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THE RELEVANCE OF DROWSINESS IN THE CIRCADIAN CYCLE OF FARM ANIMALS

BY Y. RUCKEBUSCH

Laboratoire de Physiologie et Pharmocodynamie, Ecole Nationale Vétérinaire, 31, Toulouse, France

Abstract. Electrocorticography and concurrent electromyography were used to establish the quantitative duration of the states of sleep and wakefulness during the circadian cycle, and also during the night-time, in four species of farm animals. Associated attitudes and physiological data were also recorded. Drowsiness is described as a definite stable state of wakefulness, as opposed to alert wakefulness. The state of wakefulness occupied 85 per cent of the 24-hr period in the herbivorous species studied but only 67 per cent in pigs. Cows spend the greater proportion of this wakeful period in the state of drowsiness, horses spend the greater proportion in alert wakefulness. A considerable amount of the wakeful period of farm animals well-accustomed to their environment is spent in the drowsy state, when they are not asleep or actively ingesting or searching for food.

Electroencephalographic (EEG) studies in cats have demonstrated that sleep can be divided into two stages with differing electrocorticographic (ECoG) patterns, namely slow-wave sleep (SWS) and paradoxical sleep (PS) (Jouvet 1967). SWS is characterized by a synchronized high voltage, slow activity (HVSA) type of ECoG, muscle tone is reduced and this is said to be the only stage from which animals can progress into PS. By contrast PS is characterized by a desynchronized low voltage, fast activity (LVFA) type of ECoG and absence of muscle tone. Dream-like episodes associated with rapid eye movements (REM) and phasic motor activity in the face and limbs may occur (Dement 1958). Similarly, the state of wakefulness may be considered as being comprised of two degrees, alert wakefulness (AW) and drowsiness (DR). The ECoG pattern of the transition period between DR and SWS frequently exhibits conspicuous spindling.

Stages of sleep similar to those demonstrated in the cat have been shown to occur in farm animals. The earliest work reported that horses are able to sleep while standing (Steinhart 1937; Kayser 1949). ECoG studies revealed that SWS occurs in horses adapted to a constant environment; and experimentation with simultaneous ECoG and electromyographic (EMG) recordings revealed the occurrence of PS manifested by complete loss of postural tone (Ruckebusch, Barbey & Guillemot 1970). In cows, reduced gastric motility observed during the night-time (Balch 1955) was recently found to be concurrent with short periods of PS and associated absence of muscle tone (Ruckebusch & Bell 1970). Initial experiments with goats revealed that rumination coincided with DR or slow waves recorded on the encephalogram (Bell 1960). PS of a few minutes duration was detected by Ruckebusch (1962a) working with the same species. These brief phases of PS occurred after periods of rumination usually two or three times during the night. Very brief phases of PS also occur in sheep. Ruckebusch (1962b) found in 2-day-old lambs that the average time spent in PS per 24 hr amounted to 130 min, accumulated over twenty-two individual periods. In these sucking-lambs, a marked decrease in the amount of PS per 24 hr was recorded when ruminal function began to develop, i.e. at approximately 3 weeks of age. Recordings from 12-month-old sheep confined to metabolic cages showed a further reduction to a total of 32 min, accumulated in three or four periods. Complete loss of muscular tone and reduced gastric motility were the most commonly observed phenomena during these brief phases. Jouvet & Valatx (1962) reported a case of a milk-fed, orphaned lamb where reduction of the amount of PS occurred much later than in the above-cited instance. Klemm (1966) also recorded REM from adult sleep. Ruckebusch & Morel (1968) recorded complete loss of muscular tone during SWS in 3-month-old pigs.

The aims of this study are: (1) to correlate the states of AW and DR with specific ECoG patterns, (2) to define DR in farm animals, (3) to establish the quantitative relevance of DR during the circadian cycle and also during the night-time in a normal environment, and (4) to demonstrate that DR, usually considered as a state of ECoG activity intermediate between

AW and SWS can predominate in the wakeful period in some farm animals.

Methods

Data were compiled from laboratory records of experiments conducted during the winter months, November to March inclusive, over the past 5 to 10 years. The animals were stallions, cows and ewes; three adult subjects of each species and three female gilts aged approximately three months. Subjects were selected using the following criteria: that they were healthy and of docile and calm temperament and that sufficient time had elapsed following technical procedures (more than 15 days). The horses and cows were housed in ordinary barn stalls, the sheep and pigs in metabolic cages, and all supplied ad libitum with appropriate rations.

Each animal was fitted with chronically implanted electrodes for ECoG and EMG recordings in the following manner. Three pairs of ECoG electrodes each in the form of a twisted plastic-insulated stainless-steel lead soldered to the head of a silvered screw, were bilaterally implanted via burr-holes in the parietal and frontal bones. The burr-holes were positioned at an appropriate distance for each species from the sagittal suture to avoid encountering the dorsal sagittal venous sinus. This involved invasion of the frontal sinus in horses and cows and necessitated lateral reflection of the temporal muscles in horses. In sheep and pigs, the first two pairs of screws were located on either side of the fronto-parietal sutures and in all species all three pairs of screws were associated with that area of the dorsal cerebral cortex delimited by the cruciate sulci anteriorly and the occipital poles posteriorily, their tips reaching into the sub-arachnoid space. Insulation of each soldered joint and screw-head was achieved using a drop of acrylic resin (Fortacryl, Dental Fillings Ltd, London). EMG electrodes in the form of the non-insulated tips (0·1 mm) of single enamel-insulated stainless-steel leads were implanted in pairs in the dorsal cervical musculature and in the anterior limb musculature (triceps brachii) according to the technique of Basmajian & Stecko (1962). Similar electrodes were implanted one in each eyelid insertion to record REM. All animals were habituated to wearing a distribution box and familiarized with the recording and observation conditions.

Results were registered on an EEG machine (Reega VIII, PH, Alvar, Paris). No filter was employed, time constants of 0·3 s for ECoG and 0·01 s for EMG were used and a paper speed of 2·5 mm per s. Occasionally a paper speed of 15 mm per s was used. An audio-oscillator provided a source of stimulation at a strength of approximately 80 db and 800 to 1000 Hz. Approximate numerical values for arousal thresholds were determined in the following manner. An auditory stimulus of sufficient strength to wake the animal was sounded for 2 to 3 s. When the animal had returned to sleep the same stimulus was employed to retest its efficacy, thus a range of values, depending upon the depth of sleep, was obtained. Different frequencies were employed during the night to avoid as far as possible loss of sensitivity due to habituation. Recordings were made for periods of two to three consecutive 24-hr periods per week. The behaviour of the animals was visually monitored during the day and observed on closed circuit television (Grundig FA 30) during the night. Their various attitudes and movements were noted on the recording paper. In addition heart and respiratory rates were registered.

Results

Results are grouped according to ECoG patterns for the states of sleep and wakefulness, and are presented as mean values obtained for each species in groups of three animals. Figure 1 shows the ECoG patterns associated with the four different states of the circadian cycle, and associated physiological data. Comparative data of sleep-wakefulness states and behavioural attitudes obtained during three consecutive 24-hr periods, and also during night-time are represented in Table I and Fig. 2. Table II gives an analysis of the states of DR and PS.

In all species the ECoG recordings for each of the sleep or wakeful states were found to be similar: SWS being characterized by synchronized HVSA, PS and AW by desynchronized LVFA and DR by a mixture of both LVFA and HVSA. However, minor peculiarities existed for each species. During AW clear patterns of alpha rhythm occurred in pigs, and theta rhythm in horses. In sheep spindling was associated with DR and delta rhythm occurred during this same period in cows especially when ruminating. Of particular interest is the very rapid decrease of postural tone observed in pigs; it may totally disappear before the onset of SWS. By contrast sheep lost muscular tone gradually and some activity persisted in the form of short bursts even during PS. Horses also exhibited gradual

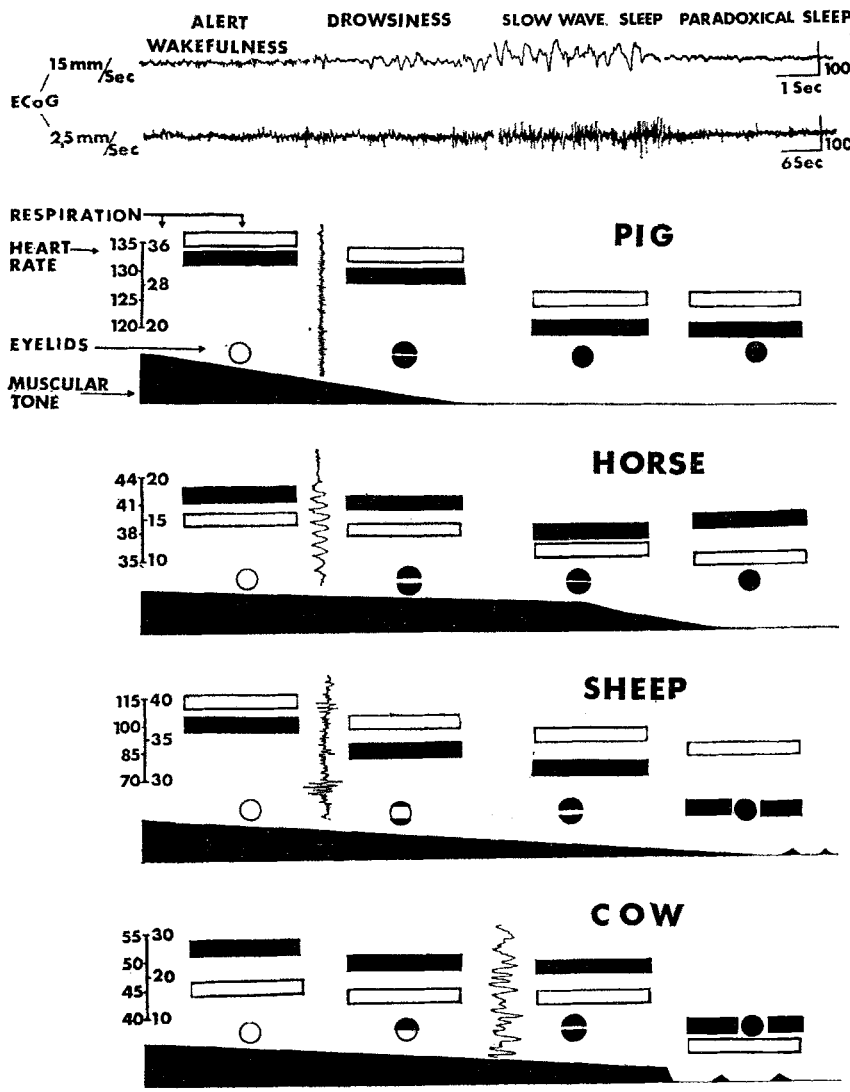

Fig. 1. Composite diagram of characteristic ECoG patterns, heart and respiratory rates, muscular tone and degree of closure of the eyelids during the circadian cycle. The different ECoG patterns for each species are shown at a speed of 15 mm/s: theta rhythm (horse), delta rhythm (ruminating cow), spindles (sheep) and alpha rhythm (pig).

loss of muscular tone until the middle of the SWS period whence it decreased to a negligible amount during PS. In cows an abrupt loss of postural tone occurred only at the onset of PS and as in sheep short bursts occurred during this period. In all four species the eyelids were open during AW and closed during PS. During DR the upper eyelid of the cow was relaxed and partial closure of the palpebral fissure was progressively more marked in sheep, horses and pigs. During SWS the eyes were completely closed in pigs and partial closure occurred to an increasing degree in sheep, cows and horses respectively.

In most cases the average heart and respiratory rates decreased with transition from the state of AW to PS. The difference in their values during AW and DR was slight. It was quite

Table I. Mean Values of Comparative Data of Sleep-Wakefulness States and Attitudes in Four Species of Farm Animals (Three Subjects of Each Species)

Species and time period	Duration and percentage					
	Wakefulness		Sleep		Attitude	
	AW	DR	SWS	PS	Standing	Recumbent
HORSE						
24-hr period	19hr 13min 80·8%	1hr 55min 8·0%	2hr 05min 8·7%	47min 3·3%	22hr 01min 91·8%	1hr 59min 8·2%
Night-time (10 hr)	5hr 14min 52·4%	1hr 54min 19·0%	2hr 05min 20·8%	47min 7·8%	8hr 01min 80·1%	1hr 59min 19·9%
COW						
24-hr period	12hr 33min 52·3%	7hr 29min 31·2%	3hr 13min 13·3%	45min 3·1%	9hr 50min 40·9%	14hr 10min 59·1%
Night-time (12 hr)	1hr 55min 16·0%	6hr 14min 51·9%	3hr 06min 25·8%	45min 6·3%	1hr 30min 12·5%	10hr 30min 87·5%
SHEEP						
24-hr period	15hr 57min 66·5%	4hr 12min 17·5%	3hr 17min 13·6%	34min 2·4%	16hr 50min 70·1%	7hr 10min 29·9%
Night-time (12 hr)	5hr 58min 49·8%	2hr 45min 22·9%	2hr 43min 22·5%	34min 4·8%	7hr 10min 59·7%	4hr 50min 40·3%
PIG						
24-hr period	11hr 07min 46·3%	5hr 04min 21·1%	6hr 04min 25·3%	1hr 45min 7·3%	5hr 10min 21·5%	18hr 50min 78·5%
Night-time (12 hr)	4hr 23min 36·5%	2hr 30min 20·8%	3hr 52min 32·2%	1hr 15min 10·5%	1hr 20min 11·1%	10hr 40min 88·9%

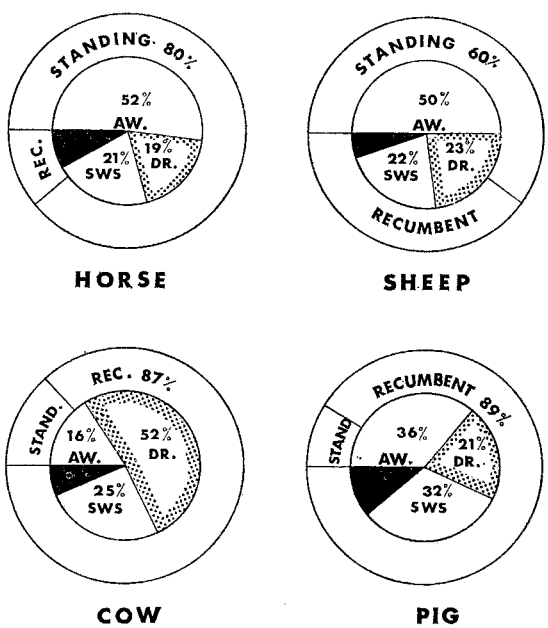

Fig. 2. Mean values of comparative data of sleep-wakefulness states and attitudes during night-time. The inner circle shows the relative duration of the ECoG pattern (PS in black) and the outer circle the relative duration of the attitudes.

pronounced at the transition from SWS to PS in the case of the two ruminant species, particularly cows. Tachycardia and polypnea were commonly observed in both horses and pigs during REM bursts in the course of PS. In all species during DR the arousal threshold to audio-stimulation remained low; it increased by a factor of approximately ten during SWS. It was observed that sheep and cows ruminate during both wakeful states. Rumination may continue even during SWS as defined by its ECoG pattern, in which case the rate is slowed, and frequently when rumination ceases cows fall abruptly into PS.

Horses, cows and sheep spend the larger part of any 24 hr in the wakeful state (88, 83 and 84 per cent respectively). This is true even during the night-time (71, 68 and 73 per cent). The alert state predominates in the wakefulness of horses and sheep, horses exhibiting a very high level during both the 24-hr period and the night (80 and 52 per cent). By contrast drowsiness predominates in cows even at night, occupying 51·9 per cent of this period, as compared with 22·9 per cent found in sheep. Pigs have a shorter wakeful period than the other species, 67 per cent for the 24-hr period, 57 per cent during the night. Drowsiness occurred mostly

Table II. Analysis of Periods of Drowsiness (DR) and Paradoxical Sleep (PS) during the 24-hr Period and during the Night-Time in Four Species of Farm Animals (Mean Values for Three Subjects of Each Species)

Species and time period	Duration and percentage		Ratio (expressed as a percentage)		Mean duration and no. of periods	
	Wakefulness	Sleep	DR/ total wakefulness	PS/ total sleep	DR	PS
HORSE						
24-hr period	21hr 8min 88·0%	2hr 52 min 12·0%	9·06	27·32	3min 29s 33	5min 13s 9
Night-time (10 hr)	7hr 8min 71·4%	2hr 52min 28·6%	26·63	27·32	3min 56s 29	5min 13s 9
COW						
24-hr period	20hr 2min 83·5%	3hr 58min 16·5%	37·37	18·90	17min 57s 25	4min 5s 11
Night-time (12 hr)	8hr 19min 67·9%	3hr 51min 32·1%	96·14	19·48	19min 40s 19	4min 30s 10
SHEEP						
24-hr period	20hr 9min 84·0%	3hr 51min 16·0%	20·84	14·71	10min 4s 25	4min 51s 7
Night-time (12 hr)	8hr 43min 72·7%	3hr 17min 27·3%	31·54	17·25	10min 18s 16	4min 51s 7
PIG						
24-hr period	16hr 11min 67·4%	7hr 49min 32·6%	31·30	22·38	5min 50s 52	3min 10s 33
Night-time (12 hr)	6hr 53min 53·7%	5hr 7min 42·7%	36·31	24·42	6min 30s 23	3 min 0s 25

during the night except in the case of pigs where it occurred in approximately equal proportions during both day and night. The ratio of DR to total wakefulness was smallest in the horse, both during the 24-hr period (9·06 per cent) and during the night (26·63 per cent) and largest in the cow, with the relatively enormous 96·14 per cent recorded during the night. The animal with the second highest ratio for both time periods was the pig. This species also showed the greatest number of periods of DR with a total of fifty-two periods of brief duration per 24 hr. Horses exhibited a large number of periods also and recorded the shortest duration averaging approximately 3·71 min. Sheep and cows showed approximately the same number of periods, but those in cows were of much longer duration (mean 18·82 min).

Horses slept only during the night, cows and sheep mostly at night. With regard to attitudes, horses spent the majority of this time standing: 80 per cent, sheep 60 per cent, while cows and pigs assumed a recumbent attitude, 87 per cent and 89 per cent, respectively. In addition, pigs spent a very high proportion of their day-time in recumbency. Sleep was generally distributed in two or three periods during the night, and during each of these periods transition from SWS to PS was usually repeated three or four times. PS occurred in horses, cows and sheep only during the night-time, but in pigs it was not restricted to this period and these animals had a higher incidence of sleep than the other species except when preoccupied with food. They exhibited the greatest number of periods of PS both during the 24-hr period (33) and during the night-time (25) and those of shortest mean duration, 3·18 min and 3·0 min respectively. The smallest number was recorded from sheep (7), and horses showed PS periods of longest duration (5·22 min). The ratio of PS to total sleep was highest in horses and lowest in sheep. Pigs also exhibited a high ratio of PS to total sleep.

Discussion

Data was compiled from animals of docile temperament and probably without any pathological past history. They were selected a posteriori for the stability of their sleep patterns and consequent consistent recordings. Each individual animal seemed to have its own specific sleep-wakefulness pattern and variation between records of one 24-hr period and another for

the same animal was much less than variation observed between two different animals of the same species. In all cases results obtained showed a daily intra-individual variation of less than 5 per cent, but a daily inter-individual variation of 10 to 25 per cent. Mean values calculated for 24-hr periods were found to be more consistent than those compiled in many early experiments from interrupted short period recordings. Firm implantation of the electrodes and their location in the subarachnoid space ensured that the ECoG tracings were well defined and clearly showed the different cortical patterns. The recordings for each species were limited to one sex and it must be born in mind that slightly different results may have been obtained if members of both sexes had been chosen as subjects.

In accordance with the results obtained, drowsiness or somnolence may be defined as an intermediary state between AW and SWS characterized by a mixture of LVFA and HVSA types of ECoG concurrent with a small decrease in muscular tone and heart and respiratory rates. Like SWS it has different depths, corresponding to the relative proportion of slow and fast waves present. It is a stable, non-evolutionary wakeful state which ends in an abrupt transition to either AW or SWS and during which the threshold to audiostimulation remains low.

During their respective circadian cycles different species exhibit different amounts of DR. The three herbivorous species examined spent approximately 85 per cent of the 24-hr period in wakefulness, either AW or DR. An equilibrium seems to exist between these two states, in the horse the shift is towards AW, in the cow towards DR. This is possibly associated with the different temperaments of these two species. The ECoG of horses shows theta rhythm which is indicative of a highly emotional nature (Brown & Shryne 1964). This same rhythm with a frequency of three to six per second has also been reported in burros during their wakeful periods (Stromberg et al. 1962). DR is the most common feature of wakefulness in adult ruminants (cattle and sheep) and even in the fetus near term ECoG records clearly show brief phases of DR (Ruckebusch 1972). In adult sheep spindling characterizes the ECoG pattern of DR. Cows reached a greater depth of DR than the other species, indicated by a higher percentage of synchronized slow waves in their ECoG tracings.

Sterman et al. (1965) observed DR in his studies of the waking patterns of cats and more recently Vital-Durand & Michel (1971) reported that following sectioning of almost all afferent nerves, cats showed a large increase in the percentage of DR, up to 40 per cent of the 24-hr period, at the expense of AW. These animals exhibited also both normal sleep states. During DR they assumed an attitude of statue-like immobility which resembled that normally observed in ruminants, indicating possibly that during their DR periods ruminants have little awareness of their surroundings which they seem to regard indifferently with partially closed eyes.

Cows and sheep frequently ruminate while in the DR state. The question whether animals fall asleep while ruminating or are capable of ruminating during sleep (i.e. SWS) is unimportant. The ECoG pattern of a recumbent ruminating cow may be either that of DR or SWS. It is always either AW or DR at the commencement of a period of rumination and in some cases can progress to that of SWS. That the ECoG pattern in the latter instance corresponds to a state of sleep is verified by the fact that when the animal stops ruminating it falls immediately into PS, the pattern of the transition period SWS to PS being identical with that recorded for the same period in a non-ruminating recumbent animal.

Loss of muscular tone, usually associated with transition to PS, frequently occurs in pigs during SWS and sometimes even occurs before the end of long DR periods. Pigs showed a shorter wakeful period (only 67 per cent of the circadian cycle) than herbivores, but the length of DR periods was of approximately the same quantitative value as that of the ruminant species. This was surprising considering the concurrent low level of muscular tone and superficial resemblance to sleep during this period.

During some phases of PS, bursts of tachycardia, superficial irregular breathing and movements of the limbs have been observed in all species. They were much more apparent in horses and pigs and sometimes tachycardia and increased breathing were recorded independently of any limb movement providing evidence that they were a direct result of dream-like episodes of central nervous origin. It may be concluded that these episodes are more vivid in horses and pigs, especially in the former species, than in the ruminants.

In as much as the percentage of PS is characteristic of different animal groups, being much

greater in carnivores than herbivores, the same does not apply to DR. Among herbivores horses exhibit a much lower percentage than cows, one possible explanation for this being the degree of awareness of the species of its environment.

Finally the proportion of DR can be increased in a single individual when in a protected environment which excludes predators and does not necessitate food-searching as is the case in domesticated breeds. It cannot be denied that the percentages of DR and also perhaps of SWS and PS observed in the laboratory are far in excess of that which may be observed in the same animal in the field.

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