

Low frequency oscillations are responsible for changes in EEG complexity during wakefulness and sleep

Melissa Ve

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ABSTRACT

Electroencephalography (EEG) is a technique for recording an electrogram of electrical activity on the scalp, which has been shown to represent the macroscopic activity of the brain's surface layer beneath.

The electrodes are typically placed along the scalp, making it non-invasive. Electrooculography, which uses invasive electrodes, is also known as "intracranial EEG."

Key Words: *Anaesthesia; Coma; Encephalopathies; Brain death*

INTRODUCTION

EEG measures voltage fluctuations caused by ionic current in the brain's neurons. EEG is a clinical term that refers to the recording of the brain's spontaneous electrical activity over time using multiple electrodes placed on the scalp [1]. Diagnostic applications typically focus on either event-related potentials or EEG spectral content. EEG is most commonly used to diagnose epilepsy, which results in abnormal EEG readings. It can also be used to detect sleep disorders, anaesthesia depth, coma, encephalopathies, and brain death. EEG was once used as a first-line method of diagnosis for tumours, stroke, and other focal brain disorders, but its use has declined since the advent of high-resolution anatomical imaging techniques such as Magnetic Resonance Imaging (MRI) and Computed Tomography (CT). Despite its limited spatial resolution, EEG remains an important tool for research and diagnosis [2]. It is one of the few mobile techniques available and provides millisecond-range temporal resolution, which CT, PET, and MRI do not. Recently, novel complexity measures have been used to analyze sleep-wake states, supplementing the traditional analysis of EEGs by frequency bands. This new method consistently demonstrates a reduction in EEG complexity during slow-wave sleep, but it is unclear how cortical oscillations shape these complexity variations. We investigate how the frequency content of brain signals affects complexity estimates in freely moving rats in this paper. We discovered that the low-frequency spectrum, which includes the Delta, Theta, and Sigma frequency bands, drives the changes in complexity during the sleep-wake cycle. Low-frequency oscillations emerge from neuronal population patterns, as demonstrated by recovering the complexity variations during the sleep-wake cycle from micro, meso, and macroscopic recordings.

Furthermore, we discover that lower frequencies reveal synchronization patterns across the neocortex, such as sensory-motor decoupling during REM sleep. Overall, our findings show that low-frequency EEG is critical in shaping the complexity of sleep-wake states across cortical scales. The sleep-wake cycle is one of the most common biological rhythms in the animal kingdom, and it is essential for the regulation of physiological functions [3]. The cycle is divided into three major states: wakefulness, Rapid-Eye Movement (REM), and Non-REM sleep (NREM). Wake is distinguished by asynchronous and irregular neuronal activity at the neocortical level. REM sleep is strikingly similar to Wake activity, with the exception that there is no muscular activity. NREM, on the other hand, has neuronal synchronous silences that match the nominative slow waves recorded in Electroencephalograms (EEG). Classical analysis divides EEG oscillations into specific frequency bands in order to understand cortical function during the sleep-wake cycle. These divisions result from oscillations being: 1) state-dependent, i.e. occurring in relation to specific sleep-wake states, 2) associated with different physiological functions, and 3) produced by distinct neuronal circuits. Frequencies up to, for example, contain the Delta, Theta, and Sigma bands, which have been linked to state-dependent oscillations [4]. Higher frequencies, such as Beta or Gamma, on the other hand, have been linked to cognitive functions even during sleep. The classical analysis of EEG per frequency band has recently been supplemented by the study of EEG complexity, which provides an up-to-date literature review. Typically, complexity analyses focus on the EEG signal as a whole rather than its frequency components (or bands). Under this framework, it has been demonstrated that the complexity of EEG varies with behavioural state, but not with animal species (including mice, rats, cats, monkeys, and humans).

Editorial Office, Journal of Clinical Psychiatry and Neuroscience, United Kingdom

Correspondence: Melissa Ve, Editorial Office, Journal of Clinical Psychiatry and Neuroscience, United Kingdom; E-mail: clinicalpsychiatry@neurologyjournals.org
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Wake, in particular, has been consistently reported to be a highly complex state, with complexity decreasing during NREM when consciousness is lost and increasing during REM sleep when a state of altered consciousness, i.e., dreams, emerges [5]. We investigated intracranial EEG complexity during the states of wakefulness, NREM, and REM sleep by dividing the ECoG recordings into low and high frequency bands. We discover that the low frequency band contains the majority of the information that determines the state's complexity, including the classic Delta, Theta, and Sigma bands. We show that this low frequency band preserves information across neuronal scales, from neuronal ensemble activity to local field potentials and ECoGs. This means that our division effectively denoises ECoG signals, allowing the underlying neural oscillations to be revealed. Furthermore, we discover novel synchronization patterns throughout the cortex. We discovered that, despite having similar complexity values at the local level, cortical sensory-motor integration is severely compromised during REM sleep. Overall, our findings support traditional EEG analyses that concentrate on low-frequency oscillations to study the sleep-wake cycle, as these frequency bands contain highly relevant information. The complexity of a signal can be quantified using its information content, such as by calculating the Shannon Entropy. Estimating the Shannon Entropy for finite and real-valued signals, such as an Electro-Corticogram (ECoG), is more difficult. Instead, we use Ordinal Patterns (OPs) to encode the ECoG signal into a finite alphabet and then calculate the entropy - known as Permutation Entropy. This quantification is affected by the OP dimension, the number of data points, and the embedding delay (resampling). We use the Permutation Minimum-Entropy (PME) instead of its classical value to increase differences between close OP distributions.

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