

Sleep and Wakefulness in the Housed Pony Under Different Dietary Conditions

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ABSTRACT

For several weeks, three ponies kept in an environment with controlled light and temperature, were studied for behaviour (time spent in recumbency and time required to consume hay or oats) and for electrical activity of the brain (cortical and sub-cortical) during the night phase of the circadian rhythm.

Recumbency was adopted by all the ponies for six or seven periods during the night. With a regimen of hay ad libitum, about four hours were cumulated in sternal recumbency and only one hour in complete lateral recumbency. Various degree of sleep, as identified by cortical and hippocampal electrical activities, accounted for 30% of the circadian cycle. Paradoxical sleep was calculated to occur during 7% of the 24 hours.

When oats were substituted for hay or during fasting for two to five days, the total recumbency time and the total sleep time (slow wave sleep and paradoxical sleep) increased. The time in lateral recumbency did not change.

RÉSUMÉ

Les auteurs ont étudié durant plusieurs semaines, chez trois poneys séjournant en permanence dans un milieu où l'on contrôlait la température et l'éclairage, la durée individuelle du décubitus et ses modalités, le temps consacré à la consommation de la nourriture (foin ou avoine), ainsi que l'activité électrique corticale et sous-corticale, au cours de la phase nocturne du nyctémère.

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Les trois poneys se couchèrent à six ou sept reprises, chaque nuit. Quand ils recevaient du foin ad libitum, ils demeurèrent en décubitus sternal durant environ quatre heures et en décubitus latéral complet pour une heure seulement. Les différents états de sommeil, tels qu'identifiés par l'activité électrique du cortex cérébral et de l'hippocampe, représentent 30% de la période d'enregistrement. Le calcul du sommeil paradoxal a révélé qu'il occupait 7.0% du nyctémère.

Le remplacement du foin par de l'avoine, ou un jeûne de deux à cinq jours, augmentèrent la durée totale du décubitus, sans modifier celle du décubitus latéral complet. Ils prolongèrent aussi la durée totale des deux états de sommeil.

INTRODUCTION

A growing volume of information is now available on the correlation between thermoregulatory and digestive behaviour (1, 3) and between the former and sleep (6, 12). Since these activities are related to energy regulation, dependency between dietary conditions and sleep may be suspected.

Each species has its own peculiar basic pattern of sleep, which can be partially suppressed or exaggerated under different management or feeding conditions. However, it is surprising how infrequently this aspect of behaviour has been investigated in large domesticated herbivores such as Equidae, for which oats and hay represent two different but natural regimens.

Continuous electrocorticography, electromyography and electro-oculography have made possible a long term study of the relationship between sleep and such dietary conditions. Other aspects, such as recumbency and feeding behaviour, were also easily recorded on a kymographic apparatus.

In this study variations in the behavioural states of sleep and wakefulness and their corresponding attitudes were studied under two different regimens in the housed pony.

MATERIALS AND METHODS

Three ponies (90 to 160 kg) of the Pottock breed, with chronically implanted electrodes, were used when respectively six months, one and six years old. Silver coated screws were epidurally placed over frontal, parietal and occipital cortices. Groups of three stainless-steel wires, insulated with enamel except for 1 mm at the tip, were aimed stereotaxically to lodge the exposed tip in the dorsal hippocampus according to the technique previously described in donkeys by Ruckebusch (8). The screws and electrodes were fixed with an acrylic resin and their position verified by radiography post-operatively and their local effect by a post-mortem histological examination.

In two ponies, screws were placed into the orbital bone to record eye movements. In all animals pairs of 120 μ stainless-steel wires were used for recording the activity of neck muscles (*brachio-cephalicus*). Animals were allowed to become accustomed to their environment for one month before surgery and were left in their usual stalls for recordings, which began one week after

implantation. The connecting cables were attached during the experimental session to a counterweight assembly to provide a minimum of hindrance. Temperature and light were under complete control during the experiments.

The position of animals (standing, in sternal or lateral recumbency) and feeding behaviour were continuously registered by means of balloons connected to a kymographic apparatus with airtight tubings. These balloons were placed in the submandibular space, at the level of the sternum and on each side of the head.

The electrophysiological data were recorded from 18:30 to 06:30 directly on an eight-channel electroencephalograph (Alvar TR) at a paper speed of 2.5 mm/sec with samples at other speeds (15 to 30 mm/sec) or were stored on a tape recorder (Philips Analog 7) in order to replay at different speeds for later quantitative analysis. Tracings were visually scored in 120 sec periods as awake (AW), drowsiness (DR), slow waves sleep (SWS) and paradoxical sleep (PS). When two or more different states were present in one period, only that state which occupied a majority of the time was considered.

Animals were maintained on an *ad lib* water and hay schedule. Results obtained with this regimen constituted the baseline performance of each animal, to which experimental data under oats feeding were compared. Periods of fasting, two to five days with water only and straw taken away,

TABLE I. Daily Mean Time of Recumbency and of Sleep (min \pm s) in Individual Ponies, Data Cumulated During Three Consecutive Nights After Adaptation to a Feeding Regimen

Pony	Feeding Regimen	Recumbency		Sleep		Paradoxical/Total
		Total*	Lateral	Slow waves	Paradoxical	
1.....	Hay	255.1 (21.4)	53.8 (9.2)	135.6 (28.1)	53.6 (5.2)	27.9%
	Oats	311.3	57.8	203.0	88.0	30.2%
2.....	Hay	237.0 (32.3)	51.7 (6.3)	144.3 (7.3)	45.9 (2.9)	24.1%
	Cats	288.0 (13.0)	53.8 (9.2)	194.3 (10.3)	66.0 (10.9)	25.4%
3.....	Hay	196.2 (7.5)	55.0 (3.5)	157.3 (15.2)	31.3 (1.4)	16.0%
	Oats	233.7 (13.7)	55.8 (3.9)	188.0 (12.2)	38.6 (2.7)	17.4%

*Total recumbency: sternal plus lateral

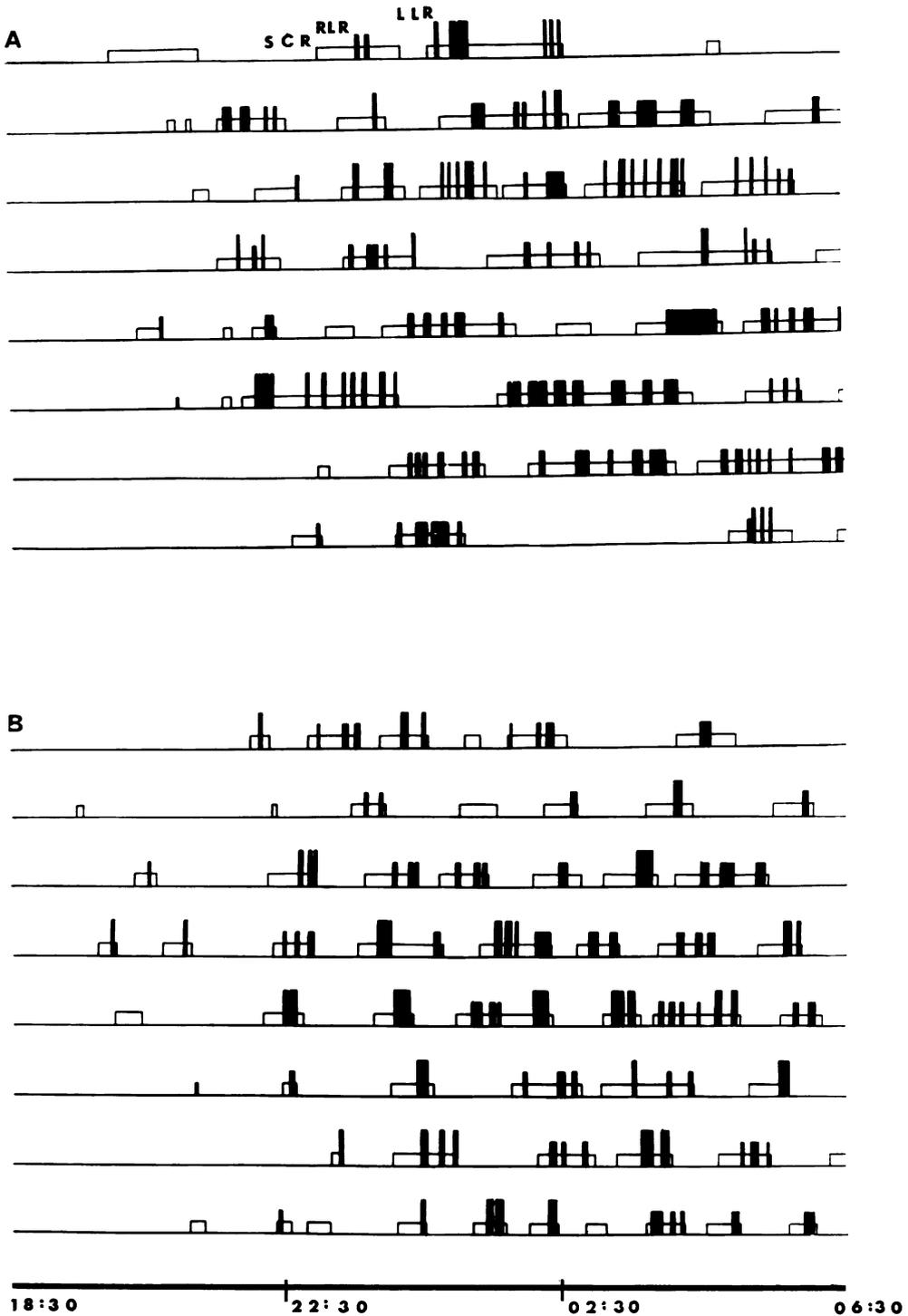


Fig. 1. Types of recumbency during eight consecutive nights (from 18:30 to 06:30) in two ponies (A and B) fed hay. SCR: sterno-costal recumbency; RLR: right lateral recumbency and LLR: left lateral recumbency.

were also considered. Oats, given twice daily, at 08:30 and 18:00, replaced hay on a 1:2 weight basis so that the total energy was about the same. Recordings were obtained during three consecutive nights, 48 hr and one week after changing to this regimen. At these times oats had appeared in the stool and the animals were well adapted to the new type of feeding.

RESULTS

RECUMBENCY

Each animal lay down at night, despite the experimental situation. In the youngest pony (six months) there was a constant alternation between feeding and recumbency. Under the hay regimen, the mean total

time spent recumbent per night was 252.0 minutes, spread over six or seven different periods. There were noticeable inter-individual variations in sternal recumbency time, associated with age (Table I) and probably with temperament. Lateral recumbency, right or left, represented about 20% of total recumbency time. Uninterrupted periods of lateral recumbency were usually short (mean: 4.6 min) but varied from one subject to the other (1-12 min). Total time spent in lateral recumbency was approximately the same in the two older subjects.

A gross pattern of recumbency was recognized through the night. At the beginning of the night a few brief periods of sternal recumbency were evident. But the major part of recumbency was seen after midnight where usually five or six periods of sternal recumbency were interrupted by several periods (8-24, mean: 14) of lateral recumbency (Fig. 1).

During the 24 hr recordings the ponies

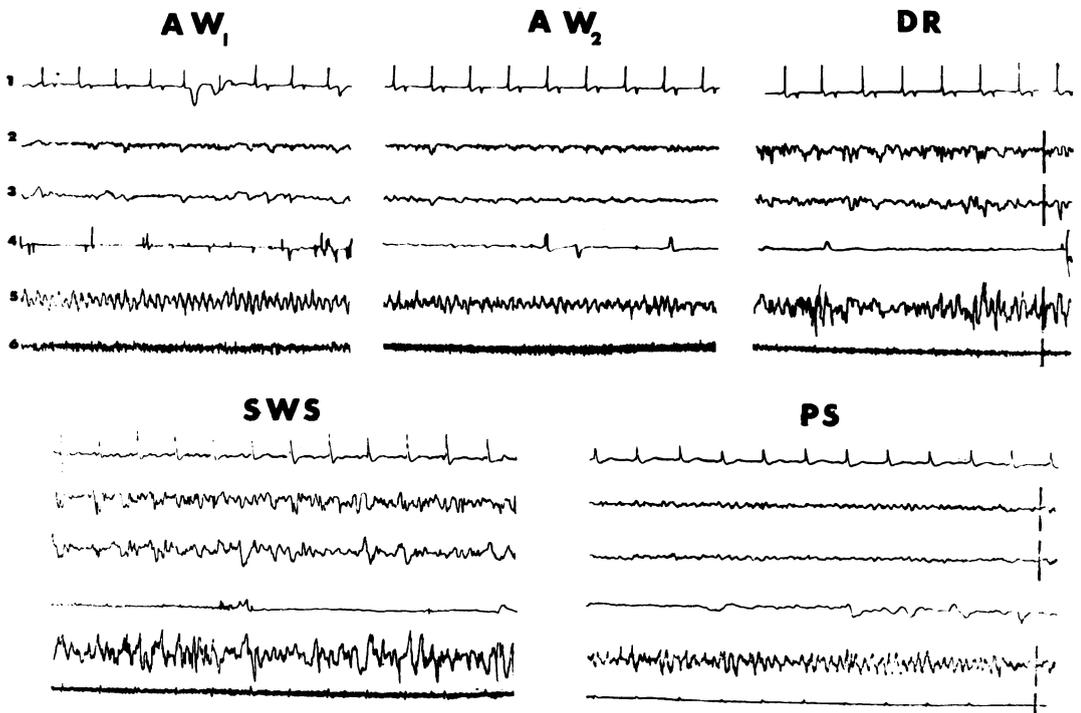


Fig. 2. Electrocardiogram and related phenomena: (1) heart rate, (2) ECoG at the frontal level, (3) ECoG at the occipital level, (4) eye movements, (5) hippocampal activity, (6) muscular tone in the pony, while awake (top) and in sleep (lower). During alert wakefulness (AW₁), hippocampal activity is synchronized. During non-specific wakefulness (AW₂), small irregular hippocampal activity occurs. During drowsiness (DR), muscular tone is slightly lowered and spindles are seen on the ECoG. During slow waves sleep (SWS), muscular tone is reduced. During paradoxical sleep (PS), muscular atonia is definite and hippocampal activity is similar to AW₁. Calibrations: 2 s. and 200 μ V

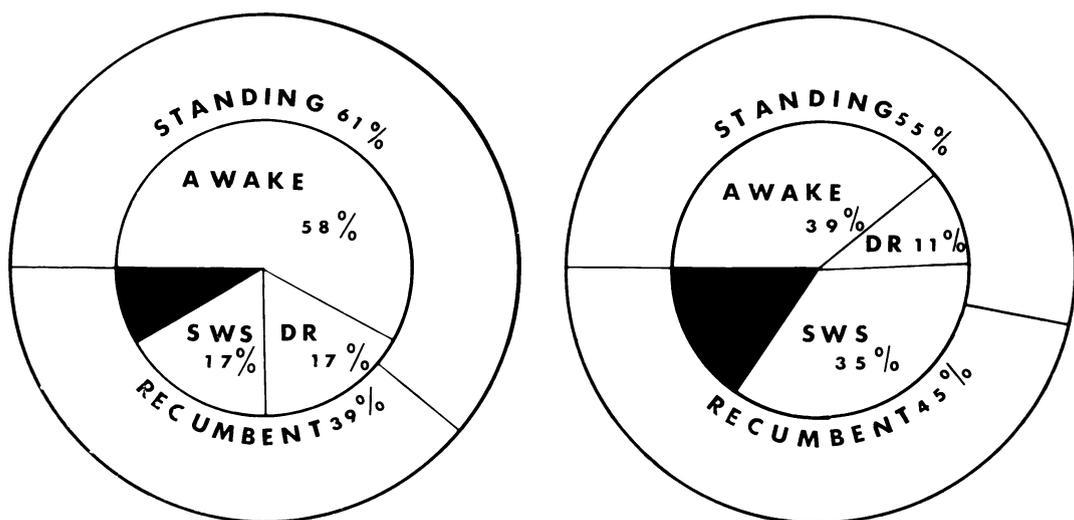


FIG. 3. Relative mean values for sleep-wakefulness states and attitudes during the night (18:30 to 06:30) exhibited by pony No. 3 when fed on hay (left) or on oats (right). The outer circle gives the relative duration of the attitudes. The inner circle shows the mean percentages of the sleep-wakefulness states as witnessed by the ECoG patterns: DR, SWS, AW1, AW2 and PS (in black, 8% on hay and 15% on oats).

showed an irregular tendency to adopt a recumbent position during the day. The younger pony would lie down at noon and in the mid-afternoon, but not every day, while the older animals did not show this behaviour.

SLEEP

Polygraphic recordings were used to separate the two distinct states of sleep: slow waves sleep (SWS) and paradoxical sleep (PS). The former was characterized at the level of the neocortex by large slow waves on which was superimposed irregular low voltage fast activity. Frequency of larger waves ranged from 3 to 8 Hz and amplitudes were between 90 and 150 μ V. Hippocampal tracings showed an irregular rhythmic slow activity (4-5 Hz) alternating with high voltage waves (150-200 μ V). As typical sleep progressed the large waves were more frequent (Fig. 2). An interesting feature of SWS in ponies is that it occurred in a standing subject, as it does in the donkey and the horse (8, 12).

Neck muscular tone persisted during SWS, but had a decreased intensity even when the animal was standing. When a subject was recumbent, neck muscular activity was either present or progressively reduced at the end of a single period of SWS. This

was particularly true if SWS was to be followed by a period of activated sleep (PS). Eyelids were usually closed during SWS and ocular movements were infrequent.

SWS did not end abruptly in paradoxical sleep. There was a progressive desynchronization at the cortical level and a gradual synchronization of hippocampal activity (intermediary phase). Onset of paradoxical sleep was signaled by a rhythmic activity in hippocampal leads (6-8 Hz, 90-120 μ V) and by complete desynchronization in neocortical tracings with a frequency higher than 30 Hz. Muscle tone was completely abolished, and pronounced rapid eye movements occurred in bursts. They had a stereotyped pattern and were frequently accompanied by movements of the ears and the forelimbs, with twitching of the lower lip.

Hippocampal rhythmic slow activity, during PS, was identical to that occurring in alert wakefulness when the subject was activated by any external stimulus (Fig. 2). Paradoxical sleep took place either in sternal or lateral recumbency, the former being more frequent during the early part of the night.

EFFECTS OF OF REGIMEN ON RECUMBENCY AND SLEEP

When ponies were fed oats, the total time spent in recumbency was increased by about

TABLE II. Percentage of Increase in Recumbency and Sleep Time in Ponies Under Oats Feeding and Prolonged Fasting, Compared to Hay Feeding

Pony	Regimen	Recumbency		Sleep	
		Sternal	Lateral	Slow waves	Paradoxical
1.....	Oats	25.0	7.4	49.7	64.1
2.....	Oats	26.4	4.1	34.6	43.5
3.....	Oats	26.7	0.1	19.0	23.3
3.....	Fasting	25.8	5.1	20.0	16.9

20%. However, the mean time in lateral recumbency did not vary significantly. The inter-individual differences observed under hay feeding were maintained so that all the subjects reacted in the same way and increased the duration of sternal recumbency (Table II). The total time spent feeding was reduced (420.3 min/24 hr versus 740.0 min/24 hr); the decrease was more marked at night (105.3 min versus 400.0 min). Time spent in sternal recumbency increased after two or three days of fasting.

Oats feeding (for 48 hr or one week) and fasting both caused a decrease in awake and drowsy states and an increase in total sleep (TS) time (SWS and PS). The polygraphic records showed that SWS and PS increased together so that the ratio PS/TS remained about 25%. The number of single phases of SWS and PS did not vary significantly; only their mean duration was increased. No differences were observed in the amount of alert wakefulness as judged by the hippocampal activity. Neither the change in regimen nor fasting modified the transition from SWS to PS.

An example of the variations in attitude and sleep-wakefulness states found during night-time in pony No. 3 receiving oats is shown in Fig. 3. It can be seen that the increase of PS paralleled that of SWS. On the other hand no DR occurred at the expense of AW.

DISCUSSION

Temporal aspects of recumbency in ponies are in accordance with results obtained in horses (2, 5, 11, 13) and donkeys (8), in which 23.0% and 31.6% respectively of the time was spent in recumbent attitude. However, the percentage time in lateral recumbency

exceeds that of donkeys (3.0%) and is slightly lower than that of horses (8.0%). This may be due to different environmental factors or may reflect the specific character of resting behaviour.

Data compiled from the three ponies over several weeks show that each animal has its own pattern of resting and sleeping. For example, pony No. 3 slept regularly about 40 min more than pony No. 2 and total time of recumbency was also higher by about one hour. The recordings were limited to males. The influence of age, as seen in the six months old pony, is in agreement with previous studies in other species (9). It can be considered with confidence that the daily intra-individual variations are less than inter-individual variations.

The 20% increase in duration of recumbency and sleep in all subjects with consumption of oats could be related to a lower cellulose content (10% for oats versus 34% for hay). In this experiment, the quantity of digestible energy is the same in each regimen and the effect of physical form of food observed one week later is not different from that seen after 48 hr. Thus a rebound phenomenon to an aggression, regardless of its nature, can be excluded. A possible explanation is that under oats feeding visceral information to the brain is reduced so that reticular substance is less active and sleep is increased. This hypothesis may also serve to explain the results observed in fasted ponies. Moreover, under oats feeding, less time is spent for choosing and ingesting food. Afferent impulses over olfactive and trigeminal nerves are diminished and consequently total sensory input is greatly decreased. This is also valid for fasting, since the straw is taken off and animals are fasted sufficiently to change the relevance of drowsiness (10).

Another hypothesis could be that oats, which are consumed more rapidly, promote more easily than hay the liberation of gas-

trointestinal hormones or/and a central satiety factor, phenomena which are described as facilitating sleep (4, 7).

The knowledge of temporal aspects of resting and sleeping and their promoting factors may be useful to increase animal production. Management and feeding are important in housed animals and very little is known about the "ideal environment". During rest and sleep, metabolic rate is at its lower level and an increase in their duration is essential for a better conversion ratio.

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