

# Sleep Patterns in the Pony with Observations on Partial Perceptual Deprivation<sup>1</sup>

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DALLAIRE, A. AND Y. RUCKEBUSCH. *Sleep patterns in the pony with observations on partial perceptual deprivation*. *PHYSIOL. BEHAV.* 12(5) 789-796, 1974. - Sleep characteristics were investigated in ponies under normal stall conditions and during partial (visual and auditory) perceptual deprivation. Polygraphic recordings of slow wave sleep (SWS) and paradoxical sleep (PS) including changes in hippocampal activity are described. A notable feature was the modulation of rhythmic slow hippocampal activity during PS. Sleep patterns are described with a relatively short sleep cycle (mean: 13.5 min). An intermediary phase (IP), lasting about 2.0 min, frequently occurred (40%) between SWS and PS. Perceptual deprivation reduced the occurrence of IP but an increase in SWS was observed. After-effects showed an augmentation in both SWS and PS.

Sleep      Equidae      Hippocampal theta rhythm      Intermediary phase      Perceptual deprivation

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THE DEMONSTRATION of the existence of slow wave sleep (SWS) and paradoxical sleep (PS) in most mammals encouraged the view that sleep is more than a state of rest accompanied by reduced responsiveness to the external environment. It drew attention to the question of the biological value of sleep, the understanding of which requires careful analysis of neurological as well as behavioural aspects.

Much more has been done on the behaviour of man and animals during prolonged exposure to a monotonous sensory environment but the literature contains only a few studies of sleep under these conditions [6,12], all of which have been conducted on man. In their review on sleep and learning, Bryson and Schacher [2], suggested that sensory deprivation is unfamiliar to adult mammals and thus should theoretically cause increased subsequent sleep. So, such a study may be of relevance to some theories on the function of sleep, specially those relating SWS to physical fatigue and PS to cognitive functions.

In the present experiment sleep patterns are examined in ponies under normal stall conditions and during a period of partial perceptual deprivation.

## METHOD

Five male Pottock ponies ranging from six months to six years of age were chronically implanted with electrodes in the following manner: under pentobarbitone Na anaesthesia (20 mg/kg) epidural silver coated screws were positioned

bilaterally over the frontal, parietal and occipital regions of the cerebral cortex. Pairs of stainless steel wires (dia. 0.1 mm), insulated with enamel except for 1 mm at the tip, were inserted stereotaxically into the dorsal hippocampus, the stereotaxic coordinates being obtained on the basis of Yoshikawa's anatomical atlas [18]. The exact positions of the electrodes were verified post-operatively by radiography, and also by postmortem examination in two animals.

Two stainless steel wires (dia. 0.15 mm) were used for recording the activity of the neck musculature (*splenius*). In two ponies, the eye movements were recorded from two screws, one fixed in the temporal and one in the lacrimal bone. The heart and respiratory rates were monitored from two needles positioned subcutaneously on each side of the thorax.

The animals, fed on hay ad lib, were left in their usual stalls which were equipped with a closed television circuit. They were free to move about with a minimum of hindrance, the recording cable being attached to a counterweight assembly. Electrophysiological data were recorded on an VIII-channel polygraph (Alvar, Paris) at a paper speed of 2.5 mm/sec with samples also taken at other speeds (15 and 30 mm/sec). Tracings were visually scored in 2-min epochs as wakefulness (W), drowsiness (D-), slow wave sleep (SWS), intermediary phase (IP) and paradoxical sleep (PS) for quantitative analysis in percentage per 12-hr. When two or more states were present in a same epoch, that which occupied the majority of the time was considered.

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The duration of single episodes were calculated from their actual onset. Frequency waves at the cortical level were studied by means of selective filters using four basic bands ( $\alpha$ : 8–13 Hz;  $\beta$ : 4–36 Hz;  $\delta$ : 0.5–3 Hz;  $\theta$ : 4–7 Hz).

For each animal studies were carried out from 20:00 to 08:00 on four consecutive nights. Each different attitude and movement was noted against its corresponding tracing. These results were used as a control for comparison with those obtained during four days of perceptual deprivation. Deprivation was achieved by physical immobilization of the ear-drum using wax, and by blind-folding with an opaque hood. This procedure prevented the cortical arousal reactions usually registered for common sounds and light changes.

Arousal thresholds during sleep were measured in one pony (E) by electrical stimuli (1–6 V, 5 msec, 20 Hz) applied to the chest wall through the implanted electrodes. Ten stimuli (1 sec duration) of each voltage were tested in random order at intervals of approximately 1 min during Dr, SWS, IP and PS. Arousal was defined as both a behavioural response (movement of the head) and electrical changes lasting 5 sec or more: increase in neck muscle activity and cortical low voltage fast activity.

## RESULTS

### *Polygraphic Correlates of Waking and Sleep*

During wakefulness, low voltage (10–30  $\mu$ V) fast

activity (25–40 c/sec: L.V.F.A.) was recorded from all cortical leads. At the hippocampal level the activity showed an irregular theta rhythm with periods of small irregular activity (S.I.A.) (Fig. 1). During alert wakefulness, i.e. the brief periods when the attention of the animal was drawn to some external event: arrival of a human, presentation of food, strange sounds, neighing of another pony or when the animal was in search for food or preparing to defecate or urinate, the hippocampal activity showed regular high amplitude waves (150–200  $\mu$ V) of a low frequency (3–6 c/sec: rhythmic slow activity, R.S.A.). At the occipital leads, L.V.F.A. was superimposed on a slower rhythm (4–6 c/sec). The most conspicuous ECoG characteristic of drowsiness was the occurrence of spindles clearly visible from the frontal leads. At the hippocampal level, large (250  $\mu$ V) slow (1 c/sec) waves masked progressively the irregular theta rhythm. As the animal fell asleep the cortical spindle activity alternated with high amplitude (200  $\mu$ V) slow waves (1–4 c/sec) and with short bursts of low voltage fast activity.

During SWS delta activity (0.5–3 c/sec) became prominent from all cortical leads, and filter analysis showed a concomitant increase in both 4–7 and 8–13 c/sec bands (Fig. 2). Slow waves of high amplitude were recorded from the hippocampus. The ECoG features of PS are low voltage fast cortical activity with intermittent theta rhythm (4–6 c/sec) in the parietal and occipital regions, and R.S.A. from the hippocampal leads. Both synchronization and

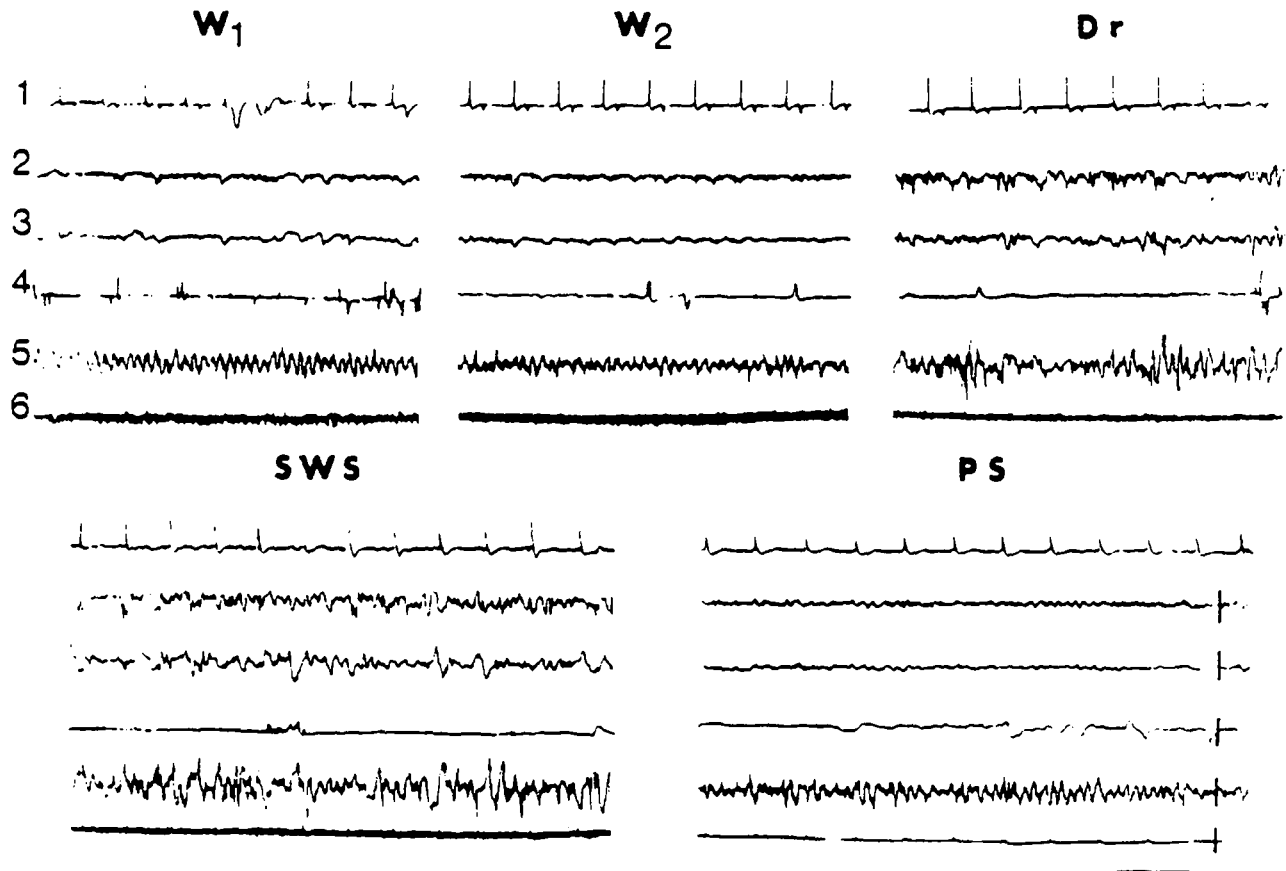


FIG. 1. Polygraphic characteristics of alert wakefulness (W<sub>1</sub>), quiet wakefulness (food intake: W<sub>2</sub>), drowsiness (Dr), slow wave sleep (SWS) and paradoxical sleep (PS). 1: EKG; 2: Occipital EEG; 3: Frontal EEG; 4: EOG; 5: Hippocampus; 6: EMG. Calibration: 1 sec, 100  $\mu$ V.

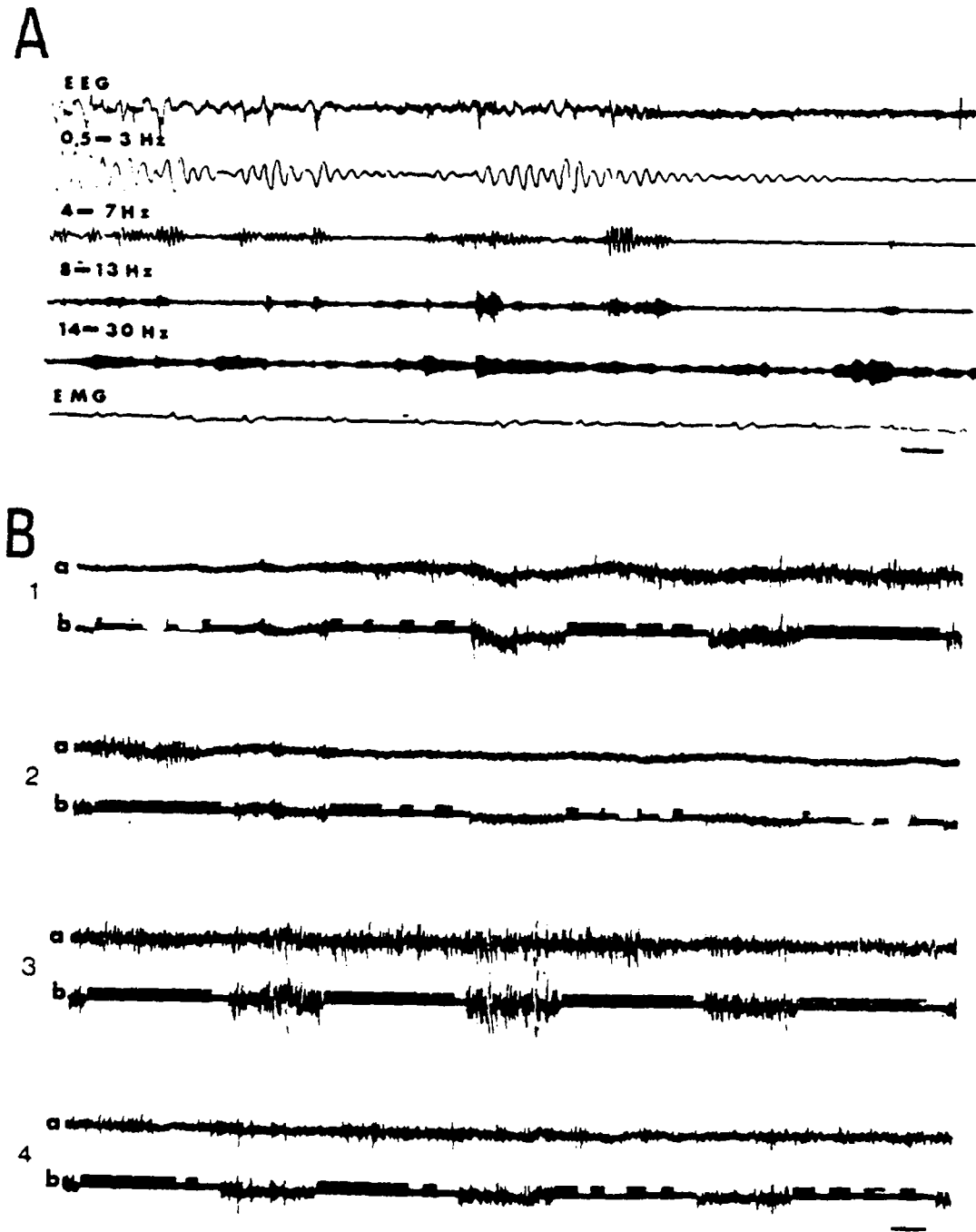


FIG. 2. Filter analysis of frontal electrocorticogram. A: Intermediary phase. ECoG: frontal leads; selective filters corresponding to  $\delta$ ,  $\theta$ ,  $\alpha$  and  $\beta$  rhythms; EMG: neck electromyogram. B: Semi-quantitative integration at 20 sec intervals of the four basic frequencies (b) of a frontal ECoG (a). 1: awake, drowsiness and slow wave sleep; 2: arousal; 3: slow wave sleep; 4: intermediary phase and paradoxical sleep. Time scale: A = 1 sec; B = 6 sec.

amplitude of hippocampal R.S.A. were intensified during phasic somatic phenomena (eye movements, muscular twitches, neighing, etc.) and occasionally interrupted by short periods of S.I.A. (Fig. 3). Before the onset of complete cortical desynchronization, a mixture of slow and fast waves occurred at the cortical level (Fig. 2) and an irregular

theta rhythm with interspersed high amplitude slow waves was seen from the hippocampus: this transition constitutes the intermediary phase (IP).

Neck muscle activity, high during wakefulness, except for periods when the animal lowers its head for food intake, was decreased proportionally to the degree of head drop

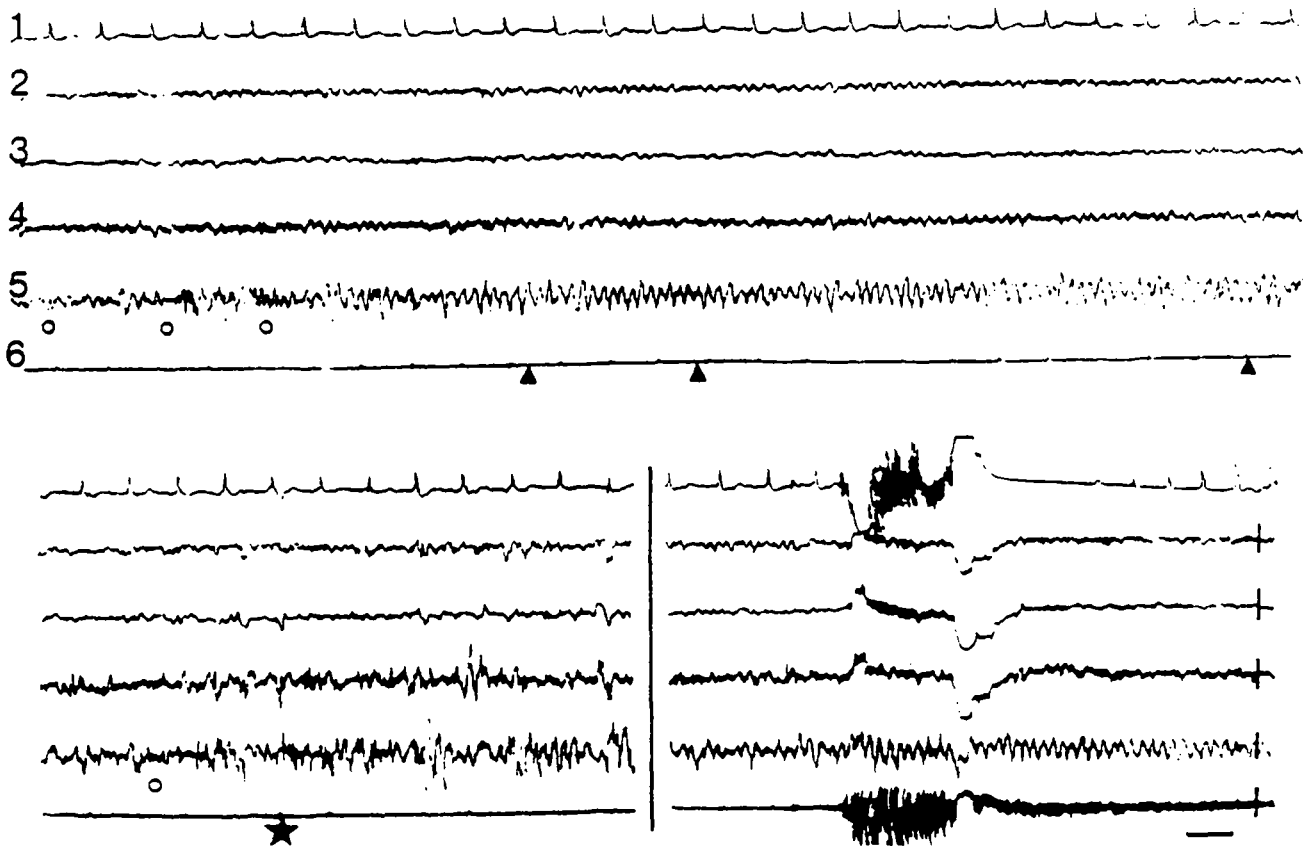


FIG. 3. Hippocampal activity during PS. 40 sec continuous recording of PS ending in drowsiness (★): 30 sec of drowsiness are omitted to show the arousal reaction. In 1: EKG; 2: Occipital EEG; 3: Frontal EEG; 4: Parietal EEG; 5: Hippocampus; 6: EMG. Phasic movements (head, ears or limbs) are indicated as (▲). Occurrence of low voltage activity (S.I.A.) at hippocampal level is showed by (o). Calibration: 1 sec and 100  $\mu$ V.

during drowsiness. A complete resolution of this activity was seen during SWS when in sterno-costal recumbency with the animals muzzle resting on the ground and in this case no change occurred during PS. In cases when muscular tone persisted during SWS and during the IP it disappeared entirely at the onset of PS. During SWS some slow eye movements occasionally occurred. During PS, intensity and frequency of eye movements increased and they were grouped in bursts. The observed phasic somatic events during activated sleep included movements of the muzzle, twitchings of the ears, contractions of the limbs and occasional whinnying. The eyelids were frequently partially open during IP and at the beginning of PS, but were always closed at the onset of rapid eye movement periods. The respiratory rate was slow and regular during drowsiness ( $25.8 \pm 0.70$ ) and SWS ( $26.0 \pm 0.58$ ) and during the latter state expiration was frequently more audible. During PS, the mean rate ( $25.2 \pm 1.18$ ) did not differ significantly from both Dr and SWS despite frequent inspiratory pauses and compensatory accelerations. Heart rate decreased progressively from the value seen during wakefulness ( $65.5 \pm 1.0$ ) to a stable value during Dr ( $56.0 \pm 0.4$ ) and SWS ( $55.9 \pm 0.34$ ). Irregularity with an unchanged mean frequency ( $55.1 \pm 1.12$ ) was the characteristic of PS. (All values given in parentheses are mean  $\pm$  standard deviation).

pooled data from four animals using 20 phases for each behavioural state.) In two animals, when recumbent, a marked respiratory sinus arrhythmia was present during SWS and this arrhythmia persisted during PS. Penile erection frequently occurred following a sleep cycle, when the animal was again standing, with subsequent micturition and defecation.

#### Sleep Patterns

The attitude of ponies during sleep is the same as for other equidae [10,11]. However the SWS state was infrequent in the standing animal and most often occurred during sterno-costal recumbency with the head resting or not on the ground. The posture taken during paradoxical sleep varied. Early in the evening (20:00–24:00), PS occurred in sterno-costal recumbency and due to the disappearance of neck muscular tone, the animal frequently readjusted its position by a behavioural arousal unaccompanied by cortical arousal. During the middle period (24:00–04:00) and the early morning (04:00–08:00) PS occurred mainly during lateral recumbency; at this time phasic somato-motor phenomena were more prominent.

The mean length of a sleep epoch was 41.0 min although some periods of uninterrupted sleep were as long as 90 min.

TABLE 1  
SLEEP PATTERN CHARACTERISTICS (MEAN  $\pm$  SE) IN THE PONY FED ON HAY AD LIB (FROM 20:00 to 08:00)

Animals	Total sleep time (min) (TST)	PS/TST (%)	Length of SWS period (min)	Length of PS period (min)	Sleep cycle length (min)	Sleep epoch length (min)	Number of sleep epochs (per day)
A	178.5 $\pm$ 11.4	24.6	5.3 $\pm$ 0.51	3.6 $\pm$ 0.22	13.0 $\pm$ 1.3	33.7 $\pm$ 3.7	7
B	237.0 $\pm$ 2.6	22.3	7.7 $\pm$ 0.22	3.9 $\pm$ 0.40	13.9 $\pm$ 1.4	49.9 $\pm$ 4.5	5
C	193.9 $\pm$ 9.1	21.5	6.5 $\pm$ 0.50	4.6 $\pm$ 0.11	11.4 $\pm$ 1.1	35.9 $\pm$ 5.5	5
D	188.6 $\pm$ 29.6	27.9	6.4 $\pm$ 1.30	4.3 $\pm$ 0.45	15.6 $\pm$ 2.1	43.6 $\pm$ 4.4	5

Total sleep was clearly distributed in two periods one occurring between 21:00–23:00 and the other between 02:00–04:00. On rare occasions (1–2%) sleep was observed at 12:00. Sleep cycle duration was calculated from the end of one PS period to the end of the next. Only cycles uninterrupted by awaking were used for compilations of data. The observed mean value was 13.5 min. The amount of PS expressed as a percentage of total sleep time (TST) was about 25% and the mean length of a single period was 4 min (Table 1).

#### Characteristics of the Intermediary Phase

In the sequential nature of SWS-PS, about 40% of activated sleep phases were preceded by an intermediary phase. There was a correlation ( $p < 0.01$ ) between the presence or absence of IP and the duration of a single PS period. The mean duration when IP was present was  $2.8 \pm 0.28$  min ( $n = 38$ ) and when absent  $4.1 \pm 0.30$  min ( $n = 48$ ).

A mixture of low voltage fast cortical activity with spindles and a few delta waves which progressively disappeared characterized the IP. At hippocampal level rhythmic slow activity occurred in bursts separated by high voltage slow waves. Neck muscular tone when present only completely disappeared a few seconds (10–20 sec) before the onset of the complete cortical desynchronization and the hippocampal theta activity characteristic of PS (Fig. 3). In most phases the eyelids were partially open and eye movements, when present were slow. Heart and respiration rates did not differ from values observed during drowsiness (Table 2). The mean duration of an intermediary phase based on pooled values from three ponies was  $2.0 \text{ min} \pm 0.7$ .

#### Arousal Threshold During Sleep

Figure 4 summarizes the arousal thresholds as measured by sets of 10 trials of electrical shocks for each voltage applied randomly to the thoracic wall. The increase in the intensity of the stimulus necessary to produce arousal during SWS was proportional to the degree of cortical synchronization. The arousal threshold was found to be slightly lower during the intermediary phase than during drowsiness. A marked decrease in responsiveness to stimuli occurred as soon as the cortical desynchronization and hippocampal theta rhythm characteristic of PS appeared.

#### Effects of Perceptual Deprivation

Three animals (A, B, C) were subjected to a four-day period of perceptual deprivation (visual and auditory) and their sleep patterns were compared with those recorded during the days before and during the days after the deprivation. Figure 5 shows the changes observed in Dr, SWS and PS. SWS was increased from a mean percentage of 20.5 to 26.4 on Days 1, 2 and 3 of the deprivation period. On the fourth day the mean time spent in SWS for all three animals (20.8%) was almost identical with the pre-treatment values. During perceptual deprivation PS showed no significant variation. Drowsiness did not vary significantly during deprivation but was slightly decreased during post-deprivation period.

The most interesting feature was the increase in total sleep time observed on Days 1 and 2 after the period of perceptual deprivation. The increase in TST was due to an augmentation of both SWS and PS. The latter showed a marked increase in its mean percentage (from 5, control value, to 17.4, deprivation value) and in the number of individual phases (from 7–8, control to 12–17, deprivation). The patterns of sleep were slightly modified during both deprivation and post-deprivation periods, namely the mean percentage of PS phases preceded by an intermediary phase which decreased from 37.0 to 17.0. The arousal threshold during sleep was measured in another animal (E). The probability of arousal resulting from a certain voltage was almost identical to that for the control period, except during the first day of deprivation when it showed an increase during drowsiness. The mean length of the sleep cycle was also increased during the deprivation period Days 1, 2 and 3 ( $17.5 \pm 2.4$  min;  $n = 46$ ) and then returned to the pre-treatment value on the fourth day, but no changes occurred after the period of sensory restriction ( $14.0 \pm 1.4$  min;  $n = 81$ ) despite the variations observed in TST.

#### DISCUSSION

The polygraphic manifestations of sleep in the pony, while resembling those of other placental mammals, exhibit two notable features: a short value for the sleep cycle length and a frequently occurring intermediary phase between SWS and PS.

The mean length of the sleep cycle (14.0 min) does not correlate with the metabolic theory of sleep rhythmicity

TABLE 2  
CHARACTERISTICS OF THE INTERMEDIARY PHASE (MEAN  $\pm$  SE)

Animal	Heart rate (beats/min)	Respiration rate (breaths/min)	Length of a single IP (min)	Percentage of PS episodes preceded by IP phases	
				Control	Sensory deprivation
A	51.6 $\pm$ 0.74	28.0 $\pm$ 1.26	2.5 $\pm$ 0.75	33.0	17.0
B	60.5 $\pm$ 0.68	24.0 $\pm$ 0.96	2.2 $\pm$ 0.72	61.0	35.0
C	65.6 $\pm$ 0.75	24.0 $\pm$ 0.20	1.5 $\pm$ 0.69	20.0	8.0

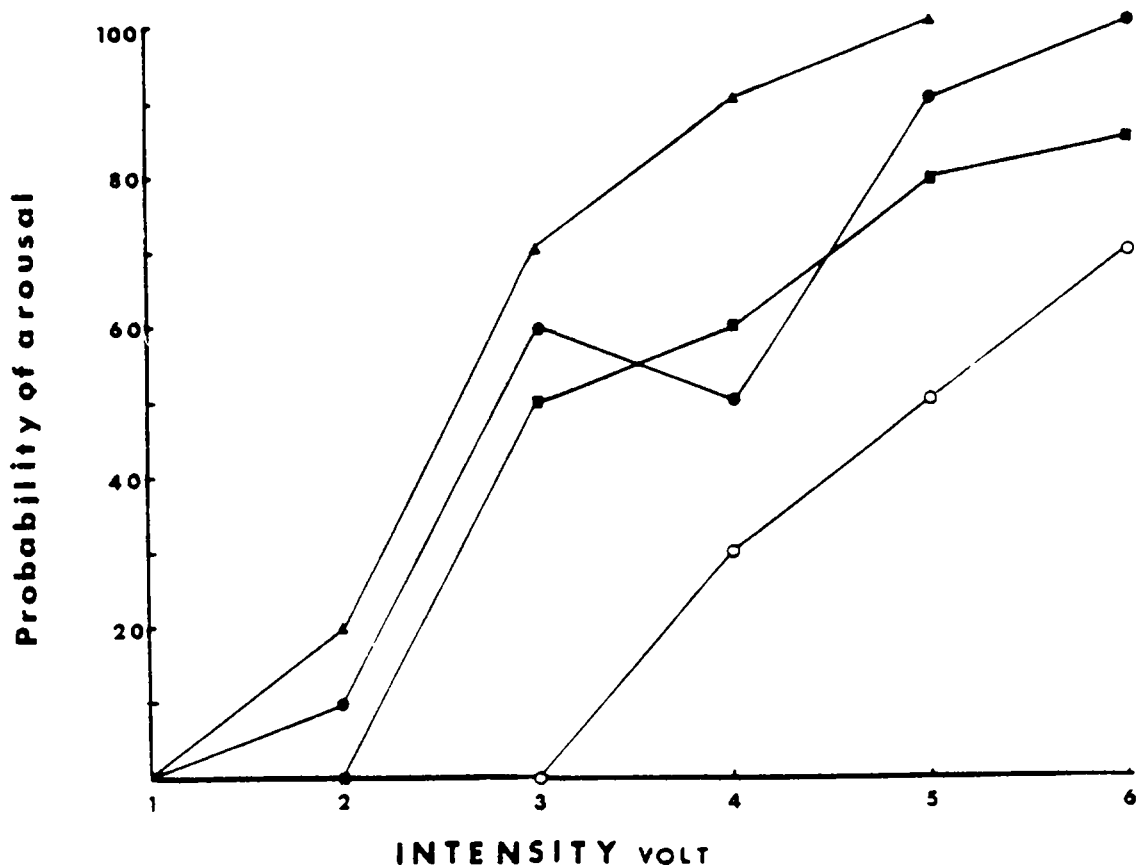


FIG. 4. Arousal threshold during drowsiness and sleep for an arousal stimulus applied during 1 sec (Pony E).  
▲ IP; ● Dr; ■ SWS; ○ PS.

[4,16]. Differences in criteria used to define a sleep cycle make comparisons difficult. However, when the sleep cycle values [4] are considered in relation to the degree of brain development from rodents to primates, as assessed by the coefficient of encephalization [8], a positive correlation is seen: rodents have values from 3–10 min with a coefficient of 6, the rabbit about 20.0 min with a coefficient of 6, the cat 21.0 min with a coefficient of 8, the chimpanzee,

86.0 min and man, 100.0 min both with a coefficient of encephalization of 32. This and the fact that injection of thyroxine decreased the interval between two successive PS episodes, suggest that these differences in paradoxical sleep rhythmicity are not related to basal metabolic rate but to the rate of turnover of an amino-acid, probably involved in catecholamine synthesis, in the nervous structures responsible for the triggering of paradoxical sleep, the rate of this

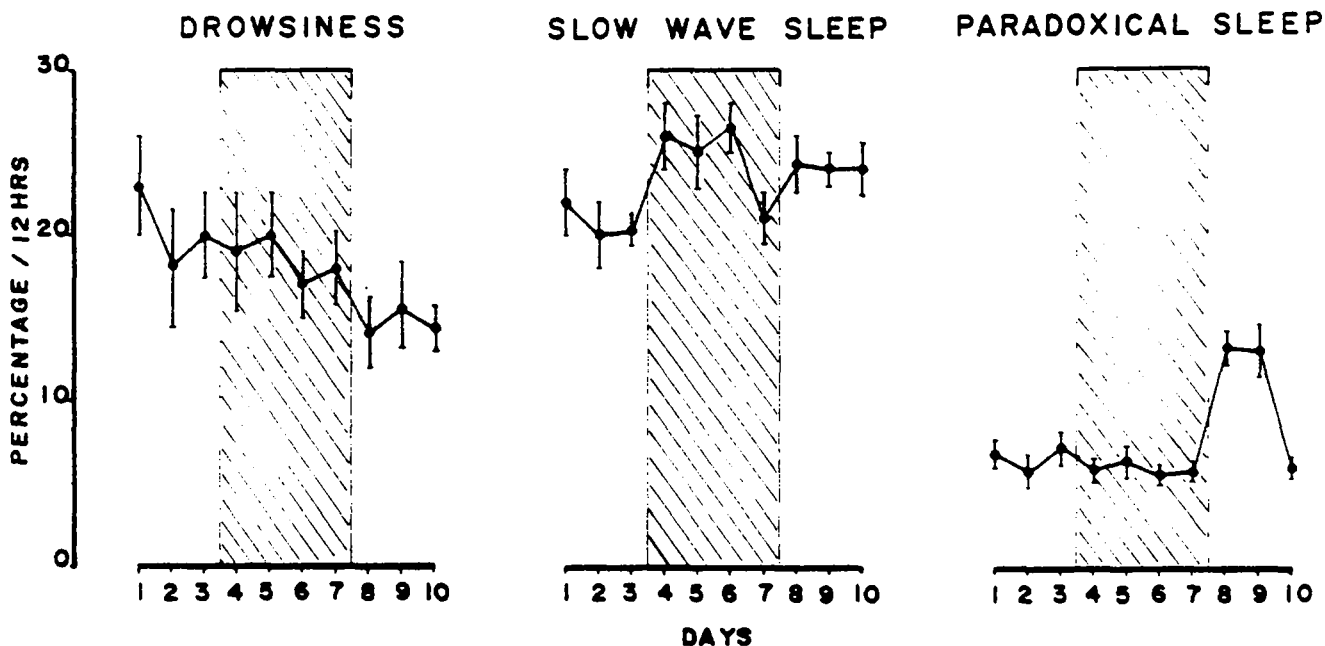


FIG. 5. Effects of partial perceptual deprivation on sleep patterns. Pooled data from three ponies. Hatched zone corresponds to the four-day period of sensory deprivation, preceded and followed by 3-day control periods.

process being influenced or controlled by higher nervous centres.

The relevance of the intermediary phase is interesting in its qualitative aspect. This transitory state with an arousal threshold slightly lower than during SWS is closer to wakefulness than an intermediary step between SWS and PS. Features such as a mixture of spindles and fast cortical activity, eyelids partially opened, heart and respiratory rates resembling those seen for drowsiness indicate rather a partial awakening prior to PS. A pre-paradoxical state has been described also in man [1], in the rat [3] and in the cat [13]. In the guinea-pig two states have been distinguished during PS, an early one in which the ECoG desynchronizes without postural atonia, and a second one in which both desynchronization and abolition of muscle tone occur. The guinea-pig, which is considered to be a poor sleeper, presents frequent awakening during sleep. The pre-paradoxical state observed in these animals may be equivalent to the IP observed in other species. The idea that the animal rapidly explores its surroundings before entering a more pronounced state of inhibition is supported by the effect of perceptual deprivation. In this case the possibility of exploring the environment is abolished and thus the number of PS episodes preceded by IP, at least in an animal well adapted to its surroundings before experimentation, is decreased.

In the sensory restricted pony, results support the suggestion of Bryson and Schacher [3], that sensory deprivation, which is unfamiliar to an adult mammal, may result in a subsequent increased sleep time. The increase in SWS, both during and after perceptual deprivation does not support the theory linking this state to physical fatigue

[17]. This change may be best explained in terms of sleep mechanisms. As far as sleep is both an active and a passive phenomenon [17], SWS can be increased independently of PS by the effects of reduced sensory input and less reticular involvement. The increase in PS is probably the essential feature of the post-deprivation period, and possibly reflects increase of information from the environment which then seemed more vivid. These results are in accordance with the observations of Tagny [14] where rats placed in an enriched environment showed an increase in both SWS and PS. In any case, this is not a rebound phenomena since both in the pony and the rat, the percentage of PS was not decreased during the period of sensory restriction.

These results may be attributed to the fact that during PS some aspects of protein synthesis in the brain are enhanced. This is supported by the work of Stern *et al.* [13] in cats, where intra-ventricular injections of cycloheximide, a protein synthesis inhibitor, induced an increase in PS time, the effect of which persisted up to ten days, while brain protein metabolism gradually returned to its normal level. Sensory deprivation may affect brain protein synthesis as shown by Levitan and *et al.* [6] who found, at early times of experiments, a higher level of amino-acids incorporation in the cortex and hippocampus of rats raised in enriched environments than those kept in impoverished conditions. However, in man, Potter and Heron [9] did not observe a rebound-like phenomenon during PS following 4 or 7 days sensory deprivation. This may be due to the fact that man is able to maintain a sufficiently high level of cortical excitation due to thought processes to prevent rebound-like phenomenon during the recovery period.

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