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Letter to the Editor

ORIGIN OF SLEEP

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Summary

Phylogenetically simultaneous origin of the waking state ("neowaking") and slow wave sleep (SWS) is supposed related to evolutionary appearance of homoiothermia in mammals and birds. Paradoxical sleep (PS) is regarded in a way of "archeowaking", that is the result of evolutionary transformation of the primitive waking state of poikilothermic vertebrates.

Key Words: evolution of sleep.

Discussion

It is well known that the main signs of both SWS and PS described initially in humans are common to all warm-blooded animals: mammals and birds (Kovalzon 1976; Latash and Kovalzon 1975). Despite some interesting features peculiar to species ecology which are described in details in several recent reviews (Mukhametov 1986; Frank 1999; Rial et al. 1993, 1997; Siegel 1999), no important complication of both quantitative and qualitative characteristics of SWS and especially PS could be seen in accordance to progressive encephalization and corticolization in mammalian evolution. For instance, a primitive marsupial mammal, american opossum, which brain retains many anatomical "reptile" traits, demonstrates the same phenomenology of both sleep states that do mammals possessing highly developed cerebral cortex, such as predators, and differs only slightly from primate and human sleep. PS percentage in opossum is very high, up to one third of the total sleep time, that is more then in adult humans (20-25%). However, it is much greater in a ferret, highly developed predator with a very complicated behavior (up to 40%) (Zepelin 2000). Until recently it was accepted generally that there are a couple of exeptions from this general rule, only two species without PS: an ancient egg-laying mammal from Australia - echidna, and highly organized mammals living in water but breathing with air - dolphins. However, the recent years convincing evidences of PS presence in another monotremal mammal, platypus, have been found, which occupy extremely large part of the total sleep time, about one half of it (Siegel et al. 1999).

Two independent teams reported about eventual finding of PS signs in echidna; however, the data which have been published recently evoke some scepticism and need more support (Berger et al. 1995; Nicol et al. 2000; Siegel 1997; Siegel et al. 1996, 1998). Anyway, as a platypus origin in monotremal evolution occurred much earlier than that of echidna (the brain of the latter specis is much larger and more complicated in its organization, and the cerebral cortex possesses important convolutions), it seems obvious that PS reduction in echidna is a secondary phenomenon and a result of adaptive radiation of this species (Penny and Hasegawa 1997).

Regarding the dolphins, recent behavioral observations and videorecordings by L.M.Mukhametov and his collaborators on four species of the cetaceans have demonstrated brief PS-like episodes in all these mammals (Lyamin et al. 1998, 2001; Mukhametov and Lyamin 1997; Oleksenko et al. 1996).

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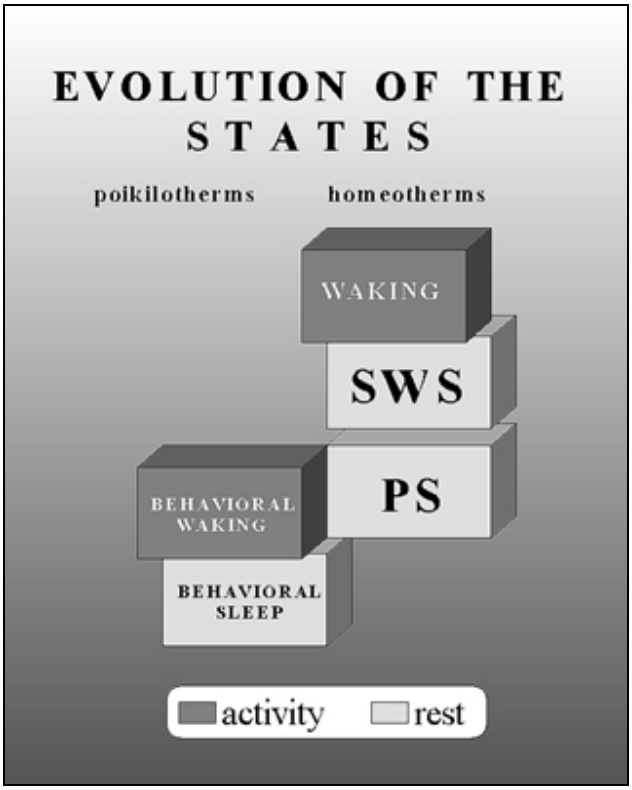
Contrary to that, sleep in poikilothermic vertebrates is clearly monotonous (Kovalzon 1976; Lyamin et al. 2002). As the cerebral electrical activity in these animals differs drastically from the mammal EEG (even if the former stay in warm environment), it is very difficult to search for any analogues of SWS and PS in cold-blooded vertebrates (reptiles, amphibians, fishes). The origin and evolution of PS seems especially enigmatic as this particular state is obviously archaic regarding its general anatomical and functional characteristics. It would be sufficient to remind that PS initiates from the most ancient caudal brain structures: rhombencephalon and medulla; special studies demonstrated that the higher cerebral structures are not critically necessary for the periodic appearance of PS-like episodes. It is well known that PS-like state (activated sleep) predominates in early ontogenesis. In adult mammals thermoregulation interrupts in PS, body becomes poikilothermic for this period. Together with the above-mentioned very high percentage of PS in the most ancient of the present mammals, egg-laying platypus and marsupial opossum, the whole data clearly indicate old evolutionary origin of PS. Consequently, this state should be the main or even the only sleep state in poikilothermic vertebrates. However, there are still no significant evidences for the presence of PS or PS-like periods in these animals though this problem is not sufficiently studied (Eiland et al. 2001; Frank 1999; Lyamin et al. 2002; Nicolau et al. 2000; Rial et al. 1993, 1997; Siegel 1997, 1999; Siegel et al. 1998).

On the other hand, if PS would be evolutionary older than SWS, what can be the function of the former state? It is absolutely clear now that PS is by no means the quiescence of the brain but the state of a high level cerebral activity, the so-called "inside-directed waking". If this is true, why poikilothermic brain needs two different kinds of activity? And when is it resting?

To resolve this controvercy, a hypothesis is offered (see the figure), in accordance to which cold-blooded vertabrates have two behavioral states: activity and rest (left side). During active state, their brain mainly realizes genetically determined behavioral programms; learning abilities, acquirement of novel experience are very limited in these species. During quite state, their body is progressively cooling, the brain is "switching off".



Evolutionary birth of homoiothermia renders the brain an ability to work during the rest periods too, so the state of inactive, "turned off" brain disappeared (left bottom block). Two evolutinary novel states appeared: wakefulness during the active circadian phase and SWS during the rest circadian phase of homeotherms related to tonic de- and hyperpolarization of the cortical neurons, respectively (right two upper blocks) (Borbély et al. 2000). It is commonly known and do not need any arguments for advocacy that mammal waking is incomparably more flexible, adaptive and susceptible to changes in evironmental conditions. In highly organized mammals obtaining a large and well-developed brain, individual experience, individual memory plays the role of the same (or even more) importance that their heredity, "species memory". Regarding the "primitive waking state" of poikilotherms, its

mechanisms did not disappear in evolution but rather loose their ability to analize exteroceptive signals and directly control the behavior; this state shifts from the circadian active phase to the rest one and turns into PS, which serves the function of reprogramming of the brain in accordance to the plans of the innate behavior, adaptation of these programms in conformity to the acquiring experience during individual development (Jouvet 2000).

Thus in accordance to the hypothesis, the states of waking ("neowaking") and SWS originates in evolution simultaneously with homoiothermia, at the same time PS represents the state of "archeowaking", the result of evolutionary transformation of the primitive waking state of poikilotherms.

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