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Background and evoked activity and their interaction in the human brain

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Abstract

Most functional neuroimaging studies have investigated brain activity evoked by certain types of stimulation or tasks. In recent years, resting brain activity and its influence on evoked activity has become accessible for investigation. However, despite numerous studies on background and evoked activities, either observed with vascular (functional magnetic resonance imaging, positron emission tomography, optical) or electrophysiological (electroencephalography, magnetoencephalography) or a combination of both methods, so far, there is no generally accepted view concerning both the precise meaning of background activity and its relationship to evoked activity. In this article, we give an overview of the current knowledge on this issue and we review recent studies examining the influence of ongoing activity on behavioral responses and the relationship between ongoing and evoked activity.

Keywords: Background; Baseline; Ongoing oscillations; Evoked activity; Resting state; Human brain

1. Introduction

Functional brain imaging techniques enable non invasive investigations of the human brain during "mental work." Typically, a task or a stimulus is administered to a subject in a block or event-related experimental design, and the resulting changes in neuronal activity are detected by contrasting a "task-state" and a "control-or baseline-state." While the term "baseline-state" comes with the connotation of no associated brain activity, it has, however, become clear that in wakeful human subjects the brain is not "silent" implying "zero brain activity." Rather, there is always some neuronal activity (spikes, synaptic activity) associated with a relatively high level of (baseline) cerebral blood flow and cerebral metabolic rate of oxygen ($CMRO_2$) even during so called "rest conditions" [1–3].

Given that baseline activity is not zero, the question arises whether spontaneous fluctuations of resting brain activity are stochastic ("noise") and, thus, can be attenuated by averaging procedures or whether there are non stochastic components. Furthermore, it is of relevance whether fluctuations of the baseline influence the shape and amplitude of evoked activity during the stimulation period. These distinctions are of great importance for many approaches of data analysis for which the presence of only "stochastic" fluctuations and the independence of evoked activity from the baseline state are implicit assumptions as in most functional magnetic resonance imaging (fMRI) analyses.

In recent years, the issue of "physiological noise" and brain activity during resting states has become accessible for investigation, and a plenitude of studies has been published. Evidence has been accumulated that (i) background activity fluctuates spontaneously, i.e., unrelated to any obvious task, and that (ii) these fluctuations are not random, rather, they seem to contain important function-related information, e.g., it has been shown that "resting states" are characterized by several distinct patterns of correlated brain activity, so called "resting state networks" [4], and that fluctuations of these over time (particularly in the low-frequency range <0.1 Hz) are influenced by (patho)-physiological conditions and by drugs [5–10]. Resting state activity has been identified by

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different methods, such as fMRI, positron emission tomography (PET), optical imaging, electroencephalography (EEG) and magnetoencephalography (MEG), and in several instances, simultaneous combinations of methods such as EEG/fMRI have been particularly useful. In addition, numerous studies have addressed the influence of ongoing activity on behavioral responses and the relationship between ongoing activity and evoked activity.

In this article, we give an overview of the current knowledge on background activity and its relation to evoked activity. We start by providing a description of different methodological approaches for studying (i) resting/ongoing activity, followed by a brief account of ways to assess (ii) evoked activity, and finally, we discuss our knowledge on (iii) interactions between background and evoked activity.

2. Measures of ongoing brain activity

2.1. Electrophysiological methods

Electrophysiological methods such as EEG and MEG measure electrical/magnetic correlates of neuronal activity. “Electrical activity” reflects ionic currents and changes in membrane potentials, producing a current dipole moment in each tissue volume that can be measured with extracranially located electrodes [11]. Due to the large number of cells contributing to dipole generation, extracranially recorded potentials presuppose synchronized electrical activities because non-phase locked sources cancel out. The time course in each sensor is a mixture of the activity of all potential sources depending on strength and orientation of the different dipole moments, as well as head geometry and conductivity parameters. Frequency analysis, such as Fourier transform or wavelet analysis, allows for a discrete spectral examination of EEG/MEG data, and there are ways to estimate source locations of signals. Mathematical decomposition methods can be used to separate multi-channel data into a set of components (sources), each given by a time course of its activity and a weighting-vector (scalp map), describing its contribution to the signal recorded at each sensor. Although unique mathematical solution for source recovery from extracranial recordings is missing, these methods provide further insight into the origin of electrical scalp potentials.

Even in the absence of stimulation, ongoing activity can be measured with EEG and MEG. EEG background rhythms have been identified already in the late 20s of last century [12]. These resting rhythms, mainly evolving from synchronous postsynaptic oscillations of cortical pyramidal cells [13,14], have been demonstrated in a large range of different frequency bands and show pronounced fluctuations over time.

2.1.1. Occipital alpha rhythm

Most prominent is the alpha rhythm which is located predominantly in occipital areas. Its frequency varies across subjects between 8 and 13 Hz. Since occipital alpha is strongest in the absence of any visual stimulation (i.e., eyes closed) and is attenuated during tasks requiring visual attention [15], it is referred to as an “idle rhythm” of the visual system [16]. Despite numerous studies, the actual role of occipital alpha rhythms in cognitive processing still remains unclear. A lower and upper alpha band can be distinguished and several studies indicate an association of the alpha activity in the upper frequency range with different types of cognitive processes, perceptual performance and intelligence [17–20]. Despite its original description as a “background” rhythm, alpha activity has also been proposed to be related to working memory by showing that alpha activity increased systematically with memory load [21–24]. The primary sources of working memory-dependent alpha activity were located in parieto-occipital areas [22,24]. Also, attentional shifts have been demonstrated to modulate oscillatory activity in the human visual cortex [25–27], and attentional mechanisms operating within the frontoparietal network have been suggested to exert a topdown control on early visual areas [27,28].

2.1.2. Rolandic background rhythms

An inverse relationship of rhythm strength and sensory input is also found for pericentral (Rolandic) EEG rhythms. With a peak frequency around 10 Hz, one of them has been termed *mu-rhythm* or *Rolandic alpha rhythm*. The other is termed *Rolandic beta rhythm* referring to its peak frequency around 20 Hz. These rhythms are located at the pre- and postcentral gyrus [29] and are known to desynchronize following hand movement or somatosensory stimulation [30–32], thus indicating a functional relationship to the sensorimotor system. The pericentral alpha rhythm seems to be mainly associated with the primary somatosensory hand area, whereas “Rolandic beta rhythm” is located slightly more anterior and, thus, seems to be more closely related to the motor system [29]. During movements, primary motor cortices exhibit a pronounced decrease of beta amplitudes followed by a strong beta power rebound when movements are stopped [33].

2.1.3. Other background rhythms

Sources of rhythmic activity with a frequency around 10 Hz can also be found in the supratemporal auditory cortex, referred to as the temporal “tau-rhythm.” This rhythm is not affected by visual input (i.e., opening of the eyes) but is transiently suppressed by auditory stimulation [34,35]. These results support the existence of distinct “idle rhythms” of the respective sensory systems.

Oscillatory activity with a frequency of roughly 3–8 Hz is termed *theta activity*. Spontaneous theta oscillations in the EEG at rest are reported to be most prominent over midline frontocentral electrodes [36]. During transition from wake to sleep onset, high-amplitude theta waves can be observed, mostly bilaterally frontal. Furthermore, this frequency range is clinically important for the analysis of background EEG