The temporal attributes of the power spectrum of human EEG signals, such as the alpha frequency, are well established and widely studied. The spatial attributes, however, remain little investigated. We use a recent physiologically based model of corticothalamic dynamics to explore the wavenumber content of brain signals, the spatial analog of the well-known frequency power spectrum. Wavenumbers are a measure of spatial scale, so the distribution of power across wavenumbers is related to the distribution of power at different physical scales in the brain. Wavenumber is inversely related to wavelength, thus small wavenumbers correspond to global scales in the brain, and large wavenumbers correspond to microscopic ones.

The model which underlies this work in the wavenumber domain incorporates distinct neural populations, nonlinearities, dendritic and axonal delays, and feedback to the cortex through the thalamus. It has previously produced excellent results in the frequency domain, including reproduction of the spectral peaks, alpha splitting, trends seen in various states of arousal, spatial coherence and correlations, and certain generalized seizure onsets and dynamics. The present study in the wavenumber domain consists of three parts: predicting the shape and behavior of the wavenumber spectrum for a range of states of arousal and for both one-dimensional and two-dimensional recording arrays; comparing our predictions with experimental data in order to infer physiology and anatomy; exploring the link between the frequency and wavenumber spectra and examining their mutual importance.

In the first part of the study we generalize the model to enable calculation of wavenumber spectra: we allow the equations defining the cortical signal to retain an explicit dependence on wavenumber, rather than integrating over wavenumber to produce the frequency spectrum. We use the generalized model to explore both electrocorticographic (ECoG) and electroencephalographic (EEG) signals, and illustrate that the two are related to one another through filtering of the signal through the head. We also explore the predicted evoked response potential (ERP) wavenumber spectrum, by applying an impulse-like stimulus to the model, then performing an inverse Fourier transform to determine the evolution of the spectrum after stimulation. We find that the predicted wavenumber power spectrum has three plateau regions separated by regions of monotonic power decrease, which we are able to explain by filtering of the signal through structures of different length scales in the brain, namely neurons of different type and characteristic range. The model indicates that each region of power decrease is due to a different neural population, hence we deduce that there are three such populations which significantly contribute to macroscopic electrical signals in the brain. Furthermore, we are able to deduce the mean range of each population, and conclude that the three populations correspond to long-range excitatory (pyramidal) neurons, mid-range excitatory neurons (probably the recurrent collateral system of pyramidal neurons), and a short-range population which contains both inhibitory (spiny stellate) neurons and those excitatory neurons with axons which extend a few tenths of a millimeter.

Secondly, we find that the model yields results with excellent agreement with ECoG, EEG, and ERP data obtained from both linear and square electrode arrays. The comparisons span several different states of arousal, all of which agree well with the model's predictions. Such comparisons enable us to probe the brain's anatomy and physiology, similarly to recent work fitting this model to data in the frequency domain. The spatial spectrum, however, is sensitive to quite different physiological factors than its temporal counterpart, and thus provides complementary anatomical and physiological information. For example, the frequency spectrum is most sensitive to time-dependent factors such as propagation intervals between various regions of the brain, and dendritic delays, whereas the wavenumber spectrum is most sensitive to spatial factors such as the mean range of influence of each of the contributing neural populations, cortical damping, and blurring due to signal propagation through the head. Consequently, both domains should be explored to gain maximum insight into brain behavior, and we encourage further wavenumber experimentation.

Thirdly, we examine how the wave dispersion relation links the frequency power spectrum and the wavenumber power spectrum. Experimental data suggest that the shape of the wavenumber spectrum can vary with frequency. The model predicts that the power should generally decrease with increasing frequency to reflect the same trend in the frequency spectrum: this is related to the action of dendrites as low-pass frequency filters. Secondly, the model predicts that maximums in the slope magnitude at low wavenumbers should occur at the same frequencies as peaks in the frequency spectrum: this prediction agrees with experiment. For typical experimental frequencies of $f < 100$ Hz, we expect wavenumber spectra to exhibit this frequency dependence only at low wavenumbers (large scales). Thus, for example, the relatively coarsely resolved scalp (EEG) spectra should be more affected than the typically more finely resolved cortical (ECoG) spectra. In order to explicitly examine the relationship between wavenumber and frequency spectra, we investigate the cortical wave dispersion relation for a number of brain states. This provide a means of easily visualizing the way in which power varies simultaneously with both frequency and wavenumber.

Thus, the model provides a framework for linking the underlying physiology with the large scale spatial behavior of the brain, and for understanding the wavenumber power spectrum. Spectral features such as plateaus arise naturally in our model, in agreement with experiment, whereas previously such features have typically been viewed as aberrant. Comparisons with experiment enable probing of the underlying physiology, and the parameters inferred are complementary to those arising from studies in the frequency domain. We therefore hope to encourage further experimentation in the wavenumber domain. We have also used the model to investigate the cortical dispersion relation, thereby unifying not only different aspects of spatial activity, but the spatial and temporal domains themselves. The wavenumber analysis presented represents one facet of a model which is able to reproduce many apparently disparate aspects of brain behavior in a unified way.