Unifying evoked responses and oscillatory neuronal dynamics

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Introduction

EEG and MEG recordings provide two general types of macroscopic data: oscillations and evoked responses (ERs), which, for the most part, are considered to be separate phenomena. However, if neuronal oscillations have a non-zero mean, any modulation of oscillations amplitude results in a deflection (i.e., baseline shift) in the frequency range of modulation. We refer to this phenomenon as a baseline-shift mechanism [1-3].

Here, using a computational modeling and empirical EEG data, we show that neuronal oscillations indeed have a non-zero mean and then we show that baseline-shift mechanism provides a link between the two most frequently studied EEG/MEG phenomena, i.e., between alpha oscillations and P300.

Methods

The baseline-shift mechanism can be summarized with a formula

$$y(t) = A(t) * (\sin(2\pi f t + \varphi) + r) = A(t) * \sin(2\pi f t + \varphi) + A(t) * r$$

where $A(t)$ – amplitude modulation, r - non-zero mean, $A(t) * r$ - baseline shift.

HNN – a computational biophysical model of a cortical patch [4]

LEMON – EEG, 60 channels [5]
50 young, 16 ♀
40 elderly, 17 ♀

LIFE – EEG, 30 channels [6]
2230 elderly participants
1152 ♀

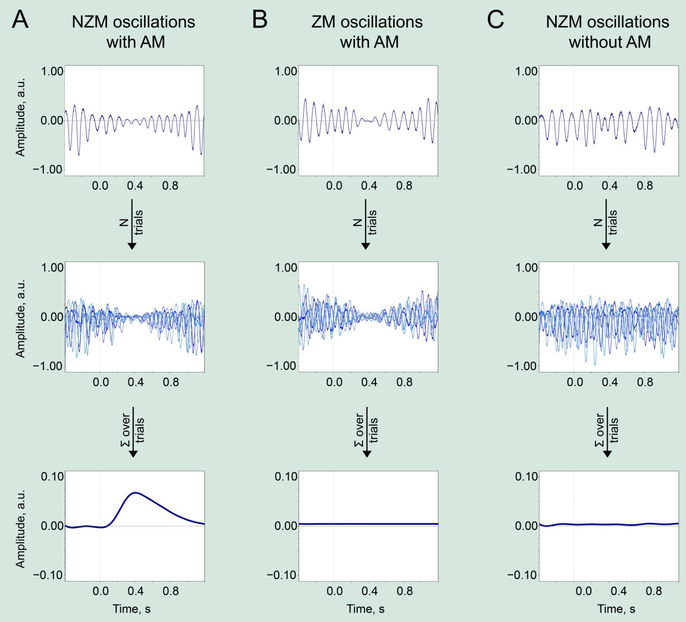

Figure 1. Two prerequisites of the baseline-shift mechanism—(1) non-zero mean (NZM) and (2) amplitude modulation (AM)—should occur together so ER would be generated. **A**. Non-zero mean oscillations when modulated in amplitude generate ER. **B**. If oscillations have a zero mean, then no ER is generated. **C**. If oscillations have a non-zero mean but do not systematically (trial-by-trial) experience modulation, then no ER is generated.

Results

1 HNN

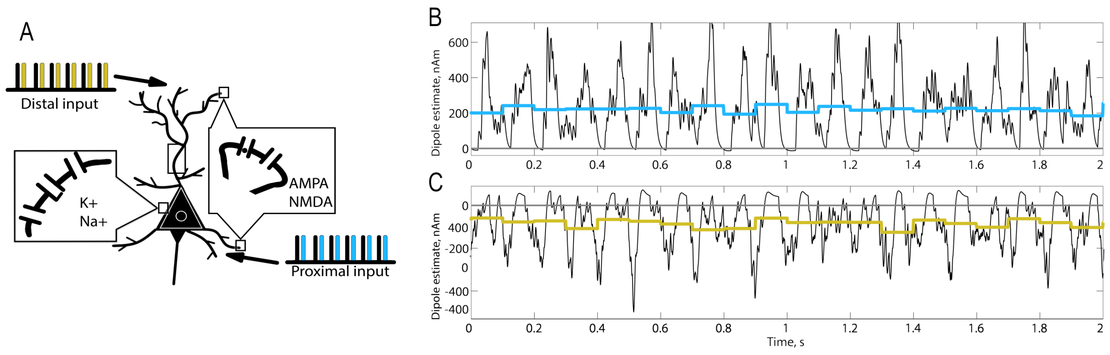

Figure 2. Various properties of neurons inevitably led to non-zero mean alpha oscillations. Oscillations were non-zero for a wide range of parameters. Parameters of the biophysical model that were manipulated: synaptic weights on AMPA and NMDA receptors, density of voltage-gated Na+ and K+ channels, length of apical dendrites (**A**). Changes in currents inside the neuron drive changes in the mean of oscillations – more input to basal dendrites pulls mean to more positive values (**B**), conversely, more input to apical dendrites causes mean to become negative (**C**).

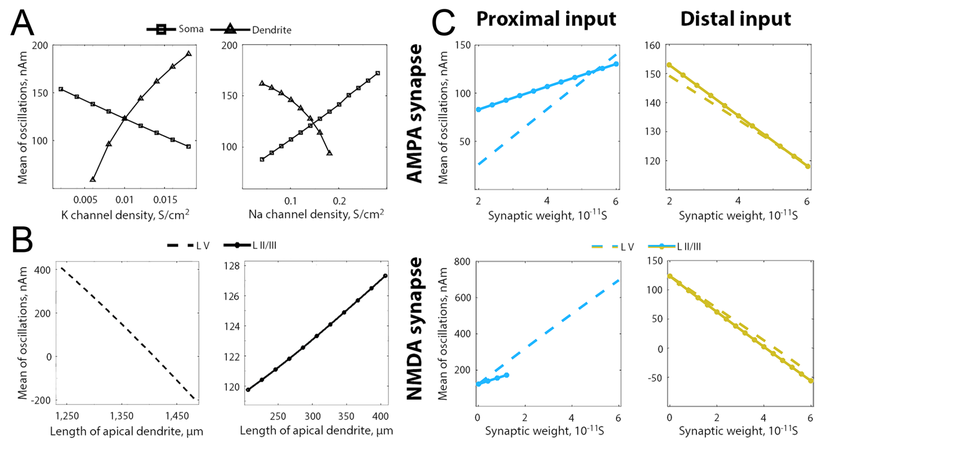

Figure 3. Relation between biophysics and morphology of a pyramidal neuron and oscillatory mean. Change in oscillatory mean of the alpha rhythm with (**A**) a change in sodium and potassium channel density on soma and dendrites on pyramidal neurons in layer V; (**B**) a change of the length of apical dendrite in pyramidal neurons in layer II/III and layer V; (**C**) depending on the strength of incoming inputs realised through excitatory AMPA and NMDA synapses. Only one parameter at a time was changing, all other parameters were kept constant and set by default. Oscillatory mean is computed from 1-second of a simulated signal. L V—layer V, L II/III—layer II/III.

2 LEMON

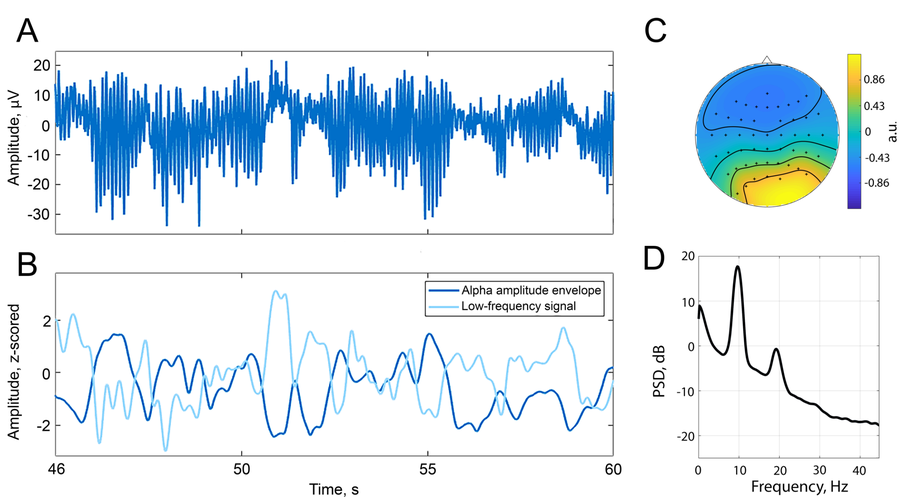

Figure 4. Baseline-shifts in EEG data. The majority of participants had at least one source of alpha rhythm with a non-zero mean (quantified with the baseline-shift index, BSI [7]). Examples of alpha-source time course (**A**), its topography (**C**) and spectra (**D**). **B**. The association between alpha amplitude envelope and low-frequency amplitude (that contains baseline shifts). Here, the non-zero mean is negative, thus, an increase in the alpha amplitude produces a baseline shift downward.

3 LIFE

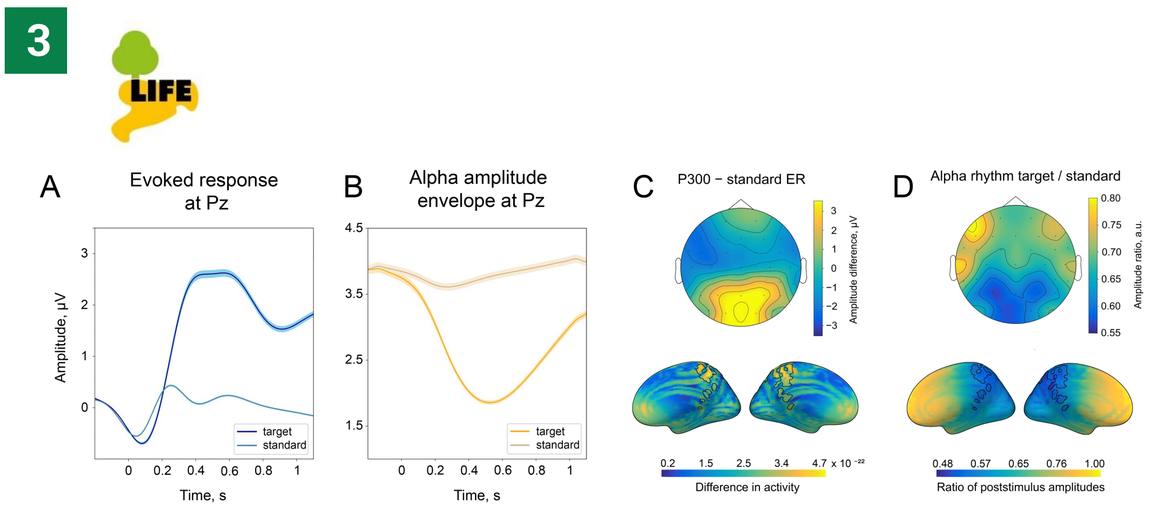

Figure 5. Temporal and spatial correlation between P300 and the alpha amplitude envelope. **A**. Time courses of P300 elicited by the target stimulus and ER after a standard stimulus at the Pz electrode, both averaged across the participants. **B**. Alpha amplitude envelope at the Pz electrode averaged across participants for the target and standard stimuli. The spatial topographies and source-reconstructed activation of P300 (**C**) and alpha rhythm amplitude (**D**) significantly overlap.

Discussion

We provided computational and empirical evidence for the existence of non-zero mean alpha oscillations in the human brain. Therefore, alpha oscillations that have a non-zero mean, if modulated by the stimulus, may give rise to many cognitive ERs [8]. In particular, our findings show that the modulation of alpha oscillations is at least partially responsible for the generation of P300 [9].

The baseline-shift mechanism is generic and applicable to all sensory modalities; thus, our results concern all sensory and motor ERs that coincide with the modulation of oscillations, such as CNV, N400, readiness potential, etc. We suggest that inferences about changes in ER amplitude or latency should be derived in conjunction with changes in oscillatory dynamics.

References

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