humans, then it is SWS rather than REM sleep which is increased[53]. It was argued[53] that the many studies on the effects of learning upon sleep generally do not 'exert' the cerebrum and probably produce little cerebral fatigue.

1 R.T. Wilkinson, in: Physiology of Survival, p.399. Ed. O.G. Edholm and A.L. Bacharach. Academic Press, 1966.
2 J.A. Horne, Biol. Psychol. *7*, 55 (1978).
3 L. Karacan, A.L. Rosenbloom, J.H. Londono, R.L. Williams and P.J. Salis, Behav. Neuropsychiat. *6*, 67 (1974).
4 R. Vigneri, V. Pezzino, S. Squatrito, A. Colandra and M. Maricchiolo, Neuroendocrinology *14*, 356 (1974).
5 R. Schilkrut, O. Chandra, M. Osswald, E. Ruther, B. Baartüssar and N. Mattussek, Neuropsychobiology *1*, 70 (1975).
6 W.C. Orr, G.W. Vogel, M.L. Stahl, W.J. Griffiths and J.R. Seely, Neuroendocrinology *24*, 347 (1977).
7 C. Lucke, B. Höffken and A. von zur Mühlen, Acta encodr. *82*, 400 (1976).
8 D.C. Parker and L.G. Rossman, J. clin. Endocr. *32*, 65 (1971).
9 J.L. Kostyo and D.F. Nutting, in: Am. physiol. Soc. Handbook of Physiology, vol.7, p.187. 1974.
10 W.M. Hunter, Proc. Nutr. Soc. *31*, 199 (1972).
11 H-J. Quabbe, Chronobiologica *4*, 217 (1977).
12 K. Adam and I. Oswald, J. R. Col. Physicians *11*, 376 (1977).
13 J.C. Waterlow, P.J. Garlick and D.J. Millward, Protein Turnover in Mammalian Tissues and in Whole Body. Elsevier, Amsterdam 1978.
14 R.D. Feigin, A.S. Klainer and W.R. Beisel, Nature *215*, 512 (1967).
15 P.J. Garlick, G.A. Clugston, R.W. Swick, I.H. Meinertzhagen and J.C. Waterlow, Proc. Nutr. Soc. *37*, 33A (1978).
16 M.H.N. Golden and J.C. Waterlow, Clin. Sci. molec. Med. *53*, 277 (1977).
17 V.R. Young, W.P. Steffee, P.B. Pencharz, J.G. Winterer and N.S. Scrimshaw, Nature 253, 192 (1975).
18 P. Webb and M. Hiestand, J. appl. Physiol. *38*, 257 (1975).
19 A. Jacobson, A. Kales, D. Lehmann and F.S. Hoedemaker, Exp. Neurol. *10*, 418 (1964).
20 L.E. Sheving, Anat. Rec. *135*, 7 (1959).
21 L.B. Fisher, Br. J. Derm. *80*, 75 (1968).
22 E.D. Weitzman, A. Rev. Med. *27*, 225 (1976).
23 F. Halberg and C.P. Barnum, Am. J. Physiol. *201*, 227 (1961).
24 R.H. Clark and D.R. Korst, Science *166*, 236 (1969).
25 L. Garma and R. Verley, Revue Neuropsychiat. infant. *17*, 487 (1969).
26 A. Borbély, Prog. Neurobiol. *10*, 1 (1978).
27 F. Baekeland and R. Lasky, Percept. Mot. Skills *23*, 1203 (1966).
28 L. Adamson, W.M. Hunter, O.O. Ogunremi, I. Oswald and I.W. Percy-Robb, J. Endocr. *62*, 473 (1974).
29 L.M. Zir, R.A. Smith and D.C. Parker, J. clin. Endocr. *32*, 662 (1971).
30 J.A. Horne and J.M. Porter, Nature *256*, 573 (1975).
31 J.M. Walker, T.C. Floyd, G. Fein, C. Caveness, R. Lualhati and I. Feinberg, J. appl. Physiol. *44*, 945 (1978).
32 C.M. Shapiro, R.D. Griesel, P.R. Bartel and P.L. Jooste, J. appl. Physiol. *37*, 187 (1975).
33 U.M. MacFadyen, I. Oswald and S.A. Lewis, J. appl. Physiol. *35*, 391 (1973).
34 P.T.S. Putkonen, E. Elomaa and P.V. Kotilainen, Scand. J. clin. Lab. Invest. suppl. 130, 19 (1973).
35 D.L.F. Dunleavy, I. Oswald, P. Brown and J.A. Strong, Electroenceph. clin. Neurophysiol. *36*, 259 (1974).
36 R.S. Ryback and O.F. Lewis, Electroenceph. clin. Neurophysiol. *31*, 395 (1971).
37 W.R. Adey, E. Bors and R.W. Porter, Arch. Neurol. *19*, 377 (1968).
38 A. Kales, J. clin. Endocr. *27*, 1593 (1967).
39 J.A. Horne, Biol. Psychol. *4*, 107 (1976).
40 W.C. Dement and S.C. Greenberg, Electroenceph. clin. Neurophysiol. *20*, 523 (1966).
41 W.B. Webb and H. Agnew, Psychophysiology *11*, 265 (1974).
42 H.S. Jones and I. Oswald, Electroenceph. clin. Neurophysiol. *24*, 378 (1968).
43 R. Meddis, A.J.D. Pearson and G. Langford, Electroenceph. clin. Neurophysiol. *35*, 391 (1973).
44 H. Agnew, W.B. Webb and H.L. Williams, Percept. Mot. Skills *24*, 851 (1967).
45 H. Agnew and W.B. Webb, Bull. Psychonom. Sci. *2*, 131 (1973).
46 W.B. Webb and H. Agnew, Science *174*, 1354 (1971).
47 E. Balzamo, R.J. Bradley and J.M. Rhodes, Electroenceph. clin. Neurophysiol. *33*, 47 (1972).
48 O.D. Creutzfeldt, in: Brain Work, p.21. Ed. D.H. Ingvar and M.A. Lassen. Munksgaard, 1975.
49 J.A. Hobson and R.W. McCarley, Electroenceph. clin. Neurophysiol. *30*, 97 (1971).
50 S. Sato, F.E. Dreifuss and J.K. Penry, Electroenceph. clin. Neurophysiol. *39*, 479 (1975).
51 R.L. Williams, I. Karacan and C.J. Hursch, Electroencephalography (EEG) of Human Sleep: Clinical Applications. Wiley, 1974.
52 H. Laborit, Res. Commun. chem. Path. Pharmac. *3*, 349 (1972).
53 J.A. Horne and B. Walmsley, Psychophysiology *13*, 115 (1976).

5. The biology of natural sleep in animals

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'Sleep is a natural, repeated unconsciousness that we do not even know the reason for.'
(K.R. Popper and J.C. Eccles[1], p.496.)

The present-day experiments on sleep are a typical example of the way in which experimental research stretches far beyond the mere description of natural processes. To fill the gap between the two approaches, some elements of comparative zoology will be considered here. Like many other vital functions, sleep is common to both humans and animals, so that a comparison can be made. This is especially the case when the comparison takes evolution into account; then conclusions can be expected from the comparative aspects of anatomy and behavioral psychology.

Sleep, as we know it in man, cannot be proved for all animals; it appears to be a 'monopoly' of vertebrates, which means that it is phylogenetically of late appearance. So long as we are dealing with homoiothermic animals, i.e. birds and mammals, we are on relatively safe ground; it becomes less certain the further we descend through the grades of vertebrates to the poikilothermic animals, through reptiles to amphibians and fish.

The drawing of this somewhat uncertain deep boundary agrees more or less with the definition quoted from Popper and Eccles[1]. If 'sleep is a natural state of unconsciousness', this presupposes a state of consciousness also. In fact, we find pre-forms of 'consciousness' – in the sense of a simple awareness of the animal's own body (including the shadow) – even in some fish[2].

For a long time, sleep was considered as a suppression effect, a passive condition. Today sleep is considered to be the result of an active process of the organism, especially for the purpose of restitution; it is also regarded as an instinctive function. For M. Holzapfel[3] investigating resting states conditioned by appetitive behavior, sleep is an instinctive function. This concept was later taken up also by Tinbergen[4] (p. 118) and is now generally accepted.

On the other hand, the question often arises whether sleep is a biological necessity for higher organisms, in other words why the restoration processes attained in sleep cannot be achieved during wakefulness, as other instinctive behavior can (such as food-intake, reproduction, migration etc.). Here it is essential to remember that almost all life processes, from heart-beating to bird migration, follow a certain rhythm. Many activities have a day-night cycle, or a dependence on the phases of the moon and sun or the tides. Sleep and wakefulness are no exception to this rule; they appear to obey the general and inevitable laws of rhythm and are controlled by a strict space-time system[5,6]. This means that sleep in animals does not occur anywhere, anyhow, at any time, but is strictly tied, not only to space and time, but even more to body position, social grouping, etc.

Among animals different sorts of sleep, such as deep sleep, half sleep (dozing), paradoxical sleep, winter sleep (hibernating), etc., can be distinguished. There are solitary sleepers and group sleepers which have various ways of damping the sense organs (eyes, ears or nose) and of filtering stimuli so that the danger signals are separated from the harmless ones. The need to be continually alert to guard against possible attack by the enemy (to perceive and be ready for flight) is not abolished in sleep, otherwise the capture of sleeping animals, or photographing them in their natural environment, would be all too easy.

It is well known that most wild animals live within defined territories of specific size and structure. Thus there is a space system of fixed points and connecting lines. The activities of animals normally follow a more or less defined pattern involving different fixed points, and according to a specific time system; in many cases this occurs precisely to the minute.

The most important fixed point is the home, for instance the mouse's hole, the fox's lair, a tree-hole or a cave. The home is the point of optimal safety where often the young are born and where the animal rests and sleeps, and to which it flees from its foes.

Home and sleeping place are often, but not always, the same. With most birds it is wrong to believe that their nest is their home and their sleeping place; it is only their fixed point for laying eggs and bringing up the young. Exceptions to this rule are woodpeckers, sparrows, tits and swallows which do sleep partly in their nests. The bird's nest exists in most cases only during a short part of the year for rearing the young.

In many birds, the sleeping place may be dozens of miles from the scene of their other activities. A classical example is the (originally) African cattle heron *(Bubulcus ibis)*, which spends the day beside the cattle or riding on an animal's back to catch insects and, in the evening – according to its space-time system – flies with hundreds of its species to the traditional sleeping tree. Of these birds, and of peacocks and several other birds, it is known that they keep strictly to their fixed sleeping place, not only for years but also for many generations.

Similar behavior is known for certain mammals, for instance bats, which sleep by day in thousands in a certain cave, or in the case of flying foxes of the species *Pteropus*, hang on certain trees. Depending on their specific space-time system, they leave these sleep trees and fly many miles to their feeding places (fruit trees), and then return according to plan to their individual branch on the sleeping tree. Hares have been seen to return to their original sleeping place – a shallow lair – over many years.

The 3 great apes, gorilla, chimpanzee and orangutan, build a new sleeping nest every evening in a few minutes, whereas most other monkeys sleep sitting on the branches of their sleeping tree. In contrast to the typical bird's nest, which contains the eggs and the young, the sleeping quarters of the great apes have no connection with reproduction.

Territorial fish, such as the coral fish, withdraw into certain holes in the rock; many bury themselves in the sand *(Coris)* or surround themselves with a protective gelatine (parrot fish), whereas fish which live in swarms, such as the herring, have no fixed sleeping place. Swifts *(Apus apus)* are now known with certainty to spend the night sleeping while flying[7]. Many ducks and gulls sleep swimming on the water.

Just as diverse as the sleeping places are the sleeping positions of different species. From standing upright on one leg (flamingo) to hanging head downwards (bats, bat parrots) all possible positions can be seen. Like the monkeys, most small birds also sit on branches, whereby the body weight, without muscular exertion, provides a mechanical hold on the branch. Other birds including the longlegged ones (flamingoes, storks, etc.) often take an abdominal lying position. It is only recently known that the ostrich, and related species, stretches its long neck on the ground in deep sleep, while the giraffe bends its neck in an arch backwards so that its head lies on its hindquarters. The classical position in sleep for mammals and humans is the lateral position; it can even be described as characteristic behavior for this class of animal. Other vertebrates are only exceptionally seen to sleep in this position, such as a few fish *(Astronotus, Malapterurus, Mola, Cetorhinus maximus)*. Lying on the stomach is the predominant position for reptiles and amphibia.

Before sleeping many animals show an appetitive behavior as is usual in instinctive conduct. In seeking the sleeping place and especially when preparing the sleeping posture, there are often complicated rituals involved. The way a dog turns around over its bed is well known. Many animals paw the ground before lying down, or (wombats, elephants) prepare a genuine pillow out of soft material. With elephants, the whole preparation for sleep occurs standing up; when the animal lies down it is already sleeping. In zoological gardens and circuses, it can often be seen that when one elephant lies down his neighbours lie down as well.

Not all vertebrates can shut their eyes because some do not have a movable eyelid. All fish, except the shark and the roach, are unable to do so and cannot even contract the pupil. With reptiles, there is no eyelid movement in snakes and some lizards, but the pupil - usually round - can be contracted to a very fine vertical slit. The hare *(Lepus europaeus)* keeps its pupil open even in the strongest light, but in sleep contracts it to the size of a pinhead. The old saying that the hare sleeps with open eyes is not correct!

A further protection against optical stimuli is achieved by many mammals with a bushy tail who can adopt a posture of sleep with their tail over their eyes. This curled-up position with the side of the face directly on the base of the tail and covered by the tail provides a muffling of olfactory stimuli. Bears sometimes hold one paw over their eyes.

As a protection against acoustic stimuli, the large-eared, sensitive mammals, such as certain marsupials *(Didelphys)*, bats *(Plecotus)*, carnivores *(Megalotis)* and primates *(Galago)*, can fold their external ears together. Many birds put their head under a wing where this is anatomically possible. From these deep-sleep postures to the light-sleep positions with uncovered eyes, there are many variations.

The covering of the sense organs is mostly complemented by a central filtering of the stimuli into harmless and potentially dangerous (enemy) signals. For instance, a sleeping elephant is not disturbed if his neighbour puts his foot on his head, but the slightest metallic sound causes immediate alarm (standing up). Even in sleep the animals remain, constantly ready to defend themselves or flee from their enemies. The permanent necessity of avoiding an enemy naturally determines the duration of sleep. Apart from the primates, which sleep in high trees or inaccessible rocks (baboons), mostly in groups, the longest sleeping period is found in the most invulnerable carnivores (such as bears) which - apart from the universal enemy, man - have few or no enemies.

The shortest sleeping time is found in vulnerable herbivores, such as antelopes or hares, which can be threatened by numerous carnivores. In these animals, one can speak of mini-sleep. Young animals usually sleep longer than adults. Gazelles and antelopes have snatches of sleep of only 2-10 min[8]. In hares it is even shorter, in giraffes and okapis somewhat longer. The giraffe has only about 20 min total sleep per night, and the okapi about 60 min. Adult elephants sleep for about 4 h, interrupted by standing to excrete faeces and urine. Guinea-pigs and cattle were, until recently, thought not to sleep at all, but this is of course not so. Not only the primates with their 10-12 h sleep (in equatorial regions), but the majority of terrestrial homoiothermic animals have a regular midday siesta of 1-2 h.

Special adaptations are needed for sleep in animals which live continually in water, particularly in aquatic mammals which, in contrast to fish, cannot breathe in water and are forced to come to the surface at short intervals to take in air.

Whereas pinnipeds (walruses, sealions, etc.) can at least sometimes come on land to sleep, this is impossible for the whole whale family. Big ones, such as *Physeter* with its 18-m length, lie sleeping on the surface with the breathing aperture at the top of the head just above the water.

Dolphins *(Tursiops)* hang asleep near the surface and thrust the head, with the breathing hole, out of the water at intervals of about half a minute, keeping their eyes closed. The behavior of the Indian river dolphin *(Platanista)* is even more extreme. G. Pilleri speaks of micro-sleep in these blind, restless swimmers[9]; he says it lasts at the most 1-8 sec. During these short pauses the sonar clicks, which are otherwise continually emitted for orientation, cease. These must be the shortest sleeping periods yet to be shown in mammals.

Two elementary forms of behavior are responsible for the specialization of sleep in vertebrates: the necessity to avoid the enemy and, in animals secondarily adapted to water, the need to breathe. Extreme conditions of climate can influence winter sleep in some mammals (mainly rodents and insectivores) and one single bird *(Phalaenoptilus nuttallii)*, but these and other special forms of sleep cannot be treated here.

The old question of whether animals dream can today be answered positively, at least for homoiothermic animals. Firstly, there are so many confirmatory observations in different types of mammal and bird that can hardly be interpreted other than as typical expressions of paradoxical sleep. Secondly, paradoxical sleep (i.e. dreaming sleep) has now been proved to occur in numerous animals by experimental electroencephalography[10].

1 K.R. Popper and J.C. Eccles: The Self and its Brain. Springer Int., 1977.

2 H. Hediger: Zur Frage des Selbstbewusstseins beim Tier, in: Psychologie des 20. Jahrhunderts. Kindler, Zürich 1978.
3 M. Holzapfel, Naturwissenschaften *28*, 273 (1940).
4 N. Tinbergen: The Study of Instinct. Clarenden Press, Oxford 1951.
5 H. Hediger, Med. Klin. *54*, 938, 965 (1959).
6 H. Hediger, Tierpsychologie im Zoo und im Zirkus. Friedr. Reinhardt, Basel 1961.
7 D. Lack, Swifts in a Tower. Chapman and Hall, London 1973.
8 F. Walther, Verhalten der Gazellen. Ziemsen, Wittenberg (Lutherstadt) 1968.
9 G. Pilleri, Die Geheimnisse der blinden Delphine. Hallwag, Bern 1975.
10 H. Hediger, Vom Traum der Tiere. Ciba Z. No. 99, pp. 3558–3566 (1945).

6. Comparative electrophysiology of sleep in some vertebrates

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An adequate investigation of the waking-sleep function in vertebrates requires, besides the comparative analysis of the behavioral manifestations, an electrophysiological quantitative analysis of the 24-h 'circadian' waking-sleep cycle, including the day (light) phase (07.00–19.00 h) and the night (dark) phase 19.00–07.00 h. The best approach is to follow the comparative evolutionist classification of vertebrates: amphibians (frog, toad); reptiles (lizard, turtle, crocodile); birds (starling, owl); mammals, as herbivores (rodents, cattle), insectivores (hedgehog), carnivores (cat, dog); primates (cercopithecoids, hominids); and man[1].

For the electrophysiological study of the waking state and sleep in animals, the same methods and criteria are used as for man. The electroencephalogram (EEG) is recorded concurrently with the electrooculogram (EOG) for quantification of the rapid eye movements (REM) during paradoxical sleep, in contrast to orthodox non-REM (NREM) sleep. For the same purpose, the 'ponto-geniculo-occipital spikes' (PGO) are recorded. The motor behavior is assessed by electromyography (EMG) and the visceral behavior (heart and respiratory rates) is under polygraphic control. An adequate quantification should involve waking (W) and total sleep (TS). Total sleep includes NREM and REM sleep. Orthodox NREM sleep is subdivided in man into initial stages (I and II) and later stages (III and IV). The latter are called slow wave sleep (SWS) or deep sleep. Paradoxical sleep (REM sleep) is characterized by initial PGO spikes, followed by a low voltage, high frequency EEG, rapid eye movements and loss of muscle tone. In higher vertebrates, the phase of rapid eye movements is associated with dreams.

1. *Amphibians*

Toads *(Bufo boreas; Hyla)* and frog *(Rana catesbiana)*. Investigations of Anurans *(Hyla* and *Rana)* showed that neither actually sleep. The tree toad *Hyla* has a more easily defined 'resting phase' than *Rana*; the EEG arousal threshold during rest is increased[2,3]. In *Bufo boreas*, 3 EEG and behavioral states were distinguished: a) Active awakened state, with maximal respiratory and cardiac rates; fast EEG frequency: 14–16 Hz; EEG amplitude: 10–40 μV; EMG: 15–20 μV. b) Relaxed wakefulness: animal motionless, yet responsive; reduced EMG amplitude (6–10 μV), as well as respiratory and heart rates; decreased EEG frequency and amplitude: 10–14 Hz, 5–10 μV. c) Resting behavior: animal unresponsive to external stimuli for 1–5 sec, relaxed posture; minimal respiratory and EEG activities: EEG: 5–7 Hz, 5–10 μV; EMG: 3–5 μV. The animals tend to be nocturnal; resting amounts to 87% in the photic phase and 24% in the scotopic phase. Thus, *Bufo boreas* does not exhibit real sleep, only a more pronounced resting state than the ever vigilant *Rana castebiana*[4].

2. *Reptiles*

A) Iguanid lizards *(Ctenosaura pectinata* and *Iguana iguana)* (n = 4). The weak EEG activity with small monophasic sharp and sawtooth waves during behavioral waking became polymorphic during behavioral sleep; the EEG decreased in frequency, but neither typical NREM nor REM sleep was recorded. Spikes and sharp waves reached peak levels (up to 385 μV) only during behavioral sleep. This association of spikes and sharp waves with behavioral sleep, without slow rhythms, in lizards, chelonians or crocodile reptiles indicates that sleep in lower vertebrates is not always correlated with slow-wave EEG, as in birds and mammals[5].

B) Tortoise *(Testudo denticulata)*. 2 EEG states, unrelated to posture, were found : 1. State of fast, low voltage EEG (6–10/sec, 40 μV) with moderate EMG and heart rate. 2. 'Spiking state' with reduced EMG and heart rate. The high spikes (60–150 μV) were led from the olfactory bulb, cerebral hemispheres and optic lobe; they disappeared during behavioral arousal. There was no clear sleep[6].

3. *Birds*

In certain bird species (pigeon and hen), in spite of great differences in brain size and functional organization, slow-wave sleep occurs but paradoxical sleep is not prevalent.