PART I

EEG Rhythms

One of the most basic laws of the universe
is the law of periodicity
György Buzsáki, Rhythms of the brain

I. INTRODUCTION

New insights in the field of electroencephalogram (EEG) discovered during the last few decades dramatically changed classical postulations which psychiatrists and neurologists used to learn in medical schools. These classical postulations presume that information processing in the human brain is carried out by impulse (spike) activity of single neurons. Oscillations of electrical events (such as EEG rhythms) were usually discarded and ignored, in the worst case, or considered as a background activity, in the best case. For example, in the fourth edition of "Principles of Neuroscience" edited by Eric Kandel, James Schwartz, and Thomas Jessel – the book that is considered as the bible for neuroscientists – electrical oscillations in EEG were missing and the chapter "The Collective Electrical Behavior of Neurons: the Electroencephalogram and the mechanisms of Epilepsy" by John Martin present in the third edition was discarded.

During the last few years the situation is slowly changing. Now we are facing the renascence of EEG. This renascence is associated with appearance of new methods in human EEG assessment and new experimental findings in animal research which allowed electrophysiologists to discover that alterations in oscillatory patterns of EEG play a critical role in maintenance of brain functions and consequently may be used as a powerful tool for diagnosis of brain dysfunctions.

From a general point of view, oscillations are present in all physical and biological systems trying to achieve the equilibrium. In almost all cases of oscillations emerge when the system is controlled by two opposite processes: the one that drives the system from the equilibrium and the one that returns it back. In this respect, EEG oscillations do not differ from oscillations in other biological systems. In the case of any observable EEG rhythm (such as alpha, beta, or theta) we always find a force that drives the neuron or the neuronal network from their equilibrium and a force that returns them back.

However, oscillations may be not only the reflection of two opposite forces in the neuronal networks but, hypothetically, can also serve as the source of combining factor in organization of neuronal networks. For example, changes in the overall local field potential created by the neurons – generators of this rhythm may entrain other neurons that do not participate directly in generation of the rhythm. This entraining synchronizes activity of all neurons of the neuronal network with the rhythm generators. In spite of several attempts to prove this suggestion, we still do not know whether it is correct or not.

This part of the book deals with EEG rhythms in frequency range from 0 to 70 Hz. The band covers several categories of electrical phenomena recorded from the scalp. These bio-electrical phenomena are conventionally divided into the following types: direct current (DC) shifts, deco-second oscillations, and slow waves, delta, theta, alpha, and beta EEG rhythms (Fig. PI.1). It should be stressed here that the notion of rhythm presumes that rhythm represents regular changes in electric potential measured by electrodes from the scalp. When Fourier or wavelet transforms are applied to EEG recordings containing rhythms these rhythms appear at the corresponding spectra in a form of peaks.

Recording of deco-second oscillations needs special amplifies. The deco-second oscillations are usually discarded in conventional EEG. Delta

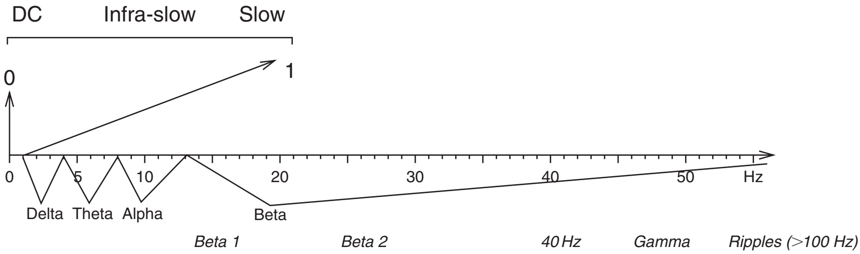

FIGURE PI.1 Frequency bands in EEG spectrum. The frequencies boundaries are not strictly determined. However usefulness of this classification was proved during the whole history of EEG.

rhythms cover the frequency range from 1 to 4 Hz, theta rhythms from 4–8 Hz, alpha rhythms from 8–13 Hz, and beta rhythms – frequency higher than 13 Hz. Theta, alpha, and beta rhythms are present in normal EEG recorded in resting (eyes closed or eyes open) state and in different task conditions. Delta rhythms in the normal brain are expressed on the spectrograms in a form of peaks only during the state of deep sleep. Although basic EEG rhythms are known since Berger's time in late 1920s their neurophysiological basis began to be elucidated only recently starting approximately at 1980s.

It should be stressed that EEG is a sensitive parameter of subject's state and EEG rhythms change dramatically when the subject falls asleep and transfers from one stage of sleep to another. For example, at stage II specific oscillations called sleep spindles emerge. Sleep spindles disappear while theta and delta rhythms develop at further stages of sleep. During wakefulness, rhythms can be a sensitive measure of brain responses to different psychological tasks. For example, occipital alpha rhythms are suppressed (desynchronized) while frontal beta rhythms are enhanced (synchronized) in response to behaviorally meaningful visual stimuli.

In the diseased brain normal mechanisms of EEG rhythms may be impaired and the rhythms may (1) become slower in frequency (so-called EEG slowing), (2) may appear in unusual places (e.g., alpha rhythms at temporal areas), (3) may become higher in amplitude (the phenomenon called hypersynchronization) and in more synchronicity with other areas (the phenomenon called hypercoherence), (4) in some severe cases (characterized e.g., by disconnection of cortical areas from subcortical structures due to stroke, trauma, or tumor) a separate slow rhythm in delta frequency (1–3 Hz) may appear. In some cases normal synchronization mechanisms may be enhanced and spike or spike/slow wave patterns appear indicating a so-called focus in the human brain which in some situations may cause a seizurer. Normative databases help an electroencephalographer to recognize those abnormal patterns and to assess the level of statistical significance of the abnormality. 3D location of generators of EEG rhythms can be assessed by different techniques such as dipole approximation and low resolution electromagnetic tomography (LORETA).

II. GLOSSARY

10–20 International system of electrode placement was accepted internationally in 1959. The name comes from the fact that any electrode is 10 or 20 percent of some distances from another.

Alpha rhythms are rhythmic activities in EEG recorded from the cortex of primary or secondary sensory areas during eyes open or eyes closed rest conditions and suppressed in response to activation of these areas. In EEG of healthy subjects alpha rhythms are found in posterior regions (occipital and parietal areas) and over the sensory motor strip (mu or sensory-motor rhythms) within the frequency range from 8 to 13 Hz. Alpha frequencies change with age: younger and older subjects have lower alpha frequencies.

Amplifier is a basic component of any EEG machine (or electroencephalograph). It amplifies a week (30–100 μV) EEG signal. $1\,\mu V = 0.000001\,V$.

Barbiturates are pharmaceutical substances that bind to so-called "sedative–hypnotic" sites at $GABA_A$ receptors and promote opening of Cl^- ion channels. They belong to a class of GABA agonists. They are used as a sleeping medication, for example, to induce anesthesia before surgery as well as minor tranquilizers or antianxiety medication.

Beta band is a band beyond 13Hz in EEG and MEG recordings. Sometimes, beta band is divided into smaller categories: low beta band (*beta 1*) from 13 to 21 Hz, high beta band (*beta 2*) from 21 to 30 Hz, and *gamma* frequency band for frequencies higher than 30 Hz.

Bispectral index (BIS) of the EEG is an empirical, statistically derived variable that provides information about the interaction of brain cortical and subcortical regions. BIS, which is expressed as a score between 0 and 100, is a consistent and reliable index of state of consciousness in normal subjects, with scores of 95 or greater typically indicating full consciousness.

Brodmann area is a region in the human cortex defined on the basis of its organization observed in microscope when a tissue is stained for nerve cells. Brodmann areas were originally defined in 1909 by a German neurologist Korbinian Brodmann and referred to by numbers from 1 to 52.

Burst of spikes is two or more discharges of a neuron followed by a period of quiescence. The burst mode of thalamic cells is generated in response to long hyperpolarization due to a rebound Ca^{++} spike. The bursts of cortical cells are induced in response to depolarizing injected currents.

Calcium spike is a rebound depolarization of the thalamo-cortical cells following strong hyperpolarization of the neurons. It is generated by a transient low threshold Ca^{++} current (I_t), ion current that is inactivated when the neuron is depolarized and becomes deinactivated during the hyperpolarization state.

Coherence is a measure of synchronization between EEG recorded in different scalp locations. It reflects a correlation between EEG powers computed for these two locations in the same frequency band.

Common average reference montage is a computational montage in which electrodes' potentials are measured in reference to "common average" potential, that is, a potential averaged over all electrodes.

Common Mode Rejection (CMR) defines the ability of a differential amplifier to be as close to the ideal (the output is zero when $V_1 = V_2$) as possible. It is expressed as ratio of the output signal when $V_1 = V_2$ (they are connected to the same source) to the output signal when only one input is non-zero. CMR is measured in dB.

Contingent negative variation (CNV) is a negative slow (with time constant of about seconds) shift in electrode potential associated with preparatory activity of the subject, such as preparation to receive a stimulus or to make a motor response.

DC potentials *are* potentials recorded from the scalp by non-polarizable electrodes (such as silver–silver chloride electrodes) in the frequency range from 0.04 to 0.16 Hz.

Delta rhythm (cortical) is EEG rhythm generated by intracortical thalamic mechanisms. It dominates in the EEG when the cortical area is disconnected from the corresponding thalamic nucleus.

Delta rhythm (thalamic) is EEG rhythm generated in the thalamus and recorded from the scalp by interplay of two ion currents in the thalamo-cortical neurons: a cation current that depolarizes the membrane potential, and a transient low threshold Ca^{++} current responsible for generation of so-called Ca^{++} spikes.

Depolarization is a decrease in neuronal membrane potential usually caused by cation (Na^{+} and Ca^{++}) inward currents associated with opening of the corresponding ion channels in membrane. The potential changes caused by these currents are named excitatory postsynaptic potentials (EPSP).

Differential amplifier amplifies the difference between two input potentials V_1 and V_2.

ERD/ERS stands for event-related desynchronization/synchronization. It is a parameter that measures the percentage of decrease/increase of the EEG power in a given frequency band in a given time interval in response to a given event.

Excitatory neurons are neurons that when spiking generate a so-called excitatory postsynaptic potential which depolarizes (makes it less polarizable) the postsynaptic membrane and consequently, drives the membrane potential toward the threshold of action potential and increases the probability of action potential discharge. Glutamate serves as a fast excitatory mediator in many cortical neurons.

Forward problem is a problem of calculating the scalp potential of a single dipole or a set of dipoles located within the cortex. The forward solution can be expressed in a physical equation and numerically solved by computers.

Hebb's law is the law formulated by Donald Hebb in 1949 to identify a possible way for forming new memories. According to the law, if presynaptic neuron A is active (exhibits neuronal discharges) and a postsynaptic neuron B is active, then the synapse AB will be strengthen.

High frequency filter is analog or digital filter that suppresses lower frequencies in EEG signal and leave the higher frequencies intact. The filter is characterized by low cut in seconds.

Hippocampal theta rhythm is rhythmic activity from 3 to 10 Hz found in mammalian hippocampus and interconnected anatomical structures.

Human frontal midline theta rhythm is spontaneous or task related short bursts of rhythmic (from 5.5 to 8.5 Hz) activity over the frontal leads with maximum at Fz. This is the only normal theta rhythm in the human adult brain. This rhythm is synchronized in response to behaviorally important events and is associated with operations such as recalling from memory or encoding memory traces.

Hyperpolarization is an increase in neuronal membrane potential. The increase is usually caused by anion (such as Cl^-) inward currents associated with opening of the corresponding ion channels in membrane. The potential changes caused by this current are named inhibitory postsynaptic potentials (IPSP).

Independent Component Analysis (ICA) is a method of solving the blind source separation problem. In EEG the problem can be formulated as finding independent cortical generators of potentials recorded at the scalp.

Infra-slow activity is a type of EEG activity which can be recorded only by special (so-called DC) amplifiers and includes oscillations with periods from few seconds to few tens of seconds. The mechanism of their generation is unknown but the association with slow metabolic processes of the brain is hypothesized.

Inhibitory neurons are neurons that when spiking generate a so-called inhibitory postsynaptic potential which hyperpolarizes (makes it more polarizable) the postsynaptic membrane and consequently, drives the membrane potential away from the threshold of action potential and decreases the probability of action potential discharge. Gamma-aminobutyric acid (GABA) serves as a fast inhibitory mediator in many cortical neurons.

Inverse problem is a problem of finding multiple elemental dipoles in the cortex (sometimes named density of neuronal generators) that approximate potentials recorded by multiple scalp electrodes. Theoretically this problem does not have a unique solution, that is, a certain scalp distribution can be achieved by infinite number of cortical distributions.

Local average reference montage is a computational montage in *which a* local average potential is averaged over a small number of electrodes in the vicinity of a target electrode and is subtracted from the potential of the target electrode. There are several types of local average montages (Laplacian, Lemos, Hjorth).

Long-term potentiation (LTP) is the increase of synaptic strength between two neurons induced by high frequency stimulation of presynaptic terminals.

Low frequency filter is analog or digital filter that suppresses higher frequencies in EEG signal and leave the lower frequencies intact. The filter is characterized by high cut in Hz.

Montage is a rule according to which EEG potentials are computed. The simplest rule (linked ears montage) is measuring electrodes' potentials in reference to two linked electrodes located at left and right earlobes.

Non-polarizable electrode is an electrode that is not easily polarizable. It means that if you apply a current through an electrode, the potential of the electrode will not change significantly from its equilibrium potential. Silver–silver chloride electrode is an example of non-polarizable electrode.

Notch filter is a very sharp filter that attenuates a certain frequency in the signal. In EEG a notch filter at 50 (60) Hz is used to filter out the noise from the electrical system in the room.

Polarizable electrode is an electrode that is easily polarizable. It means that if you apply a current through an electrode, the potential of the electrode will change significantly from its equilibrium potential. Gold electrode is an example of polarizable electrode.

Polarographic method of measuring extracellular oxygen is a method of measuring oxygen in living tissues, in which an electric current induced by application of −0.63 V is proportional to the concentration of extracellular oxygen.

Reaction of desynchronization corresponds to suppression of the corresponding rhythm.

Referential recording is a recording of EEG signal when the second (reference) electrode is usually located on the earlobes, mastoids, or the tip of the nose, that is, far away from the neuronal source. This is in contrast to sequential recording when two electrodes are located on the scalp near EEG generators in the cortex.

Sampling rate is the rate at which raw EEG signal is sampled (quantified). According to Naiquist theorem the sampling rate must be twice as much as the highest possible frequency of recorded EEG signal.

Slow waves of sleep is an EEG activity in a frequency range less than 1 Hz but higher than 0.3 Hz which dominates in EEG during deep sleep. This type of activity is generated by cooperative mechanisms in the recurrent cortical circuits and includes periodic fluctuations between UP and DOWN states.

Spectra are computed by means of fast Fourier transformation that decomposes EEG signals into series of sinusoidal functions with different frequencies, amplitudes, and phases. Spectra show how amplitude, power or phase of the sinusoidal harmonic depends on the sinusoid's frequency in the EEG signal.

Thalamus is a subcortical brain structure that controls the flow of sensory information to the posterior parts of the cortex through sensory-related nuclei and regulates activity in the prefrontal areas though a distinct set of nuclei.

Thalamo-cortical neurons are neurons of the thalamus that project to the corresponding cortical area and receive back the excitatory connections from this area.

Theta band in EEG is a band from 4 to 8 Hz.

Vertical organization of the cortex reflects the fact that pyramidal cells of the cortex with their long apical dendrites are oriented perpendicular to the cortical surface with distinct layers playing different roles in receiving inputs and sending outputs.