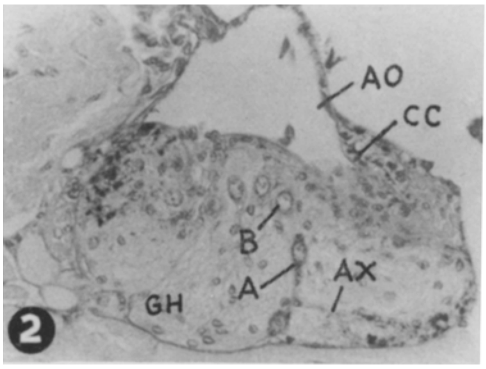

Fig. 2. T. S. through aorta (AO), corpora cardiaca (CC) and hypocerebral ganglion (GH) showing neurosecretory cell types (A, B) in the latter. ×270.

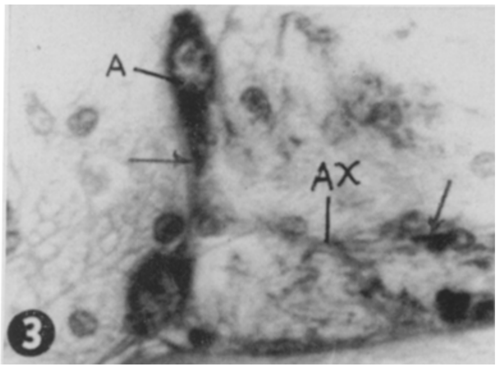

Fig. 3. A part of Figure 2 enlarged to show the A cells (A) and axons (AX) filled with neurosecretory material (arrows). ×520.

Zusammenfassung. Neurosekretorische Zellen der Typen A und B werden im Hypocerebralganglion von *Gryllus bimaculatus* beschrieben. Die Axone der A-Zellen führen das Neurosekret durch die Nervi hypocerebri und enden im Corpus cardiacum. Die Ganglien des reifen Männchens enthalten mehr Neurosekret als die des reifen Weibchens.

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[2] I am grateful to Professor S. M. H. KHATIB for providing laboratory facilities and critical guidance.

Arousal as a Cyclic Phenomenon During Sleep and Hibernation in the Hedgehog (*Erinaceus europeanus*)

The length of total sleep time (TST) has been claimed to be related to the degree of cortical development, the more primitive the cortex the greater the period of TST[1]. If this is so, the TST of the European hedgehog should be high, and 80% per day has in fact been reported by direct observation[2]. The sleep cycle duration, i.e. the interval between 2 successive paradoxical sleep periods uninterrupted by a waking period of longer than 1 min, has been suggested to be related to basic metabolic rate[3], animals with a low rate having a long sleep cycle. The hedgehog (53.1 kCal/kg^{0,75}/day)[4] would be expected to have a longer sleep cycle than the guinea-pig, an animal of similar body weight (69 kCal/kg^{0,75}/day)[5]. For the majority of the year, the European hedgehog has a body temperature of 34 °C. During winter, when the surrounding temperature drops below 13 °C, it enters hibernation, and its temperature is maintained 1–2 °C above that of the external environment, with which it varies.

This work was carried out to establish the sleep-wakeful pattern by EEG techniques and to evaluate the influence of metabolic rate on sleep cycle duration.

Methods. 9 hedgehogs, captured in autumn, were housed in small individual transparent enclosures and supplied ad libitum with a standard diet of canine prepared food. Under ether anaesthesia a pair of silvered screws was positioned on either side of the sagittal suture over the frontal lobes for recording ECoG. Electrodes were fixed in the neck muscle and subcutaneously on either side of the thorax for EMG and ECG respectively. A strain-gauge attached to the animal's back served as a pneumograph. Body temperature (BT) was measured from thermocouples placed within the abdominal cavity. A polygraph (REEGA VIII, ALVAR) was used for recordings at speeds of 2.5 mm/sec and 60 mm/sec. Heart and respiratory rates were counted over periods of 12 sec and checked every 2 min. The response (jerk reflex) of the animals to an auditory stimulus (click) involved a general contraction of the orbicularis dorsi muscle and was recorded for all experimental situations. Continuous recordings for periods of 1 week were made at 3 different BT: in autumn at BT = 34 °C, next in winter after the animals had spontaneously entered hibernation at BT = 13 °C and finally the hibernating animals were placed in a refrigerator reducing their BT to 8 °C.

Results. At BT = 34 °C, the following states were identified: alert wakefulness (AW), drowsiness (DR), slow wave (SWS) and paradoxical sleep (PS). An attitude of lateral recumbency was assumed for the last 3 states. AW was characterized by high voltage (> 100 μV) fast activity (> 25 c/sec) and usually corresponded to feeding or exploratory behaviour it was the only state for which the cervical muscular tone was high. During DR the ECoG evolved progressively and the spindles (100 μV, 40 c/sec) occurred systematically at each respiratory pause (Figure 1). Towards the end of this period the occurrence of the spindles was inconsistent and their morphology had altered (50 μV, 16 c/sec). The ECoG during SWS showed typical high voltage (100 μV) low frequency (2–4 c/sec) waves with microwaves superimposed. PS was recognized by low voltage (50 μV) high frequency (> 20 c/sec)

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[1] F. SNYDER, in *Physiology and Pathology of Sleep* (Ed. A. KALES; Lippincott, Los Angeles 1968), p. 266.

[2] P. SUOMALAINEN, in *The Nature of Sleep* (Eds. G. E. W. WOLSTENHOLME and M. O'CONNOR; Churchill, London 1961), p. 307.

[3] T. WEISS and E. ROLDAN, Experientia *20*, 1 (1964).

[4] G. HILDWEIN and A. MALAN, Arch. Sci. Physiol. *24*, 133 (1970).

[5] J. PELLET and G. BÉRAUD, Physiol. Behav. *2*, 131 (1967).

Sleep pattern characteristics and cardio-respiratory rates in the European hedgehog at normal body temperature (34 °C) (mean value ± SE)

	Awake	Drowsiness	Slow wave sleep	Paradoxical sleep
Mean percentage per day ($n = 47$)	33 ± 6	25 ± 7	30 ± 4	12 ± 6
Heart rate (min) ($n = 720$)	224.7 ± 16.4	217.3 ± 12.5	224.2 ± 5.9	204.0 ± 8.6
Respiration rate (min) ($n = 720$)	62.6 ± 16.9	55.5 ± 12.8	36.1 ± 2.3	27.1 ± 2.7

cortical activity and phasic activities: initially isolated or grouped movements of the spines, later movements of the hose and limbs, masticatory movements and shaking of the whole body. Extension of the third eyelid across the eyeball and nystagmus consistently occurred.

During all four states only slight variations in heart rate occurred. This contrasted with the progressive decrease in respiratory rate as the transition between the states occurred (Table). The jerk reflex was recorded during all 4 states. It was particularly marked during DR and was accompanied by K complex and disappearance of spindles on the ECoG, apnoea for 3–6 sec then tachypnoea (360/min) for 12 sec after which the normal respiratory rate (60/min) was restored. In both SWS and PS the threshold of the response was increased, and despite the jerk reflex the animal for all intents and purposes remained asleep (Figure 1). TST was 42% with a ratio PS: TST of 1:3.5 or 28.6%. The distribution of the sleep and wakeful states showed the animals to be polyphasic and predominantly nocturnal. The sleep cycle duration was 17 ± 3.7 min ($n = 47$) and the mean duration of a period of SWS was 12 ± 4.2 min, of a period of PS 5.03 ± 2.5 min.

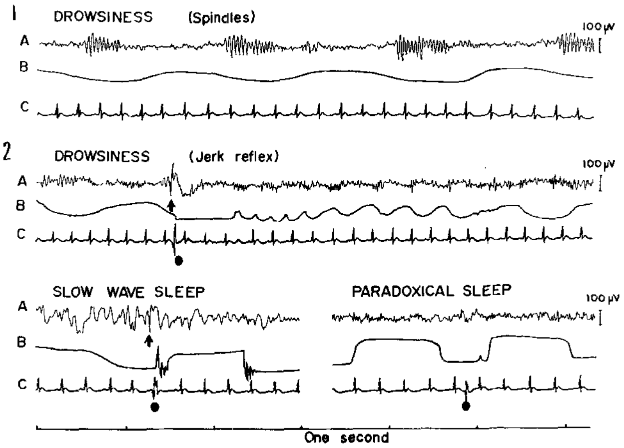

Fig. 1. Polygraphic characteristics of drowsiness and sleep states in the hedgehog (*E. europeanus*) and responses associated with the jerk reflex evoked by an auditory stimulus. A) ECoG (frontal lobes); B) respiration; C) electrocardiogram. 1. Presence of spindles linked to the respiratory pause during DR. 2. Jerk reflex (●) associated with an auditory stimulus. K complex (↑).

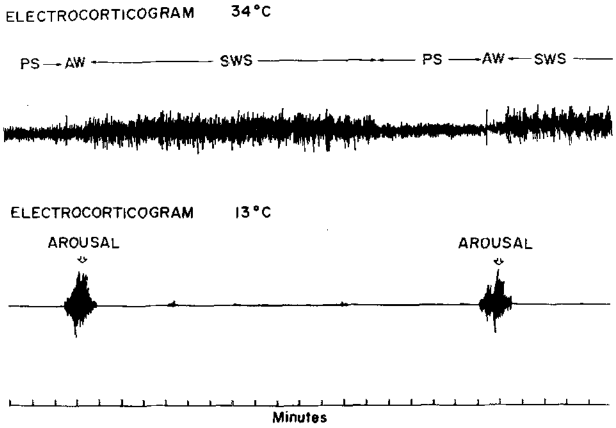

Fig. 2. Sleep cycle of *E. europeanus* at a body temperature of 34 °C and rhythmical arousals during hibernation at 13 °C. AW, wakefulness; SWS, slow wave sleep; PS, paradoxical sleep.

Entrance into hibernation at an external temperature of 11 °C was accompanied by disappearance of the ECoG and a reduction in heart rate from 200 to 11/min. However, a cyclic phenomenon persisted, recurring at intervals of 18.9 ± 1.1 min ($n = 36$) and lasting for periods of 1.5 min (Figure 2). Each period was preceded by an increase in heart rate to 20/min, occurring 1 min before the cortical and behavioural arousal. The ECoG trace resembled that of AW, and after several masticatory movements, the animal performed several 'balling up' movements on itself accompanied by deep inspiration. At a body temperature of 8 °C, the arousals occurred more or less randomly and only after intervals of several hours.

Discussion. The ECoG of the 4 sleep-wakeful states show several differences from those recorded in other mammalian species, notably the high amplitude waves during AW and the occurrence of spindles linked to respiration during DR. Disappearance of muscle tone during DR and the particular sensitivity to auditory stimuli in all states are points of added interest.

The discrepancy between these results and the visual estimation[2] of a TST of 80% may be explained by the fact that this species spends long immobile periods in the wakeful state. A TST of 43% has been recorded for the desert species *Paraechius hypomelas*[6], and assuming that both the authors concerned included DR in calculating TST, the present finding (67%) falls between the two. The higher sleep time recorded for the European species is probably due to the fact that it is a hibernator. Its reflex response to the auditory stimulus unaccompanied by cortical arousal during sleep probably also results from this fact.

The absence of continuous ECoG during moderate hypothermia (13 °C) prevents the recording of a sleep-wakeful state. Nevertheless the cyclic arousals recurring at intervals of 19 min may be compared with the very short awakenings which always follow PS at intervals of 17 min in the hedgehog at normal body temperature. A

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[6] E. S. Tauber, F. Michel and H. P. Roffwagg, Psychophysiology *5*, 201 (1968).

similar phenomenon has also been described in bats[7]. Assuming this comparison is justified, it may be concluded that the 'arousal cycle' has a Q_{10} equal to 1 and is an endogenous rhythm little influenced by the environment. The absence of any relationship between the level of metabolism and these cyclic phenomena, the fact that the sleep cycle is almost identical with that of the guinea-pig (16 min), and the small coefficient of variation of the cycle at 13 °C, suggest that the length of the sleep cycle is more related to the index of encephalization[8] than to metabolic rate.

Résumé. L'étude des états de vigilance chez le hérisson (*E. europeanus*) à la température centrale de 34 °C et de 13 °C montre que la durée du cycle de sommeil (17,0 ± 3,7 mn) durant l'été est très proche de celle du cycle d'éveil (18,9 ± 1,1 mn) pendant l'hiver. Cette analogie est en faveur du caractère purement endogène d'un tel rythme.

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23, chemin des Capelles, F–31076 Toulouse Cedex (France),
17 July 1974.

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[7] D. R. Brebbia and E. T. Pyne, Psychophysiology *9*, 122 (1972).

[8] A. Dallaire, P. L. Toutain and Y. Ruckebusch, Physiol. Behav. *13*, 395 (1974).

[9] Supported by grant from the Ministère de l'Agriculture (DGEER).

Artificial Lung Ventilation During Diaphragmatic Paralysis

Section of one phrenic nerve increases the activity of the respiratory centre. According to Dolivo[1], the reason for this phenomenon is the following: when half of the diaphragm is paralyzed the respiratory volume of the lungs also decreases, and in this way the inhibitory reflex from the lungs on the respiratory centre diminishes. Actually, artificial respiration with a constant lung volume in a rabbit with an open chest prevents the increase of the activity of the respiratory centre evoked by the section of the phrenic nerve. But, as shown in the present papaer, a constant artificial respiration when the chest is intact (that is in conditions in which artificial respiration is made during reanimation in patients with paralysis of the respiratory muscles) does not prevent the increase of the activity of the respiratory centre. Under these conditions, besides the reflex from the lungs, the accumulation of carbon dioxide plays a great role in the increase of the activity of the respiratory centre evoked by the paralysis of the diaphragm.

Methods. The experiments were performed on 10 adult rabbits anesthetized with 30–40 mg/kg Nembutal. After tracheotomy the respiratory frequency (F) and the tidal volume (V_t) were measured and then the animals were subjected to passive ventilation in which the frequency and the volume of the respiratory pump coincide with the same parametres of spontaneous respiration. Section of the phrenic nerves was performed at a low level in the neck, just before the nerves enter the thoracic cavity. Electromiograms were recorded by bipolar steel-wire electrodes affixed to the intercostal muscles. Blood samples were obtained from femoral arteries. Blood pH and $PaCO_2$ measurements were made in micro Astrup.

Results and discussion. One min after bilateral section of the phrenic nerves, there is a marked decrease of V_t (from 12.0 to 5.0 ml). Correspondingly the pH decreases (from 7.32 ± 0.04 to 7.20 ± 0.03) and the $PaCO_2$ increases (from 38.0 ± 3.5 to 51 ± 8.3) (Table I). Simultaneously the electrical activity of the intercostal muscles increases sharply (Figure). To normalize the $PaCO_2$ and the EMG, one must increase the volume of the respiratory pump from 12.0 to 22.5 ml (Table II, Figure). If the passive ventilation was not increased, the animals died in 0.5–1 h after bilateral phrenicotomy.

Thus the size of the passive ventilation which satisfied animals with intact respiratory muscles does not satisfy animals with diaphragmatic paralysis. Diaphragmatic paralysis in rabbits leads to a decrease of lung compliance, alveolar hypoventilation and hypercapnia. Thus not only the reflex from the lungs but accumulation of carbon dioxide plays a great role in the increase of the activity of the extradiaphragmatic muscles during diaphragmatic paralysis.

On the basis of these observations, the following conclusions were reached: 1. As is known, patients with respiratory paralysis require artificial ventilation which is much greater than the ventilation calculated on the

Table I. The influence of bilateral phrenicotomy on the respiration in rabbits

	Tidal volume (ml)		Respiratory frequency (resp./min)		pH		Pa CO_2 (mm Hg)	
	Before	After	Before	After	Before	After	Before	After
Mean	12.0	5.0	46.0	46.0	7.32	7.20	38.0	51.0
SD	± 2.4	±0.5	±15.0	±15.0	±0.04	±0.03	± 3.5	± 8.3
P		0.001		0.5		0.001		0.001
n = 10								

pHa, pH arterial blood; Pa CO_2, partial pressure of carbon dioxide in arterial blood; Mean, mean values; SD, standard deviations; *P*, significance of differences from values for normal animals; *n*, number of animals.

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[1] M. Dolivo, Helv. physiol. pharmac. Acta, *10*, 366 (1952).