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# Neuronal Activities Underlying the Electroencephalogram and Evoked Potentials of Sleeping and Waking: Implications for Information Processing

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COENEN, A. M. L. *Neuronal activities underlying the electroencephalogram and evoked potentials of sleeping and waking: Implications for information processing.* NEUROSCI BIOBEHAV REV 19(3) 447-463, 1995. — The low amplitude, high frequency waves of the electroencephalogram (EEG) indicative of wakefulness, are produced by a summation of potentials of thalamocortical neurons, which fire in a “tonic mode” of depolarization. In this mode, the transfer of information from the peripheral sense organs to the sensory cortex is facilitated, due to a tonic lowering of the discharge threshold of thalamocortical neurons. The transfer decreases during drowsiness when thalamocortical units are more hyperpolarized and have higher thresholds. In this state, neurons fire synchronously in a “burst mode,” which is expressed in EEG spindling. During slow wave sleep sensory blocking reaches a maximum, when thalamocortical cells are yet more deeply hyperpolarized, although that what still passes to the cortex allows a shallow, subconscious, evaluation. The collective burst firing is more irregular, which results in large and slow EEG waves. In contrast, during rapid eye movement (REM) sleep the depolarized tonic mode of firing commonly associated with waking, is again reached. Similar to EEG-patterns, the architecture of evoked potentials is dependent on the state of alertness. During waking, components in event related potentials (ERP) are moderate in amplitude, while during slow wave sleep larger waves are visible. This is caused by more synchronized unit responses with sharper phases of excitations and inhibitions, which results from increased hyperpolarizations. In contrast, visual ERPs belonging to REM sleep closely resemble those of wakefulness. In analyzing unit responses of thalamocortical neurons, it appeared that neuronal excitations are expressed in negative components of the ERP, while inhibitory neuronal activities are associated with positivity. Transient phenomena in the EEG, such as ERP waves, spindles and spike-wave discharges, are the expression of synaptic potentials in superficial cortical layers, where numerous synapses of afferent thalamocortical fibers are localized on the apical dendrites of deeper lying pyramidal neurons. It is suggested that the morphology of these EEG components is primarily due to the discharge characteristics of thalamocortical relay cells, whereby excitations underly negative waves and inhibitions positive waves. The notion of a general correspondence between thalamocortical neuronal activities and the polarity of transients in the cortical surface EEG, allows prudent speculations regarding components of ERPs. Two examples are given: the contingent negative variation (CNV) and the P300 of an ERP which can be elicited by an infrequent stimulus. The EEG negativity in the CNV, regarded as a readiness potential, is interpreted as the expression of a general neuronal activation, while the positivity of the second EEG phenomenon may be considered as associated with inhibitory processes related to specific processes of stimulus recognition.

Electroencephalogram  
Information processing

Neuronal activity

Sleeping and waking

Transfer ratio

Event related potentials

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## INTRODUCTION

MORE than 100 years ago, the British physiologist Caton (11) recorded electrical waves from the brains of rabbits and

monkeys. When he discovered that these potentials were vulnerable to such phenomena as anoxia and anesthesia, he realized that the waxing and waning of the waves was related to the activity of the brain. Some years later and unaware of

Caton's work, the Polish physiologist Beck (4) performed research on the electrical currents of the cortex of dogs and he described the blocking of the waves at the presentation of a sensory stimulus. However, the extensive research of Beck which was mainly published in Polish, has received little attention. The German psychiatrist Berger (5) extended the method and is nowadays regarded as the father of electroencephalography. He used both animals and humans as experimental subjects and published the first graphs with alpha-waves. Berger introduced also the name *Elektronekephalogramm* for the registered signal.

Presently, the recording of the electroencephalogram (EEG) is one of the most frequently applied methods in brain research. Ample evidence exists that the EEG is generated by excitatory and inhibitory synaptic potentials of large population of neurons. The summed electrical activity of numerous nerve cells results in a field potential which penetrates the brain surface and can be measured on the scalp. It is assumed that the main contribution to the scalp recorded EEG stems from numerous neurons located in cortical layers and particularly from large pyramidal neurons perpendicularly directed to the cortical surface, with extended dendritic arborizations in superficial layers parallel to the cortical surface (10,55,59). How the EEG characteristics of the various sleep-wake states are composed by the potentials of large numbers of individual neurons is still under study. In this paper, the correlation of patterns between the EEG recorded from the scalp and the underlying neuronal activity, is investigated for the conventionally distinguished sleep-wake states. Implications of changes in neuronal activity for the processing of information during these states are also discussed.

#### NEURONAL ACTIVITIES AND THE ELECTROENCEPHALOGRAM

Most research on the neuronal basis of the EEG is performed in lower mammals such as cats and rats. Basically, these animals show a relationship between EEG and vigilance to that in primates and humans. This means that active wakefulness is accompanied by low amplitude high frequency (beta) waves in the EEG, whereas the EEG of slow wave sleep is composed of high voltage, low frequency (delta) waves. The pattern of alpha waves, in humans characteristic for a relaxed awake state, does not occur in these lower animals. On the

other hand, spindle transients with a frequency of 12 to 14 Hz, in humans associated with the shallow sleep of Stage 2, appear in animals not only during light slow wave sleep, but also during the waking state just before entering sleep (72). Related to spindle activity are aberrant phenomena such as spike-wave discharges; these epileptic paroxysms often occur in both the human and the animal EEG. A prominent pattern in the EEG of cats and rats is theta-rhythm, but this pattern originating in the hippocampus, relates in a different way to behavior than theta EEG waves in humans. In the latter species these waves transiently occur in EEG recordings at the border of sleep, while in cats and rats the main behavioral domains of hippocampal theta-rhythm are active wakefulness and rapid eye movement (REM) sleep (12,69).

Steriade and colleagues (60-65) have performed extensive research on the state of nerve cells during sleeping and waking. During waking, thalamic and cortical cells are in a state of tonic depolarization with relatively stable membrane potentials of around  $-60$  mV. Neurons fire in a tonic or relay mode, implying a sustained and high spontaneous activity (32) (Fig. 1). This variable discharge pattern with a low synchronization between cells, is the reason why EEG electrodes, which summate the electrical activity of numerous cells, only record small, but irregular and heavily fluctuating waves. The tonic mode of firing is the substrate of beta waves. The occurrence of spindles marks the transition from wakefulness to sleep. Spindles become manifest when thalamocortical cells undergo a moderate hyperpolarization with a membrane potential lower than  $-60$  mV (51) (Fig. 2). Longlasting hyperpolarizations are regularly interrupted by rebound bursts of high-frequency spikes; a pattern that is measured as spindling by EEG electrodes. This mode of activation characterized by rhythmical fluctuations of the voltage of cell membranes, resulting in pause-burst discharges of many cells, is called an oscillatory or burst mode. Researchers are convinced that the origin of spindle oscillations is located in the thalamus, but the mechanism of generation is subject of disagreement. Andersen and Andersson (2) postulate that intrinsic properties of a thalamic network can lead to spindling with a main role for inhibitory interneurons, while Steriade and Buzsáki (61) claim that neurons in the thalamic reticular nucleus possess pacemaker properties.

Related to spindles are aberrant phenomena often occur-

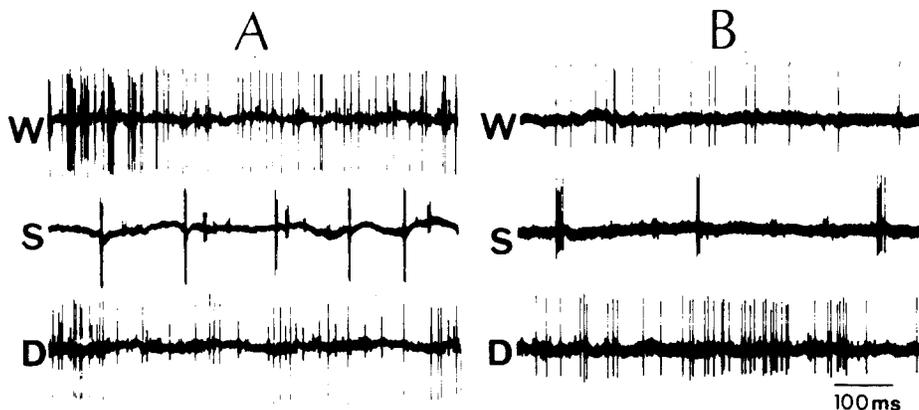


FIG. 1. Extracellular recordings of spontaneous activity of two thalamocortical neurons of the cat (A and B), during waking (W), slow wave sleep (S) and REM sleep (D). Note the high tonic activity during waking, and in particular during REM sleep. Observe also the low burst-like activity during slow wave sleep. [Adapted from Glenn and Steriade (32)].

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