

THERMAL ENVIRONMENT, SLEEP AND ENERGY METABOLISM IN PIGLETS

V. KOTRBÁČEK and Z. HÖNIG

Department of Physiology, University of Veterinary Science, 612 42 Brno, Czechoslovakia

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Abstract

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Effects of different thermal conditions on rapid-eye-movement (REM) sleep and its influence on the level of energy metabolism in piglets are described.

Heat production, respiratory quotient (RQ) and body temperature were measured in 1- to 9-d old piglets during the individual REM sleep episodes and compared with the respective values obtained in non-rapid-eye-movement (NREM) sleep. Two-hour measurements were carried out in metabolic respiratory chambers under comfortable thermal conditions and upon exposure to cold.

Thermal comfort was provided by heating the floor to 37 °C to 38 °C for 1- to 5-d old piglets and to 34 °C to 36 °C for the older animals. The air temperature in the chamber ranged between 25 °C and 26 °C. Exposure to cold was produced by decreasing the floor temperature to 28 °C.

Under cold exposure the total duration of REM sleep was reduced by 50 to 60 %. Both the number of REM sleep episodes and their duration were decreased. Heat production in REM sleep was invariably reduced. Under exposure to cold this decrease was highly significant ($P < 0.01$) owing to the disappearance of muscular tremor. However, concurrent decrease in body temperature, recorded in 1- to 3-d old piglets, was not significant.

In the thermoneutral environment a significant ($P < 0.05$) decrease in heat production was observed during REM episodes occurring shortly after food intake. By depressing the postprandial thermogenesis, REM sleep contributes apparently to more effective utilization of the food energy.

Lower RQ values observed in REM sleep are related to lower glucose oxidation under muscular atony.

Sleep, thermal environment, oxygen consumption, RQ

Effects of ambient temperature on the duration of sleep and its rapid-eye-movement (REM) — non-rapid-eye-movement (NREM) pattern have been described in both animals and man (Parmeggiani and Sabbatini 1972; Szymusiak and Satinoff 1981; Muzet et al. 1983, 1984). From these and other studies it appears that a comfortable thermal environment not only prolongs total sleeping time but also increases the contribution of REM sleep during which thermoregulation is switched off or at least its efficiency is reduced. In a non-comfortable thermal environment, on the other hand, the contribution of REM sleep to total sleeping time is reduced in direct dependence upon the degree of activation of the thermoregulatory mechanisms.

The observations that sleep and, in association with it, the intensity of energy metabolism are markedly affected by thermal stimuli also in newborn piglets have been published in our previous reports (Kotrbaček 1984; Kotrbaček et al. 1986). That this applies not only to total sleeping time but also to the pattern of sleep was evidenced by different electroencephalographs obtained in piglets sleeping in a thermoneutral environment and in the same animals sleeping in the cold. To throw more light on the matter, we decided to study the effects of different thermal conditions on the duration and frequency of REM sleep. Another objective was to find to which extent this sleep alters the efficiency of thermoregulatory mechanisms of the piglet. Therefore we compared the changes in heat production and body temperature in REM sleep with those occurring in NREM sleep.

Materials and Methods

Ten Large White piglets were included in the experiment and observed from 1 to 9 d after birth. They were separated from the sow after receiving colostrum and transferred to the laboratory at 1 d of age. They were kept there in individual cages on wire-slatted floors. Half of each wire-slatted floor was covered with a heated floor allowing regulation of the surface temperature. Up to the 5th postnatal day the temperature of the heated floor was maintained at 36 °C to 38 °C and afterwards at 34 °C to 36 °C. The ambient temperature was about 25 °C. The piglets were fed a liquid diet prepared from Selasan, a dry milk feed mixture for early weaning, at 6.00 h and then at 2-h intervals till 22.00 h on an ad libitum basis. When they were 1 d old, their upper eyelids were drawn up and their lower eyelids were drawn down with simple stitches so that their eyes were kept constantly open. This surgery took about 10 minutes and had no demonstrable effect on either the process of falling asleep or the duration of sleep, compared with intact animals. The observation of the eye movements was a simple and sufficiently exact method of determining the onset and the whole course of REM sleep without daily disturbance of the animals by procedures such as electroencephalography.

The experimental data were obtained in a metabolic respiratory chamber adapted so that the piglets could be constantly observed without being disturbed. The upper lid of the chamber was made of translucent plexiglass and mirrors were placed along both longitudinal walls of the chamber at the level of the head of the animal so that its eyes could be observed whatever its position was. Thermal comfort in the chamber was assured by the heated floor in the bottom of the chamber and by warming the air in the chamber by means of a water bath into which the chamber was immersed. Its conditions for 1- to 5-d old piglets were chosen in the light of our previous observations (Kotrbaček 1984) and were as follows: surface temperature of the heated floor, 37 °C to 38 °C; air temperature, 25 °C to 26 °C; cooling effect of the environment as assessed by means of an electric dynamic katathermo-

meter (Česnek and Novák 1971), 150 to 170 W.m⁻². In piglets over 5 d of age the surface temperature of the heated floor of 34 °C to 36 °C was enough to produce a thermoneutral environment. Cold load was produced by decreasing the temperature of the floor to 28 °C at practically unchanged air temperature and at an only slightly increased cooling effect of the chamber (190 to 210 W.m⁻²).

Under these two different environmental conditions the level of the energy metabolism of the piglets was determined in NREM sleep, i.e. at the time that the eyeballs were at complete rest with the pupils turned to the medial angles or towards the eyelids, and in REM sleep characterized by rapid movements of the eyeballs and other stereotypically repeated activity such as twitches of the mimic and limb muscles. So that more susceptible older animals might be disturbed as little as possible, body temperature measurements with a thermistor were taken only in piglets between 1 and 3 d old. All observations, i.e. the onset and end of REM sleep episodes, NREM sleep, waking and the state of wakefulness were recorded at 1-minute intervals directly on the chart paper covering O₂ consumption and CO₂ output. The shift of the paper by 1 cm per minute allowed both the regularity of all observations and the exact sum of the individual sleep episodes at the end of the experiment. The experimental design itself was as follows: after a 12-h night fast the piglet was placed into a metabolic chamber where thermoneutral conditions were produced as described above. After the piglet became quiet and fell asleep, i.e. about 10 minutes later, its resting heat production was assessed. Afterwards the piglet was fed the liquid diet from a graduated baby bottle directly in the metabolic chamber and



Fig. 1. A piglet sleeping in a thermal comfort.

its O₂ consumption and CO₂ output were recorded for 60 minutes together with the exact information on its REM sleep, NREM sleep and wakefulness. The same procedure was used in the cold environment which was produced after 15 minutes reserved for the change of the thermal conditions and for another feeding of the piglet. The results obtained under the two thermal conditions covering the number

and duration of REM episodes, O_2 consumption, CO_2 output and RQ values in REM and NREM sleep were evaluated separately for piglets aged 1 to 3 d, 4 to 6 d and 7 to 9 d. In each group the means \pm standard errors (S.E.) of heat production were computed and the significance of the differences of the means between REM and NREM sleep was assessed by Student's t-test.

Results

Under the conditions of thermal comfort the piglets fell into NREM sleep within a few minutes of their insertion into the chamber. They slept mainly on their sides throughout the experiment (Fig. 1). The first REM sleep episode appeared, on average, 11 minutes after food intake. Characteristic features of REM sleep were not only rapid movements of the eyeballs but also twitches of the rostrum, ears and

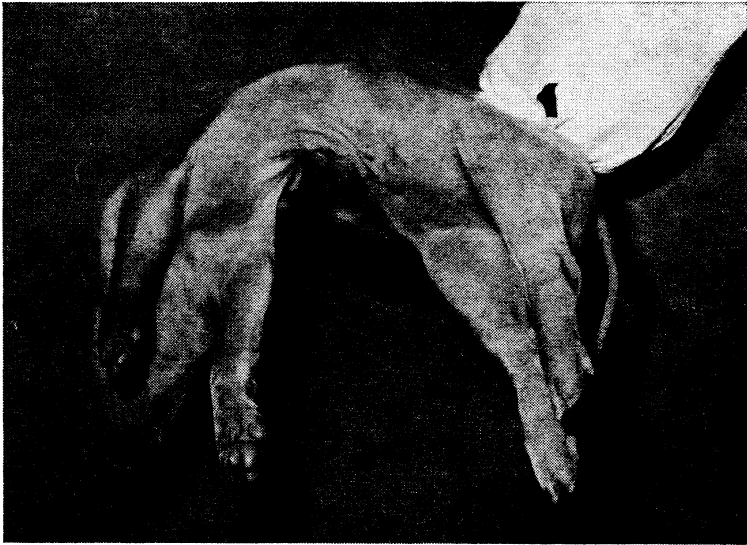


Fig. 2. Relaxation of muscle tone of the piglet in REM sleep.

later also of the limbs. This spontaneous muscular activity was accompanied by relaxation of tone of the skeletal muscles. This condition became manifested by atonical weakness of the body which was particularly conspicuous when the piglet was grasped with the hand (Fig. 2). The respiration was irregular with frequent apnoeic pauses.

In the cold environment the piglets became recumbent on their bellies with their limbs tucked under the body (Fig. 3). Gradually they developed muscular tremor which persisted even in NREM sleep episodes. The first REM sleep episode appeared, on average, 25 minutes after food intake. As in the thermoneutral environment, the REM sleep episodes were accompanied by disappearance of muscular tremor and by total relaxations of the skeletal muscles.

Total duration of REM sleep depended on the thermal conditions. It was decreased significantly ($P < 0.001$) by the cold stimulus (Fig. 4), falling to about one half and one third of the time recorded under thermoneutral conditions in 1- to 3-d old piglets



Fig. 3. A piglet sleeping in cold.

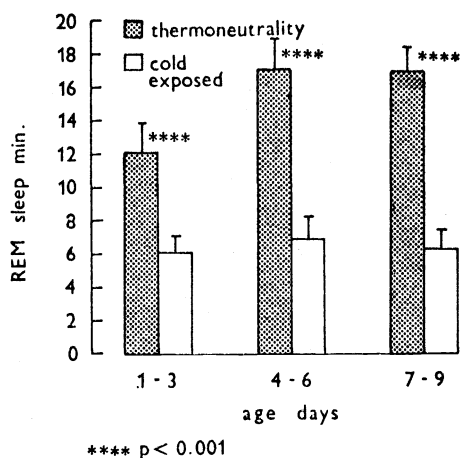


Fig. 4. Effect of two different thermal conditions on the duration of REM sleep in piglets observed for 60 min.

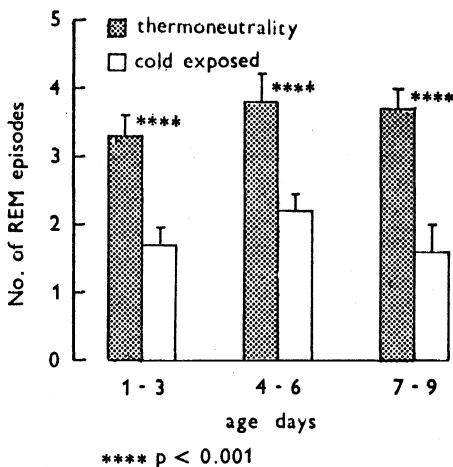


Fig. 5. Effect of two different thermal conditions on the number of REM sleep episodes in piglets observed for 60 min.

and in the older animals, respectively. A significant ($P < 0.001$) decrease occurred in the number of REM sleep episodes (Fig. 5) and, except in the youngest piglets, also in their duration.

Heat production expressed per unit of metabolically active body mass ($\text{kg}^{0.75}$) changed, as expected, mainly in dependence on the experimental thermal conditions. In addition, it was affected by the sleep phases under study: in REM sleep it was generally lower than in NREM sleep (Fig. 6). In the thermoneutral environment

the differences reached significance ($P < 0.02$) only in 7- to 9-d piglets. All experimental piglets, however, showed a significant ($P < 0.02$) decrease in heat production in REM sleep episodes following food intake (Fig. 7).

The differences found upon exposure to cold (Fig. 6) were invariably highly significant ($P < 0.01$). The decrease in heat production in REM sleep was rapid and so pronounced that it distinctly separated REM sleep episodes from the preceding and the following NREM sleep (Fig. 8). Sudden muscular relaxation accompanying REM sleep contrasted with muscular tremor which was intense before and particularly after the end of each sleep episode. In a number of cases the piglets awoke from REM sleep, showing increased motoric activity.

In association with the onset of REM sleep changes were also observed in the relation between O_2 consumption and CO_2 output. The more rapid decrease in CO_2 concentration resulted in decreased RQ level in piglets of all three age groups and under both environmental thermal conditions (Table 1). Changes in the mean RQ values were not significant when evaluated separately for the individual age groups but became highly significant ($P < 0.01$) when the data recorded for the three age groups were cumulated. The changes in body temperature during sleep observed in the youngest age group were not significant, even though a decrease in the mean values in REM sleep by $0.1\text{ }^\circ\text{C}$ to $0.2\text{ }^\circ\text{C}$ occurred in most of the animals observed.

Table 1. Decrease of RQ in REM sleep in piglets in a thermoneutral environment and upon exposure to cold

Age (days)	Thermoneutrality		Cold exposed	
	REM	NREM	REM	NREM
1—3	0.849 ± 0.012	0.874 ± 0.013	0.901 ± 0.012	0.932 ± 0.014
4—5	0.855 ± 0.014	0.888 ± 0.013	0.909 ± 0.011	0.944 ± 0.013
7—9	0.828 ± 0.008	0.855 ± 0.006	0.867 ± 0.013	0.903 ± 0.007

Discussion

In keeping with the findings of Szymusiak and Satinoff (1981) and Hale et al. (1984) in laboratory animals and with those of Haskell et al. (1981) and Muzet et al. (1983) obtained in humans the duration of REM sleep of our experimental piglets was markedly affected by thermal conditions. Under comfortable thermal conditions in our study REM sleep accounted for 20 % and 28 % of total sleeping time in 1- to 3-d old piglets and the two older age groups, respectively. It should be pointed out that our data were obtained by short-term measurements carried out immediately after food intake which in itself supports REM sleep as evidenced by the experiments of Rubenstein and Sonnenschein (1971). At 8-h measurements conducted previously under the same thermal conditions the contribution of REM sleep to total sleeping time was slightly lower: 18 % in the

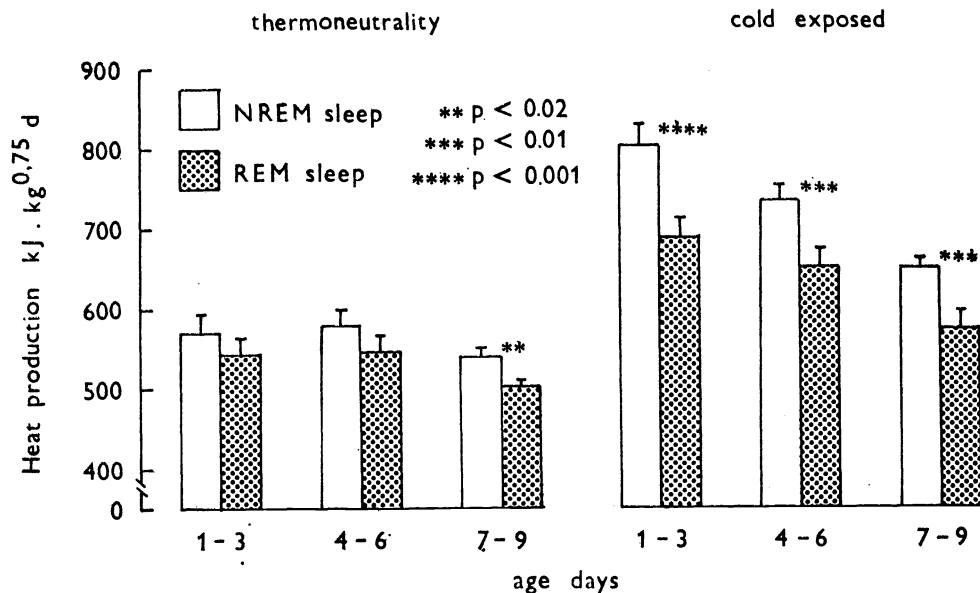


Fig. 6. Decrease of heat production by piglets in REM sleep in a thermoneutral environment and in cold.

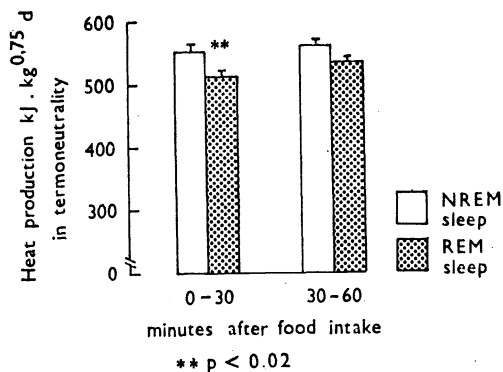


Fig. 7. Decrease of heat production by piglets in REM sleep during the postprandial period.

first week and 22 % in the second week after birth (Kotrbaček 1989). These results are comparable with those of 24-h measurements of sleep episodes in piglets reported by Ruckebusch and Morel (1968) who found that the contribution of REM sleep to total sleeping time was 20 %. This contribution apparently decreases with age. In 2-month old pigs it accounts for 10.9 % of total sleeping time according to Robert and Dallaire (1986).

Exposure of the piglets to cold produced a substantial decrease in the duration of REM sleep: in the youngest age group by about 50 % in consequence of a 50 % decrease in the number of REM episodes; in the older piglets by more than a half

cold exposed piglet 5 d of age

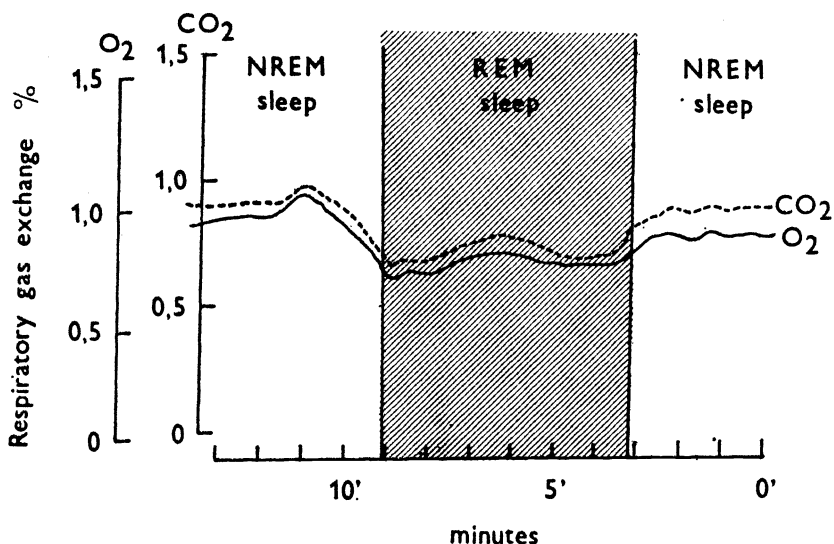


Fig. 8. Decrease of the respiratory gas exchange rate in REM sleep in piglets exposed to cold.

because also the duration of the individual REM episodes was shorter. During the exposure of the piglets to cold total sleeping time could not be exactly assessed because of their frequent waking and prolonged time of drowsiness. REM sleep, however, was easy to detect even under these conditions. Besides eye movements and muscle twitches it was characterized by general relaxation of the skeletal muscles and by disappearance of muscular tremor. Since muscular tremor is the main thermogenic mechanism in piglets, the REM sleep of our cold-exposed animals was invariably accompanied by an abrupt decrease of heat production. Moreover, the youngest piglets showed a regular, though not significant, decrease in body temperature. These findings are in keeping with the observations of Parmeggiani and Rabini (1967) on the blockade of muscular tremor during REM sleep in cats and with the reports of Glotzbach and Heller (1976) and Heller et al. (1983) who demonstrated changes in the efficiency of thermoregulation in REM sleep also in other animal species.

The decreased number of REM episodes and their shortening in our experimental piglets were therefore a necessary physiological response to cold for the sake of maintaining homeothermia. The importance of this adaptation including the aforementioned more frequent waking and increased motoric activity after REM sleep is underlined by the fact that during these sleep episodes no thermoregulatory behaviour of the piglets was observed. The position of the body (Fig. 3), effectively limiting heat loss in the wake state as well as in NREM sleep, is not actively maintained in REM sleep; muscle atony makes it impossible. This peculiar »paralytic state« during which piglets can, among other things, be handled without being wakened (Fig. 2) increases also their vulnerability. In our view it is in REM sleep that piglets are particularly at risk to be overlain.

The importance of REM sleep has been generally seen in its effects on the development and activity of the CNS (Parmeggiani 1982). Deprivation of this

sleep produces a non-specific increase in cerebral excitability resulting in behavioural changes (Drucker-Collin 1975).

Of no major functional importance of REM sleep, particularly in young animals, is its role in energy conservation. This statement finds support in numerous references cited by Horne (1977). The switching-off of tremor which in our experimental piglets led to decreased heat production during their exposure to cold could also be regarded as a saving of energy. Its actual effect, however, is doubtful because this »saving« had to be compensated for by increased heat production in NREM sleep or after wakening for the sake of maintaining homeothermia. Nevertheless, a decrease in heat production in REM sleep occurred even under thermoneutral conditions (Fig. 6). Of importance, in our view, is the fact that the first REM episodes appeared shortly after food intake, which in piglets is always associated with enhanced muscular activity resulting in enormously increasing heat production. Muscle atony which is induced by REM sleep is in itself a highly effective means of perfect immobilization leading to a rapid decrease of energy output. Under our conditions, however, the movement associated with food intake was limited to a minimum. Moreover, it does not seem likely that the observed decrease of heat production in REM sleep could be accounted for entirely by decreased tonus of the skeletal muscles. If this should be the case, a decrease in heat production must have been observed also in fasting animals. We therefore assume that the energy-saving effect of REM sleep may consist in lowering early postprandial thermogenesis as becomes apparent from Fig. 7. In view of frequent feedings in piglets this decrease may have a considerable effect on their feed energy utilization.

The regular decline of RQ characterizing the onset of REM sleep would only confirm a decreased glucose oxidation, i.e. a saving of the energy source. However, excluded cannot be the involvement of hypoventilation occurring in REM sleep in consequence of respiratory muscle atony.

The conclusions from our results are as follows: In piglets, as in the young of other animal species, REM sleep is a function of thermal environmental conditions. Both its total duration and the frequency and duration of REM episodes decrease rapidly when piglets are exposed to cold. This adaption is necessary to maintain homeothermia because shivering thermogenesis is blocked in REM sleep. The significant decrease in heat production in a thermoneutral environment during REM episodes occurring shortly after food intake suggests a possible contribution of this sleep to more efficient utilization of the energy received. The lower RQ is apparently a result of decreased glucose oxidation in REM sleep. Our findings in piglets support the general concept of REM sleep as an important energy-saving mechanism in the young.

Tepelné prostředí, spánek a energetický metabolismus selat

V předložené práci jsme sledovali působení rozdílných tepelných podmínek na REM spánek a vliv této spánkové fáze na úroveň energetického metabolismu selat.

U 1–9denních jedinců jsme měřili tepelnou produkci, RQ a tělesnou teplotu v průběhu jednotlivých REM fází a srovnávali je s uvedenými parametry zjišťovanými v NREM spánku. Dvouhodinová měření probíhala v metabolické respirační komoře za komfortních tepelných podmínek a při chladové zátěži.

Tepelný komfort jsme 1 až 5denním selatům zabezpečovali podlážkou, vyhřívanou na 37 až 38°C, selatům starším pak podlážkou 35 až 36°C teplou. Teplota

vzduchu v komoře se pohybovala mezi 25 a 26° C. Chladová zátěž byla vyvolána snížením teploty podlahy na 28° C.

Vlivem chladu se ve sledovaném období celková doba REM spánku snižovala o 50 až 60 %. Klesal počet REM fází a klesala i doba jejich trvání. Tepelná produkce v REM spánku se pravidelně snižovala. V chladu dramaticky s vysokou statistickou významností a to v důsledku vymizení svalového třesu. Současný pokles tělesné teploty, zjišťovaný u 1–3denních selat však statisticky významný nebyl.

V termoneutralním prostředí docházelo k významnému poklesu tepelné produkce v REM epizodách následujících krátce po příjmu potravy. Tlumením této postprandiální termogeneze se REM spánek zřejmě podílí na efektivnějším využívání energie krmiva.

Snížování hodnot RQ v REM fázi uvádíme do souvislosti s nižší oxidací glukózy při svalové atonii.

Термическая среда, сон и энергетический метаболизм поросят

В представленной работе проводились исследования воздействия разнообразных температурных условий на REM-сон и влияние данной фазы сна на уровень энергетического метаболизма поросят.

У особей в возрасте 1—9 суток измеряли продукцию тепла, RQ и температуру тела в ходе отдельных REM-фаз, сопоставляя их с приведенными параметрами, установленными в ходе NREM-сна. Двухчасовые измерения проводили в метаболической респираторной камере при комфортных термических условиях и при нагрузке холодом.

Термический комфорт поросятам в возрасте 1—3 суток обеспечивали настиллом, подогреваемым до 37—38 °C, поросятам постарше — настиллом с температурой 35—36 °C. Температура воздуха в камере достигала 25 и 26 °C. Нагрузка холодом была вызвана понижением температуры настила до 28 °C.

Под влиянием холода в исследуемый период общая продолжительность REM-сна понижалась на 50—60%. Уменьшалась численность REM-фаз и понижалась также их продолжительность.

Теплопродукция во время REM-сна регулярно понижалась; во время холода драматически с высокой статистической значимостью, вследствие исчезновения мышечного дрожания. Параллельное понижение температуры тела поросят в возрасте 1—3 суток не отличалось однако статистической значимостью.

В термонеutralной среде наблюдалось статистически значимое понижение теплопродукции на REM-фазах непосредственно после приема пищи. Это свидетельствует о доле REM-сна в более эффективном использовании энергии кормов.

Понижение величин RQ в REM-фазе приводим в связи с более низким окислением глюкозы при атонии мышц.

References

- ČESNEK, J. — NOVÁK, L.: Electrical katathermometer, its construction and some examples of its use in physiological experiment. *Physiol. bohemoslov.*, **20**, 1971: 57.
 DRUCKER — COLLIN, R. R.: The possible participation of REM in regulation of cerebral excitability. *Biol. Inst. Est. Med. Biol.*, **28**, 1975: 335—346.

- GLOTZBACH, S. F. — HELLER, H. C.: Central nervous regulation of body temperature during sleep. *Science*, **194**, 1976: 537—539.
- HALE, B. — MERIRIAN, D. — POLLARD, M. J.: Sleep-waking pattern and body temperature in hypoxia at selected ambient temperatures. *J. Appl. Physiol.: Respirat. Environ. Exercise Physiol.*, **57**, 1984: 1564—1568.
- HASKELL, E. H. — PALCA, J. W. — WALKER, J. M. — BERGER, R. J. — HELLER, H. C.: Metabolism and thermoregulation during stages of sleep in humans exposed to heat and cold. *J. Appl. Physiol.; Respirat. Environ. Exercise Physiol.*, **51**, 1981: 948—954.
- HELLER, H. C. — GRAF, R. — RAUTENBERG, W.: Circadian and arousal state influences on thermoregulation in the pigeon. *Am. J. Physiol.*, **245**, 1983: R321—R328.
- HORNE, J. A.: Factors relating to energy conservation during sleep in mammals. *Physiol. Psychol.*, **5**, 1977: 403—408.
- KOTRBÁČEK, V.: The effect of changes in the complexly defined thermal environment on body and skin temperature and energy metabolism in piglets. *Acta vet. Brno*, **53**, 1984: 31—39.
- KOTRBÁČEK, V. — NAU, H.-R. — LYHS, L.: Einfluss ausgewählter thermischer Umweltbedingungen auf den Schlaf beim neugeborenen Ferkel. Abstract of Papers, IV. International Symposium "Ontogenesis of Farm Animals", Brno, 1986, p. 9.
- KOTRBACEK, V.: REM spánek u selat a jeho fyziologický význam. *Veterinářství*, **39**, 1989: 29—31.
- MUZET, A. — EHRHART, V. — CANDAS, J.: REM sleep and ambient temperature in man. *Int. J. Neurosci.*, **18**, 1983: 117—126.
- MUZET, A. — LIBERT, J.-P. — CANDAS, V.: Ambient temperature and human sleep. *Experientia*, **40**, 1984: 425—429.
- PARMEGGIANI, P. L. — RABINI, C.: Shivering and panting during sleep. *Brain Res.*, **6**, 1967: 789—791.
- PARMEGGIANI, P. L. — SABBATINI, L.: Electromyographic aspects of posture, respiratory and thermoregulatory mechanisms in sleeping cats. *Electromyography and clinical neurophysiology*, **33**, 1972: 1—13.
- PARMEGGIANI, P. L.: Regulation of physiological functions during sleep in mammals. *Experimentia*, **38**, 1982: 1405—1408.
- RUBENSTEIN, E. H. — SONNENSCHN, R. R.: Increased REM sleep in the cat after food intake. *Proc. of the 25th Cong. of Physiol. Sci.*, **9**, 1971: 482.
- RUCKEBUSCH, Y. — MOREL, M. T.: Etude polygraphique du sommeil chez le porc. *C. R. Soc. Biol. Paris*, **162**, 1968: 1346—1355.
- ROBERT, S. — DALLAIRE, A.: Polygraphic analysis of the sleep - wake states and the REM sleep periodicity in domesticated pigs (*Sus serofa*). *Physiology Behav.*, **37**, 1986: 289—293.
- SZYMUSIAK, R. — SATINOFF, E.: Maximal REM sleep time defines a narrower thermo-neutral zone than does minimal metabolic rate. *Physiology Behav.*, **26**, 1981: 687—690.

Dr. Z. Hönik deceased August 5, 1989.