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Abstract. We simulated radial traveling waves of local currents on the folded surface of the human cerebral cortex. The magnetic fields on the surface of the head were calculated by individual MRI. Model MEGs were compared with experimental data using two-dimensional correlation. The maximum values of correlation coefficients were determined for traveling wave velocities of 0.2 m/s with epicenters in the occipital lobes of the brain, including in regions V1, V2. In these cases, a jump in the levels of maximum correlations in time and space was noted. At a speed of 6 m/s, the maximum values were smallest, and the change in the level of correlations was smoothed out. The results of the study show the advantage of the intra-cortical hypothesis of the brain traveling waves.

Keywords: cortical traveling waves, intra-cortical hypothesis, MEG

1 Introduction

Traveling waves of local brain potentials have been experimentally found in animals from snails [1] to the higher apes [2] and man [3]. These waves can be recorded only when using intracortical electrodes [4] or voltage-dependent dyes [5].

Macroscopic traveling waves observed in recording of EEG, MEG, and ECoG are visualized using interpolation and most likely reflect the effects caused by

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extracellular currents in the conductive volumetric environment of the brain, its shells, skull and head integuments. The visibility of macroscopic traveling waves is conditioned by the equivalent rotating dipoles formed due to the movement of cortical traveling waves along the complex folded surface of the brain [6, 7]. The validity of this approach based on experimental data was shown by us in a number of works [8, 9].

On the other hand, the hypothesis of macroscopic traveling waves, which has no direct experimental support, is used to interpret the results [10]. If the propagation of excitation, creating mesoscopic traveling waves of local brain potentials, is due to the transverse processes of unmyelinated axonal fibers (the propagation speed of action potentials < 1 m/s), then macroscopic traveling waves explain the transmission of signals through the white matter of the brain to the propagation velocity of action potentials > 1 m/s). In this work, we evaluated hypotheses about macro- and mesoscopic cortical traveling waves by simulating such waves on a three-dimensional model of the cortical surface of the human brain and reconstructing the MEG to compare model data with experimental data.

2 Materials and Methods

We used one healthy, right-handed subject for the MEG analysis. Registration was done on a 306-channel MEG using an Elekta Neuromag Vector View setup (Elekta Oy, Finland), which was located in a magnetically shielded room. MEG recording was carried out for 9 minutes in a state of quiet wakefulness with closed eyes. High-resolution structural MRI of the head was obtained on a Magnetom Verio 3 (Siemens) tomograph based on a T1-weighted sequence (R = 1900 ms, E = 2.21 ms, voxel size 1x1x1 mm). According to MRI data, a model of individual surfaces of the head and brain was built with a resolution of about 300 thousand vertices. In turn, each vertex was an epicenter, for which the distributions of the current density in the form of radial traveling waves with propagation velocities of 0.2 or 6 m/s and an average frequency of 11 Hz were calculated. The model waves propagated over a distance of 2 cm for a lower speed and 20 cm for a higher one. We conditionally called the first model "mesoscopic", because for it, a limited wave propagation of no more than 20 mm was assumed. In the second case, the model wave covered almost the entire surface, and in numerous works such traveling waves are called "macroscopic" [11].

The direct MEG problem was solved using the boundary element model separately for each hemisphere [12] in the Brainstorm software environment [13]. The technique is described in detail in our works [8,9,14].

As a result, we obtained 306 values of the magnetic field per 100 ms at the locations of the sensors, that were used to register the MEG in the experiment. Model MEGs were compared with experimental data, by calculating two-dimensional correlation (`corr2` function in MatLAB) each time shifting the analysis window by 2 ms. We found the maximum correlation value for each moment of time and the corresponding vertex on the simulating surface of the subject's cerebral cortex. Thus, the MEG recording was analyzed for 5 min. The obtained data of a set of correlation coefficients were analyzed in order to reveal the advantage of one of the models.

We compared the growth of the maximum values of the correlation coefficients for each of the models separately for each hemisphere. We assessed the normality of the distribution of the correlation coefficients for each of the models and the differences in their mean values using the ANOVA method. The difference between the maximum values of the correlations and their probability for each model were analyzed. We obtained the spatial distribution and dynamics of changes in the positions of the traveling waves epicenters for two types of simulations with the maximum similarities between the model and experimental MEG signals.

3 Results

In our analysis, we used model waves from 145885 epicenters for the left hemisphere and 154674 epicenters for the right hemisphere for two velocities and two propagation distances. Two-dimensional correlations were calculated for 15 segments of 20 s between experimental and model signals. For each segment, 9950 correlation values were obtained per epicenter. Thus, 21 773 336 250 coefficients were obtained for the left and 23 085 094 500 values for the right hemispheres for one propagation velocity and the same number of solutions for the second model. For each time interval of 2 ms, the epicenter with the maximum value of the correlation was found separately for each hemisphere of the brain.

The increase in the levels of correlations was significantly different for the compared models (Fig. 1). The level of maximum correlations at a certain moment of time for the simulations of traveling waves with the speed of 0.2 m/s was, on average, significantly higher ($p < 0.0001$) than for the simulations with the speed of 6.0 m/s for the both hemispheres (Fig. 2).

In the mesoscopic model, the mean correlations were 0.6079 for the left hemisphere and 0.5931 for the right. For the model of macroscopic waves in the right and left hemispheres, the average correlations were at the level of 0.3502 and 0.3635, respectively.

Epicenters for traveling wave velocities of 0.2 m/s were determined in the occipital and parietal lobes of the brain with levels $r > 0.7$. For a given velocity, 516 such waves were found in the left hemisphere. Most of these epicenters were located in the calcarine fissure and parieto-occipital fissure, which correspond to the areas of the visual cortex V1, V2 (Fig. 3). Epicenters arose in different places of these areas, mainly shifting by a distance of no more than 20 mm and a maximum distance of 70 mm (see "VideoJ02" in Supplementary Materials). At a speed of 6 m/s, the maximum values were lower, and for the level $r > 0.7$, only 84 epicenters were identified in the left hemisphere, which were evenly distributed between the frontal and occipital poles (Fig. 4). Position changes in most cases were either local, up to 5 cm, or remote, up to 15 cm, i.e. "jumped" between

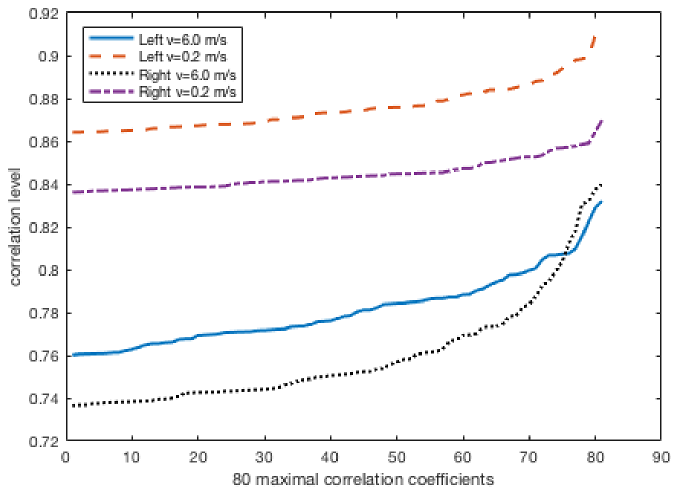

Fig. 1. Comparative increase in correlations for traveling wave models with velocities of 0.2 and 6.0 m/s in the left and right hemispheres.

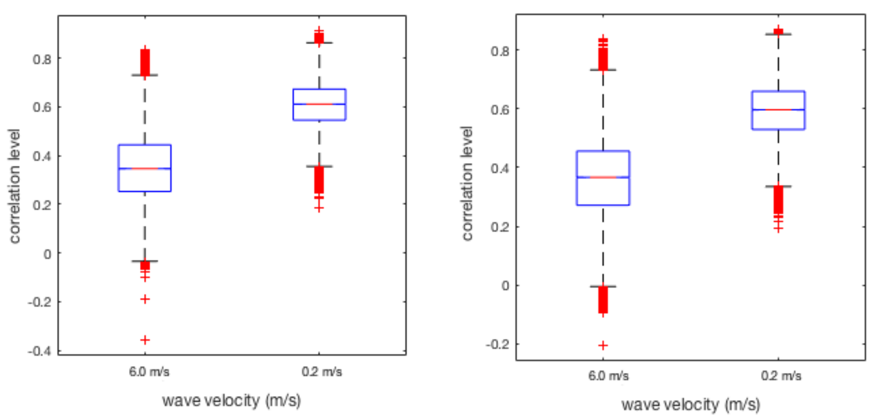

Fig. 2. Comparison of mean correlation values using ANOVA for traveling wave models with wave velocities of 6.0 m/s (1) and 0.2 m/s (2) in the left hemisphere (left) and the right hemisphere (right).

the frontal region and the occipital region (see "VideoJ60" in Supplementary Materials).

The dependence between the numbers of the traveling waves epicenters in the left hemisphere having the correlations with the MEG data, which is greater

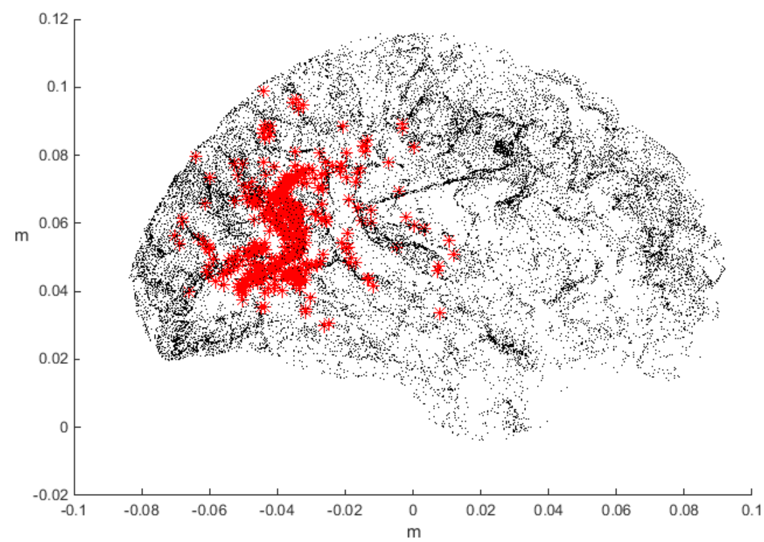

Fig. 3. The epicenters of mesoscopic traveling waves in the left hemisphere and its space dynamic for $r > 0.7$, $v = 0.2$ m/s.

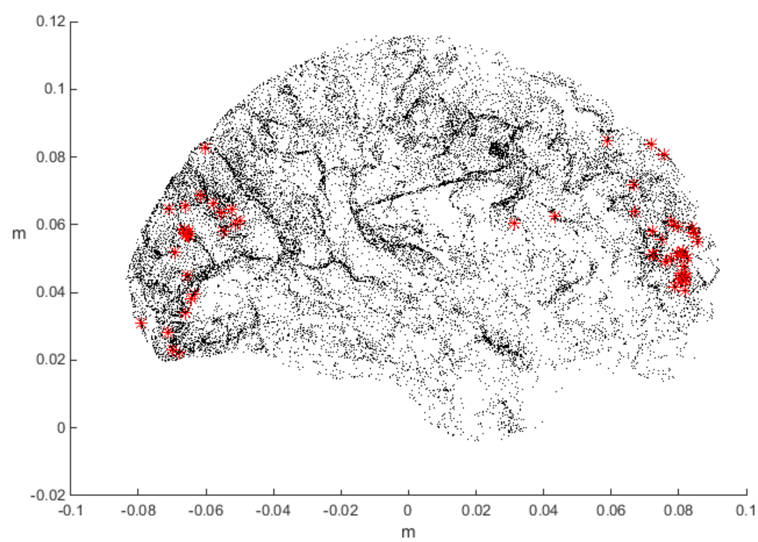

Fig. 4. The epicenters of macroscopic traveling waves in the left hemisphere and its space dynamic for $r > 0.7$, $v = 6.0$ m/s.

than a given threshold and the value of the threshold for the wave velocities $v = 6.0$ m/s and $v = 0.2$ m/s is presented in Fig. 5. The relation between these numbers of the epicenters as a function of the threshold correlation is displayed in Fig. 6.

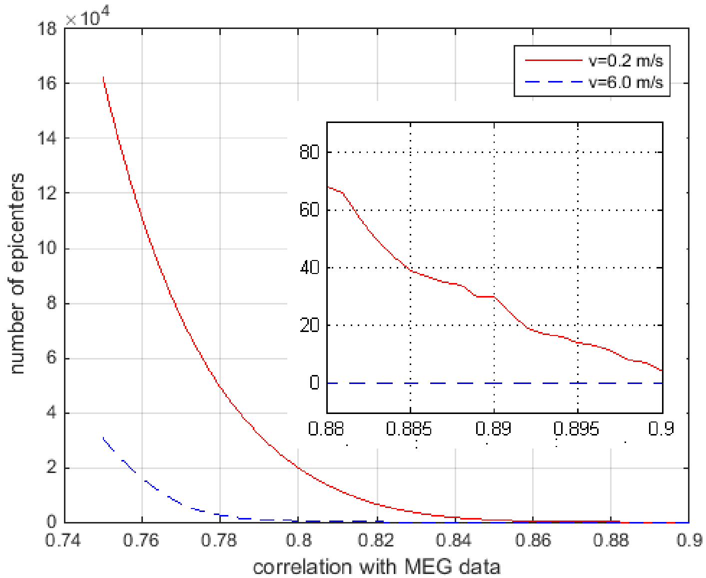

Fig. 5. The numbers of the epicenters of mesoscopic (solid line) and macroscopic (dashed line) traveling waves in the left hemisphere having the correlations greater than a given threshold as functions of the threshold.

Thus, in the left hemisphere, the number of epicenters of the traveling wave with the velocity of 0.2 m/s having a high correlation with the MEG data (i.e. $r > 0.75$) is at least 5 times higher than the corresponding number for the traveling wave velocity of 6.0 m/s. Moreover, by the correlation of 0.8, the number of mesoscopic waves becomes almost 40 times higher than the number of macroscopic traveling waves.

For the right hemisphere, we obtained the results qualitatively similar to the ones demonstrated in Fig. 3 – 6 for the left hemisphere.

4 Discussion

Although we have not received absolute evidence in favor of the mesoscopic wave model, the superiority of this model is supported by the data given in Section 3.

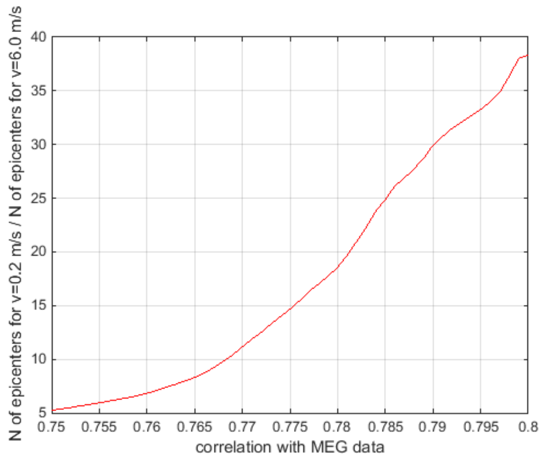

Fig. 6. The relation between the number of mesoscopic waves epicenters and the number of macroscopic waves epicenters in the left hemisphere having the correlations greater than a given threshold as functions of the threshold.

It must be admitted that both models give very similar magnetic field distributions on the head surface and the crucial experiment that will deny the existence of macroscopic cortical waves will be a joint analysis of ECoG records and microelectrode arrays [3] using our calculation methodology.

The analysis using the mesoscopic paradigm, unfortunately, is still limited to one hemisphere, although it is known that the majority of waves arise in symmetrical regions of both hemispheres [6, 15]. Such an analysis is possible, but it requires much more computational resources.

The localisation of the traveling waves epicentres in the occipital cortex is clear, because we analyse the alpha rhythm that is associated with the visual cortex and has the largest amplitude in normal humans in comparison with other similar rhythms. The localisation of the epicentres of the model macroscopic waves reflects the distribution of the magnetic field of the alpha rhythm observed in the occipital and posterior frontal regions. This distribution can also be explained by the presence of powerful current sources in the occipital cortex, which imitates macroscopic waves.

Traveling waves are associated with the mechanism of attention on a mental image. In addition, the brain compares the sensory and mental images [16]. Earlier, we showed a special role of the visual cortical projection periphery in this process [17].

In our work, we observed chaotic jumps in the epicentres of traveling waves in the visual cortex when the subject is at rest with his eyes closed. It is known from the literature that both evoked visual responses and saccadic eye movements are accompanied by traveling waves [18]. In this case, the amplitude of the EEG (EP) and MEG (EMF) is much less than that of the alpha rhythm.

Typically, the perceived sensory image is projected onto the central cortical field of the retinotopic projection. Only in cases of lateral vision, the epicentre of the traveling wave appears at the periphery of the cortical projection of the visual field, which causes a noticeable effect of increasing the EEG amplitude [16].

5 Ethical approval

Human studies were reviewed and approved by the Ethics Committee of the Institute of Higher Nervous Activity and Neurophysiology, Russian Academy of Sciences. The participant provided written informed consent to participate in this study.

6 Supplementary Materials

The "jumps" of the mesoscopic and the macroscopic traveling wave epicenters corresponding to Fig. 3 and Fig. 4 in the time interval of 5 minutes are presented in the time-scale 1:100 in the supplementary video files "VideoJ02" and "VideoJ60", respectively.

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