doubted. One must acknowledge however that the exact nature of this function is still very mysterious. The hypothesis that a process of restoration is necessary after a period of prolonged vigilant activity is still of current interest. But what kind of restoration could it be? That of brain or that of body? The study in man of day-night fluctuations in the secretion of growth hormone, which is known to control the anabolic processes of an organism, has led J.H. Horne (in this survey) to decide on a restoration of the brain. But we still do not know the nature of the alteration of the physiological neuronal processes which require correction by means of sleep. The discovery of this alteration, which may not be far off, would no doubt represent a fundamental progress in the understanding of the higher nervous activities.

2. Electrophysiological semeiology of sleep

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Summary. The main characteristics of electroencephalograms, electro-oculograms and electromyograms in human sleep are described. This electrophysiological semeiology permits the identification of the different stages in normal sleep. In animals, sleep is generally less differentiated; the possibility of recording subcortical structures allows the observation of additional phenomena such as hippocampal theta activity and PGO spikes. Evoked brain electrical activity is less well known than the spontaneous activity in sleep. Recent technological developments offer many interesting possibilities in the processing of the EEG and other physiological signals.

Soon after the development of the electroencephalogram (EEG) by Berger[1] it was recognized that brain electrical activity shows typical patterns depending on the level of alertness. Loomis et al.[2] recorded the brain activity of sleeping subjects and described 5 different stages, from wakefulness to deep sleep, termed stages A to E, respectively. In these early days, the usefulness of recording other physiological parameters together with the EEG was not obvious. It was shown later that during sleep there are periods, reccurring at regular intervals, during which the eyes display rapid movements, whereas they are unactive the rest of the time.[3] This discovery permitted the identification of a stage of sleep previously missed, paradoxical sleep, and clearly indicated the necessity of recording several physiological parameters in order to monitor the changes in alertness.

Based on these techniques a new classification was developed and is still mostly used to-day[4,5]. This classification distinguishes 2 main parts in sleep: NREM sleep also called slow sleep after the French terminology, and REM sleep or paradoxical sleep. REM stands for rapid eye movements, and REM sleep designates the stage during which rapid eye movements occur, whereas NREM sleep represents the remaining stages, normally lacking rapid eye movements. After a slight modification of the classification of Loomis, NREM sleep was subdivided into 4 stages, numbered 1-4, corresponding roughly to stages B-E of Loomis.

A polygraph recording consists of the simultaneous monitoring of several physiological parameters by means of convenient amplifiers and display devices. With the great variety of transducers now available, a large number of organs or physiological modifications in the body can be recorded. Only 3 basic parameters are necessary for defining the stages of sleep: EEG, eye movements or electro-oculogram (EOG), and muscle activity or electromyogram (EMG). Depending on the purpose, many other variables can be taken into consideration; to mention just a few: electrocardiogram, respiration movements, air flow through the nostrils, composition of expired air, and penile tumes-

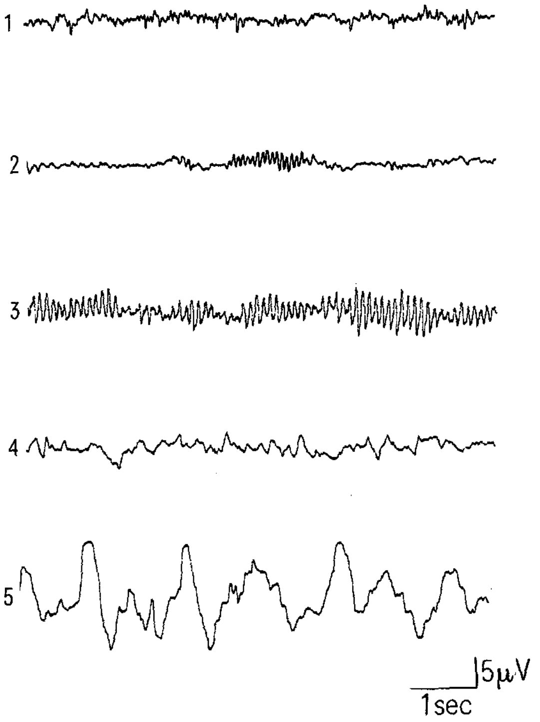

Fig. 1. Samples of the main EEG frequencies of interest in the different states of alertness. *1* beta activity; *2* spindle; *3* alpha rhythm; *4* theta activity; *5* delta activity.

cence. Biochemical measurements can also be made during sleep by withdrawing small blood samples at regular intervals by means of an indwelling catheter.

Two kinds of brain electrical activity can be distinguished: spontaneous activity and evoked activity. On the scalp, spontaneous activity can be recorded at any time in the form of more of less regular waves. Sensory stimulation can induce modifications, known as evoked potentials, of this activity in the few hundreds of milliseconds following the stimulation. Both spontaneous and evoked activities have characteristic variations which are functions of alertness.

The most obvious feature of the spontaneous EEG is its frequency (figure 1). 4 frequency bands are used to classify the different types of activities: delta (1–4 c/sec), theta (4–8 c/sec), alpha (8–12 c/sec) and beta (above 12 c/sec). Partly because the tissues interposed between the surface of the cortex and the electrode on the scalp act as a low-pass filter, the amplitude of these waves is generally greater for slow frequencies than for high frequencies.

The EEG of a subject who is awake with his eyes open and who is involved in some activity is not easy to study because it is mostly obscured by muscle artifacts, eye blinks and rapid eye movements. It is possible to record subjects in this situation with appropriate telemetric transmission systems, and filtering of the signals. When the brain is actively processing information, its electrical activity consists of rapid waves of small amplitude in the beta band (figure 1,1). This type of activity is said to be desynchronized. Some slower waves in the theta band can be observed from the temporal area. If the subject sits or lies down, relaxes and closes his eyes, a very characteristic rhythm, the alpha rhythm, appears from the posterior part of his head (figure 1,3). However closing the eyes is not sufficient in itself for this rhythm to appear, because if the subject is tense or anxious his tracing will continue to show fast beta activity. At the onset of drowsiness, the alpha rhythm tends to increase in amplitude, become more diffuse on the scalp, more abundant and slower in frequency. Later, as sleep proceeds toward stage 1, the alpha rhythm begins to disappear.

During wakefulness, the level of muscle activity is high, with an especially large variability. Some trained subjects lying down but fully awake can relax so completely that their muscular activity falls to very low levels. Eye movements constitute a sensitive indicator of the level of alertness. In active wakefulness, only rapid eye movements can be recorded, without any slow eye movement. A slight decrease of the level of alertness is accompanied by the appearance of slow rolling movements of the eyeballs, mostly in an horizontal plane.

Stage 1 is an intermediate stage between wakefulness and the deeper stages of sleep. It lasts only a few minutes in normal subjects, but can be much longer in insomniac patients. In stage 1, brain electrical activity consists mainly of theta waves of moderate amplitude (figure 1, 4). Some alpha activity can still be present but disappears progressively. Rapid eye movements seen in wakefulness are replaced by slow and mostly horizontal eye movements.

Stage 2 is characterized by 3 different patterns: vertex sharp waves, spindles and K-potentials. Vertex sharp waves (figure 2, 1) appear at the beginning of stage 2 as mono- or biphasic waves whose frequency is in the theta band, focusing around the vertex. Spindles are bursts of activity with a frequency of 14 c/sec (figure 1,2), and a duration of roughly between 0.5 and 1.0 sec. The name 'spindle' was given to this pattern because the waves at the beginning and the end are smaller than the waves in the middle. Spindles can occur isolated on a background of slower activity, but they are also frequently associated with K-complexes (figure 2,2). These complexes are slow waves of large amplitude in the delta band, appearing simultaneously on all areas of the scalp. Most of them are spontaneous, but they can also be elicited by minor sensory stimulation, such as noise. In fact, it is likely that a number of apparently spontaneous K-complexes are induced by nerve impulses of visceral origin.

The number of spindles per min is approximately 5 in normal stage 2, and the number of K-complexes is between 2 and 3, but with a large variability. As stage 2 proceeds, delta waves progressively fill the gap between K-complexes and so there occurs a very progressive transition to stages 3 and 4. In these

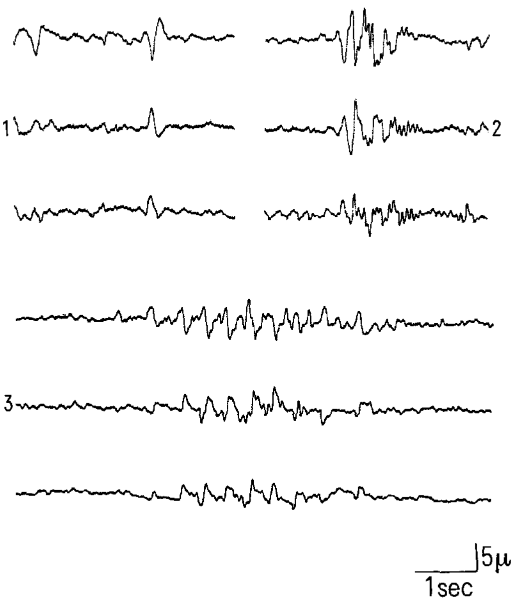

Fig. 2. 3 waveforms characteristic of sleep stages. *1* vertex sharp wave in stage 2; *2* K-potentials immediately followed by a spindle, also in stage 2; *3* saw-tooth waves in paradoxical sleep. Each sample consists of 3 bipolar leads from the anterior (top), middle (middle), and posterior (bottom) part of the scalp.

2 stages, the dominant EEG activity consists of delta waves (figure 1,5), and the distinction between stages 3 and 4 lies only in the abundance of slow waves. However, this distinction is not only academic, but also has physiological implications: stage 4 is very sensitive to age and, between 20 and 40 years, drops to a low level. On the other hand, stage 3 is very stable across different age groups, but is sensitive to pathological conditions. Electronic analysis of sleep EEG has revealed that spindles are also present in stages 3 and 4, with approximately the same abundance as in stage 2. Since they are superimposed on slow waves, they are difficult to detect with the naked eye.

In normal NREM sleep, there are no rapid eye movements, and muscle tone is usually at a low level, but not completely abolished. A reduced muscular activity persists even in the deepest stage 4. This contrasts with paradoxical sleep, when brain electrical activity consists mainly of theta waves similar to the activity of stage 1. In some subjects, the alpha rhythm can also be present in this stage, with the same spatial distribution as in waking. On this background, particular waves named saw-tooth waves can be intermittently observed, more or less clearly associated with bursts of rapid eye movements. They are not observed in everybody; they consist of trains of theta waves with a steep rise and a slower return to the base line. In addition to these EEG features, paradoxical sleep is characterized by a complete abolition of muscle tone and by phasic events such as muscular twitches and rapid eye movements. These movements are grouped in bursts or are isolated; in contrast to wakefulness, they are mixed with slow eye movements, and their speed has a larger variability.

On the whole, the main features we have seen in the electrophysiological semeiology of sleep in man are also present in animals. There are, however, some important differences. The alpha rhythm is less obvious in the cat, so that it is difficult to recognize with the eye alone; in the rat it is absent. The differentiation of NREM sleep into 4 stages is observed in monkeys, but not in lower mammals. In the rat, for instance, it is possible to distinguish a stage consisting of spindles with a few slow waves, and another stage with more abundant slow waves. K-potentials do not exist in this species.

Recording subcortical structures is easy in animals, whereas in man it is performed only for diagnosis purposes, especially in severe epilepsy. 2 remarkable electrical activities detected in animals must be mentioned in this respect. The first one is the hippocampal theta rhythm. During wakefulness and in paradoxical sleep, the electrical activity of the hippocampus consists of highly synchronized theta waves of high amplitude, whereas in NREM sleep this activity is desynchronized, having slow waves intermingled with some sharp waves. The regularity of this rhythm is even greater in paradoxical sleep than in wakefulness. In this state, 2 different levels can be distinguished on the basis of this activity. In active wakefulness, when the animal is exploring its surroundings for instance, the theta rhythm is very regular, but becomes less regular in quiet wakefulness. In the few human subjects who had electrodes implanted in their hippocampus, a similar activity was detected.

Another important phenomenon detected in animals is ponto-geniculo-occipital waves (PGO waves). They are sharp waves recorded in several subcortical structures in some animal species. They have not been observed in the rat, and are mostly studied in the cat or in the monkey. They have not been unambiguously seen in man, but waves resembling those seen in animals have been described[6]. In the cat, PGO waves begin to appear shortly before the onset of paradoxical sleep, and are manifest in the whole paradoxical episode. They are closely associated with rapid eye movements, but this is not the case in every species. In the monkey, for instance, this association is more complex[7].

The study of the evoked brain electric activity in sleep is far less advanced than our knowledge of spontaneous activity. This study requires more sophisticated techniques since the signals of interest are of very small amplitude and are usually indistinguishable from the signals given by the simultaneous spontaneous activity. Averaging of a large number of responses is a procedure most commonly used to overcome this problem. In addition, the measurement of latencies is sensitive to small distortions introduced by the conditions of recording and analysis, especially by the use of filters. This could partly explain some of the differences between the findings of authors.

Few reports have compared evoked potentials to standardized stimuli in the different states of wakefulness and sleep. The early components of the response to auditory stimuli increased as a function of intensity of stimulation in all stages of sleep. For any given intensity, the responses were larger during wakefulness, of smaller and comparable amplitude during all stages of NREM sleep, and smallest during paradoxical sleep[8]. This result, and other ones, show that during sleep there is an overall reduction in the amplitude of electrical responses to sensory stimulation. However, the various components of the responses can be influenced differently. Particularly late responses can be enhanced in sleep under certain conditions. Drowsiness can increase late negative components in the auditory evoked responses[9]. More experiments are necessary in order to throw more light upon the relationships between the state of alertness and the evoked potentials.

Most of these results have still been acquired by the eye-cortex system. Recent technological developments offer many interesting possibilities in the treatment of

EEG and other physiological signals. Electronic measurement devices connected to small laboratory computers have been set into operation for routine sleep scoring[10,11]. These systems are linked to a data base and greatly facilitate the statistical evaluation of a large number of records. In addition, new procedures have been proposed for the calculation of sleep stages as functions of time, in order to describe more accurately their temporal organization[12]. These and other developments allow much more precise measurements to be obtained, particularly of EEG waveforms, including evoked potentials, and open wide the possibility of new observations.

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3. Behavioral phenomenology of sleep (somatic and vegetative)

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The study of behavioral phenomenology represents the most classical approach to the problem of sleep[1,2]. Such an approach has never lost heuristic incisiveness, as behavior is an expressive modality of the organism whose functional significance can often directly be envisaged by the observer. Moreover, the somatic and vegetative (autonomic) events of sleep are still instrumental in the process of decoding into operational propositions the related patterns of electrochemical activity of neural structures.

The phenomenal evolution shows that the onset of sleep (phase I) is followed by 2 contrasting sets of sleep events (phases II and III) occurring in cycles of ultradian rhythmics and characterized by a functional dichotomy in terms of control theory. In fact, phase III is the result of a functional change which has mainly open loop vs closed loop operations. A reversible release of brain stem structures due to the temporary inactivation, during phase III, of hypothalamic homeostatic mechanisms underlies such a dichotomy in the intact organism[3–5]. This inactivation may be considered the result both of the change in hypothalamic integrative activity occurring in late phase II and of ascending influences related to the brain stem activity of phase III. The pacemaker role of the hypothalamus with regard to the phenomenal evolution of sleep is indirectly shown by the modifications of the sleep cycle elicited in homeothermic organisms by deviations in ambient temperature from thermal neutrality[3–5].

The functional condition of phase III of sleep implies not only that the instability of effector functions is the more marked the less they are endowed with autoregulation and/or controlled by reflex mechanisms, but also, which is more remarkable, that homeostatic regulation is temporarily suspended and replaced by a poikilostatic mode of operation. The alternation of such functional conditions can be considered as a homeostatis-poikiostasis ultradian rhythm. On this basis, phenomenal differences of phase III between species are accounted for by inborn patterns of morphofunctional organization of brain stem and spinal operative levels. Moreover, reflex responses during phase III are the more affected the greater their normal subordination to hypothalamic levels of integration. So, the functional condition of phase III reveals phylogenetically determined degrees of autonomy. In conclusion, during this phase of sleep the encephalon is coping only with its own functional needs (consummatory act of sleep[6]) through a neurochemical process which is incompatible with its specific integrative action.

I. Somatic phenomenology

The somatic phenomenology of sleep concerns primarily motor and postural activities. During phase I the behavioral repertory consists of the search for a safe ecological niche and preparing the body for the natural sleep posture. The latter differs between species, but it is nevertheless clearly related to thermoregulatory and/or safety needs. Therefore, specific behavioral and physiological thermoregulatory capabilities, innate and learned[7] motor and postural behavior and predator-prey relationships[8] are all basic factors underlying the shaping of this phase of sleep. The complexity of such performances implies the integrated activity of several encephalic structures[9,10].

Phase II (synchronized sleep) is characterized by a low level of motor and postural activity resulting in the suspension of the active contact of the organism with the environment. The sleep posture is influenced determinantly by thermoregulation[11]. So, the decrease in muscle postural activity is the result of a change in the regulation of muscle innervation rather than the