Traveling Waves in the Resting State Are Initiated by the Connectome

Elizaveta Panfilova, Evgenii Burlakov and Vitaly Verkhlyutov

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Panfilova, E.A.[1,3], Burlakov E.O.[2], Verkhlyutov, V.M.[3]

[1]Pirogov Russian National Research Medical University, Moscow, Russia
[2]University of Tyumen, Tyumen, Russia
[3]Institute of Higher Nervous Activity and Neurophysiology of RAS, Moscow, Russia

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Introduction

There are two points of view on the large-scale spatial dynamics of spontaneous and evoked EEG and MEG activity. The intra-cortical hypothesis assumes the propagation of traveling waves [1] in the cortex on a meso-scale due to intra-cortical axons (velocity < 1.0 m/s, 0.2 m/s characteristic speed). This propagation results in rotating electric dipoles that are projected onto the scalp, giving rise to the large-scale wave dynamics. The other point of view (namely, cortico-cortical hypothesis) assumes the propagation of large-scale waves due to cortico-cortical axons (velocity > 1.0 m/s, 6 m/s characteristic speed) [2]. The latter wave speed is observed in EEG, MEG and ECoG, but is not confirmed by direct recording (using intracortical microelectrodes or Utah arrays). Previously, we tested the validity of the above two approaches and showed a significantly higher-level correlation of the MEG experimental data by the results obtained using the meso-scale model [3]. However, a close look at the meso-scale model showed that the initiation of traveling waves could be related to the structure of the connectome.

Methods

For the MEG analysis, we used one healthy right-handed subject. The registration was carried out with a 306-channel MEG. The MEG recording had been carrying out for 9 minutes in the state of quiet wakefulness with closed eyes. A high-resolution structural MRI of the head was obtained using 3T tomograph. Based on the MRI data, a model of individual surfaces of the head and brain with the resolution of about 300 000 vertices was built. Each vertex was assigned to be an epicenter, for which the distributions of the current density in the form of radial traveling waves with propagation velocities of 0.2 m/s (distances of 2 cm) and an average frequency of 11 Hz were calculated. We used radial traveling waves for simulation, since they are typically observed in recordings by microelectrodes and by optical methods in animals [1], and also by the Utah multielectrode arrays in humans [5]. The forward MEG problem was solved using the BEM separately for each hemisphere in the Brainstorm software environment. The model MEGs were compared with the experimental data by calculating two-dimensional correlation each time shifting the analysis window by 2 ms. The technique is described in detail in our previous works [4].

Results

As an example, we demonstrate a reconstructed traveling wave of the alpha rhythm with an epicenter located in the central part of the retinotopic projection at $r>0.7$, $p<0.001$ the border of fields V1 and V2 (highlighted in purple and green, respectively) at rest with the eyes closed (Fig. 1A, B). Analysis of the 9-minute of MEG segment made it possible to identify a multitude of epicenters of such waves in the calcarine and parieto-occipital sulci (in the primary and secondary fields of the visual cortex). The epicenters were located chaotically, but strictly in the fields V1 and V2 of the cortex at *r*> 0.8, *p* <0.005 (Fig. 1C).

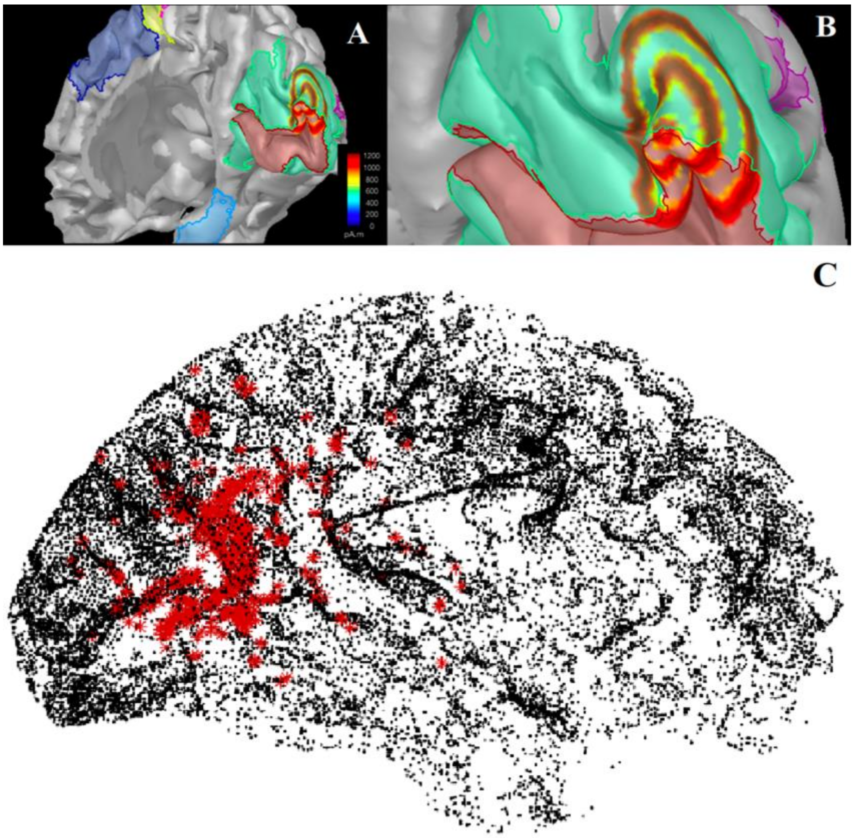

Fig. 1. Single traveling wave of alpha rhythm in the right hemisphere. The red color codes the local field potentials-LFP (A). An enlarged view of the occipital lobe, the radial wave is distorted by the complex surface of the hemisphere (B). Spatial distribution of the epicenters of traveling waves (red stars) prevailing in the left hemisphere during 9 min of the MEG recording (C).

Conclusion

Our previous study comparing two traveling wave models showed an unexpected effect of jumps in the epicenters of the traveling wave [3]. These results are in good agreement with the data on the dynamics of traveling waves in the human brain [5]. Alpha waves are specific to the visual cortex, and we previously considered their epicenters to be relatively stable [6]. The new result shows that, like saccades, when viewing images, there are changes in the position of the traveling waves epicenters in the visual cortex. The scale of traveling waves propagation we confirmed is comparable to the spatial dimension of the resting state networks, and we can assume the role of traveling waves in the local synchronization of such networks. Macroscale traveling waves are explained by the spatial dynamics of mesoscale cortical waves due to intracortical interactions. In turn, the role of connections between the visual cortex and the thalamus, which are part of the connectome, in the emergence of the alpha rhythm is well known [7]. In addition, these waves can be originated by cortico-cortical connections that are elements of the connectome. Thus, we assume that cortical traveling waves of the alpha rhythm are initiated by the connectome [8] and, of course, should be considered as one of the important elements of large-scale brain models (Fig. 2).

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