin unihemispheric slow wave sleep is prerequisite for the maintenance of autonomous respiration[3]. This hypothesis does not hold for the fur seal, whose normal respiration, in contrast to that of dolphins, is not affected by bilateral delta-wave activity. Thus, the functional significance of the state characterized by unilateral slow wave EEG in fur seal is unclear.

Our knowledge being far from complete, the finding of interhemispheric asynchrony of the sleep slow wave activity in the northern fur seal indicates that this phenomenon is not specific for dolphins only, but also characterizes some members of the Pinnipedia, another order of marine mammals. These two orders are very different in constitutional aspects. At the same time, the interhemispheric asynchrony of slow wave sleep is absent in the Caspian seal and in the harp seal, which are much closer to the northern fur seal morphologically. This gives us grounds for concluding that the origin of the unihemispheric sleep can largely be explained on an ecological basis.

Elucidation of factors in the aquatic mode of life which are responsible for the development of the unihemispheric EEG slow waves calls for comparative physiological studies of sleep in other members of the Cetacea, Sirenia and Pinnipedia.

1 Mukhametov, L.M., Supin, A.Y., and Strokova, I.G., Proc. USSR Acad. Sci. *229* (1976) 767 (in Russian).
2 Mukhametov, L.M., Supin, A.Y., and Polyakova, I.G., Brain Res. *134* (1977) 581.
3 Mukhametov, L.M., and Polyakova, I.G., J. high nerv. Activ. *31* (1981) 333 (in Russian).
4 Sokolov, V.E., and Mukhametov, L.M., J. evol. Biochem. Physiol. *18* (1982) 191 (in Russian).
5 Mukhametov, L.M., Supin, A.Y., and Polyakova, I.G., Proc. USSR Acad. Sci. *266* (1982) 752 (in Russian).
6 Ridgway, S.H., Harrison, R.J., and Joyce, P.L., Science *187* (1975) 553.
7 Huntley, A.C., Costa, D.P., Walker, J.M., Walker, L.E., and Berger, R.J., APSS 21th Annual Meeting, Hyannis 1981.

0014-4754/85/081034-02$1.50 + 0.20/0