

Wavenumber power spectrum of the EEG, ECoG, and ERP.

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Abstract

We use a physiologically based model of corticothalamic dynamics to explore the wavenumber content of EEG signals. The predicted wavenumber spectrum has three plateaus separated by regions of monotonic power decrease, which we explain by filtering of the signal through neurons of different type and characteristic range. The predicted spectrum agrees well with EEG, ECoG, and ERP data. We investigate the effect of imposing cortical boundary conditions, by examining the resulting modal structure of the spectrum. We deduce that boundary conditions do not affect the main spectral features of our model under most circumstances, and can thus be ignored.

Keywords: Wavenumber Spectrum; Spatial eigenmodes; EEG; Continuum Model.

I. INTRODUCTION

The wavelike nature of electrical activity in the brain has long been documented [2], and its temporal dependence has been extensively investigated via the frequency power spectrum; however, its spatial dependence has been relatively little studied. We investigate it here via the wavenumber power spectrum, the spatial analog of the frequency spectrum. We use a physiological continuum model of corticothalamic dynamics [3–5]. When considering cortical activity, one must appreciate that the cortex is bounded inside the skull; boundary conditions

may affect cortical dynamics considerably, especially at global scales. To determine the validity or otherwise of modeling the cortex as being infinite in extent, we investigate the effect of boundary conditions on the wavenumber spectrum by examining its modal structure.

II. INFINITE CORTEX

The model assumes randomly interconnected excitatory and inhibitory neurons. Scales below a few tenths of a millimeter are averaged over to yield a continuum treatment that extends from this scale to that of the whole cortex, as in previous models [2]. Thus, the firing rate of signals emitted by single long-range excitatory e neurons (or mid-range excitatory m neurons, or short-range excitatory and inhibitory i neurons), which depends on their individual cell body potentials, is averaged to give local mean values of the outgoing pulse field ϕ_a , with $a = e, m, i$. The propagating pulse density field ϕ_a is then assumed to be proportional to measured large-scale potentials, such as the ECoG.

We include loops between the cortex and the thalamus, as shown in Fig. 1. A key result of the model is the following transfer equation [4] which describes how a cortical signal ϕ_e , which depends on wavenumber \mathbf{k} and frequency ω , responds to subthalamic input ϕ_n :

$$\frac{\phi_e(\mathbf{k}, \omega)}{\phi_n(\mathbf{k}, \omega)} = \frac{L_e G_{es} P}{1 - L_m G_{mm} - L_i G_{ii}} \frac{1}{k^2 r_e^2 + q^2 r_e^2}, \quad (1)$$

where G_{ab} is the differential response in neurons a due to a unit input from neurons b ; L_a describes the low-pass frequency filtering of dendrites a ; the mean axon length of long-range excitatory neurons is written r_e (≈ 8 cm), with similar expressions for the mid-range ($r_m \approx 2$ mm) and short-range ($r_i \lesssim 0.5$ mm) populations; P describes feedback from the thalamus; and q describes wave propagation and delay through the corticothalamic loops. Explicit expressions for these quantities and derivations of the wavenumber equations are given elsewhere [3,4], and their details are not essential here.

The wavenumber spectrum for comparison with ECoG data was derived according to

$$P(\mathbf{k}) = \int \left| \sum_a W_a \phi_a(\mathbf{k}, \omega) \right|^2 d\omega, \quad (2)$$

where the W_a weight the signals generated from each neural population to account for their differing prevalence, structure, and orientation [4]. For comparison with EEG and ERP data, a spatial filter was included to model volume conduction through the skull [3]:

$$F(\mathbf{k}) = \frac{k_0^2}{k^2 + k_0^2}. \quad (3)$$

Comparisons of the predicted spectra with experimental data are shown in Fig. 2. The solid bold line represents the average of EEG data [8] recorded from four awake subjects, and the dashed bold line represents the average of ECoG data [1] recorded from four anesthetized subjects and one awake subject; the two curves are normalized here to have equal power at 100 m^{-1} . The thin solid line represents the spectrum predicted by the model: the portion $k < 100 \text{ m}^{-1}$ has been filtered for volume conduction since it is being compared with EEG data, whereas the portion above this has not, since it is being compared with ECoG data. This was done to enable the EEG and ECoG spectra to be easily compared with one another, and to illustrate that the shape of the model spectrum agrees well with data over nearly three decades of k . The predicted spectrum has three knees, each of which corresponds to the onset of filtering through the axons of the three neural populations [3,4]. The wavenumber spectrum has also been shown to agree well with measured spectra across different states of arousal, as well as with data from the N170 peak of a visual evoked response potential [5].

III. BOUNDARY CONDITIONS

We now investigate the effect of imposing boundary conditions on the cortex; i.e., we relax the assumption that the cortex is infinite in extent. Initially, we assume periodic boundary conditions on a rectangular cortex of size $l_x \times l_y$, and expand the dynamic equations of the model in a series of spatial eigenmodes with time varying coefficients, similarly to previous work in the frequency domain [6]. This yields discrete wavenumbers over the range $\mathbf{k}_{mj} = (2\pi m/l_x, 2\pi j/l_y)$, where m and j are integers. A one-dimensional spectral projection is thus unevenly distributed over wavenumber magnitude $k = |\mathbf{k}|$. Other boundary conditions could be investigated using appropriate coefficients.

Figure 3 shows the theoretical cortical spectrum from the infinite model (solid line). The modal spectrum is in fact a set of delta functions at each k_{mj} ; we show their coefficients in Fig. 3 (filled circles), for $l_x = l_y = 0.8$ m. We show the large-scale, low- k portion of the spectrum, which is the part most affected by the boundary conditions. The discrete structure of the modal spectrum is immediately apparent at low k , as is the uneven distribution over wavenumber of the 1D projection, though at $k \gtrsim 40$ m⁻¹ the discrete points merge and become nearly indistinguishable from the infinite spectrum. The qualitative features of the spectrum are all preserved; it retains the typical plateau-knee-power-law shape, which repeats for each of the three contributing neural populations (e , m , and i). Significantly, the main features of the spectrum are robust under variation of the cortical size, even for $l_x, l_y < 0.2$ m where boundary effects have been observed in the frequency spectrum [6]. Quantitatively, the position of the knee is invariant under boundary size change, and the slope of the power-law decrease regions is likewise.

The curve shown in Fig. 3 is for parameters corresponding to anesthesia. Varying the parameters around their nominal anesthesia values also produces near-coincident spectra. Similarly, varying the parameters around the nominal parameters for other states of arousal produces robustly near-coincident spectra for most parameter variations; notable exceptions occur when the brain is very close to an instability boundary. In such cases, the mode at $k = 0$ m⁻¹ lies below that of the unbounded spectrum; however, all higher modes ($k \gtrsim 8$ m⁻¹) lie on the continuous spectrum. The discrepancy between the spectra at $k = 0$ m⁻¹ is therefore only apparent for marginally stable states, such as waking eyes-closed, and not for states which lie further from the instability boundaries [7], such as eyes-open and anesthesia. In any case, the minimum wavenumber the cortex can support is $k \approx 7$ m⁻¹, since the 60 cm head circumference is approximately 90 cm on the cortex due to cortical folding, and thus the discrepancy between the discrete and continuous spectra at $k = 0$ m⁻¹ is immaterial.

Higher modes can be affected by boundary conditions when the cortical damping rate γ_e is reduced to $\lesssim 50$ % of its nominal value, and even then only for marginally stable states such as waking eyes-closed. For an eyes-open state, γ_e must be $\lesssim 30$ % of its nominal value to

see an effect at the scale of the first mode. Such reductions in γ_e can sharpen the excitatory knee in the bounded spectrum relative to the infinite one, with a correspondingly flatter plateau region at $k \lesssim 10 \text{ m}^{-1}$. This agrees with results from the frequency domain, where boundary conditions have been shown to contribute to slight substructure in the alpha peak when damping is low [6]. The other parameters do not affect the spectrum.

IV. DISCUSSION

We have used a continuum model of corticothalamic dynamics with three distinct neural populations to investigate wavenumber power spectra. The three plateau-power-law regions in the spectrum are due to filtering through axons at the characteristic scales of each of these populations.

The model can faithfully reproduce wavenumber spectra observed in a variety of experiments, including EEG, ECoG, and ERP. Significantly, the parameters used are not changed to match the data from each experiment; they vary only between states of arousal to reflect corresponding physiological changes, and are very similar to those used in previous modeling studies of the frequency domain. Thus, the model unifies wavenumber and frequency analyses from very different scales, recording arrays, and experimental protocols.

As a further study, boundary conditions were imposed on the cortex to determine their effect on the spectrum. The expected discrete structure was observed at low k . All the spectral features were robust under imposition and variation of boundary conditions, both qualitatively and quantitatively, under most circumstances. A similar investigation in the frequency domain [6] yielded the same conclusion, which lends confidence that we can approximate the cortex as infinite without a significant loss of information.

ACKNOWLEDGMENTS

The authors thank M. Breakspear, C. J. Rennie, and D. L. Rowe. This work was supported by a University of Sydney Sesqui Grant and an Australian Postgraduate Award.

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FIGURES

FIG. 1. Diagram of corticothalamic connections showing the cortex, reticular nucleus, and relay nuclei. There are two corticothalamic loops, and an intrathalamic loop. Gains are shown on the diagram.

FIG. 2. Predicted and experimental wavenumber spectra. The solid bold line is average EEG data (Shaw, 1991); the dashed bold line is average ECoG data (Freeman et al., 2000). The thin line is the predicted spectrum. Power is normalized for both experimental and theoretical spectra.

FIG. 3. Investigation into the effects of boundary conditions. The solid line is the spectrum for an infinite cortex, and the filled circles are the discrete points representing the coefficients of the delta functions in the modal spectrum for the bounded cortex.





