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SIMULATING RESTING CORTICAL BACKGROUND ACTIVITY WITH FILTERED NOISE

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Phase slip and beat phenomena are ubiquitous in many forms of wave superposition. Likewise, it is trivially true that cumulative summation of white noise gives rise to “brown noise” ($1/f^2$ power spectrum). We assume that the background electrocorticogram (ECoG) to a first approximation results from integration of innumerable action potentials by dendrites. This paper presents a simulation that relates these phenomena with cortical function. We report that cumulative summation of random numbers simulates resting ECoG, and that phase interference in the distributed frequencies of oscillation in bandpass-filtered brown noise gives null power spikes like those in the ECoG from test subjects. The null spikes coincide with the onsets of frames in which the spatial amplitude patterns are classifiable with respect to conditioned stimuli. We report similarity in the waveforms and amplitude distributions of null spikes upon filtering brown noise in bands corresponding to the theta, alpha, beta and gamma ranges in experimental and simulated ECoG. We estimate a threshold in null spike minimal amplitudes below which perceptual frames having gamma oscillations may recur at theta rates..

Keywords: brown noise; electrocorticogram (ECoG); null spikes; power spectral density (PSD); Rayleigh noise

1. Introduction

A prominent feature of brains at rest or prior to engaging in overt or covert behaviors is their background activity. The remarkably high consumption of metabolic energy that is required to sustain the background activity has been referred to as “dark energy” in analogy to use of the term in astronomy (Raichle, 2006). The objective in the present study is to compare simulated ECoG with “spontaneous” background rabbit ECoG recorded in control states preceding task performance (Freeman, 2005) and human

ECoG in a subject at rest (Freeman et al, 2006). The project is an extension of prior simulation (Freeman, 2006) of the rates of correct classification with respect to conditioned stimuli of spatial patterns of amplitude modulation (AM) in rabbits.

Here our simulated data consisted of the cumulative sum of random numbers (zero mean, unit SD) processed by filters with pass bands in various ratios of the Nyquist frequency (half the digitizing frequency). We were particularly interested in replicating the “ $1/f$ ” power-law distributions of the power spectral densities (PSD) of rabbit and human ECoG and the predicted self-similarity of wave forms resulting from filtering the ECoG in different frequency bands in the brain state of awake rest and slow wave sleep.

We assumed that microscopic neuronal action potentials of a large population in the resting brain could be approximated by white noise, and that the associated synaptic potentials could be approximated by the cumulative sum giving brown noise (Schroeder, 1991). The sampling interval for the ECoG was 2 ms in rabbits and 5 ms in the human subject. These intervals were consistent with the average duration of the action potential plus its absolute and relative refractory periods and gave a Nyquist frequency of 250 Hz or 100 Hz. The resulting random variable had a PSD with a slope of -2 in log-log coordinates ($1/f^2$, “brown noise”), indicating self-similarity across spectral bands. We inferred that pass bands were formed in the beta and gamma ranges by inhibitory feedback from cortical inhibitory neurons to pyramidal cells, forming multiple negative feedback loops with distributed delays (Freeman, 1975).

The effect of band pass filtering was to create “Rayleigh noise”, in which beats occurred when amplitudes approached zero. Beats were most clearly observed in the analytic amplitudes given by the Hilbert transform of the experimental and simulated ECoG. The sum of outputs of two periodic oscillators would give a null value recurring at the difference frequency. The band pass filtered signal was equivalent to the sum of a distribution of independent oscillators, for which the output aperiodically approached zero in a “null spike” (Freeman, 2006).

These null spikes and associated indeterminacy in coordinated analytic phase differences (CAPD) have been related to the onsets of the formation by phase transitions of behaviorally related AM patterns of ECoG (Freeman, 2007). In this study we tested for self-similarity across the four frequency bands of clinical interest (theta, alpha, beta and gamma) and sought for a method to estimate a threshold in the minimal amplitudes of null spikes in the gamma pass band, if indeed the null spike is a trigger for phase transition (Freeman and Vitiello, 2008)

2. Methods

Brown noise simulated by summing pseudo-white noise was filtered with a finite-impulse-response band pass filter (MATLAB `fir1`). Spectra were calculated with the multitaper window (Percival and Walden, 1993) (MATLAB `pmtm`) and displayed in log-log coordinates. The choice of the order of the filter depended on the digitizing step of 2 ms or 5 ms and the pass band. Empirically we found that order 500 gave invariance of the distribution of minimal amplitudes in null spikes over all four pass bands, which

we calculated in multiples of the Nyquist frequency (100 Hz and 250 Hz) approximating the clinical pass bands (Table 1).

Table 1. Filter settings based on Nyquist frequency (Nf)

Band	Band pass	2 ms step	5 ms step	display, s
low gamma	25-50 Hz	1/10-1/5 Nf	1/4-1/2 Nf	2
beta	12.5-25 Hz	1/20-1/10 Nf	1/8-1/4 Nf	4
alpha	6.25-12.5 Hz	1/40-1/20Nf	1/16-1/8 Nf	8
theta	3.125-6.25 Hz	1/80-1/40Nf	1/32-1/16 Nf	16

These ratios gave the advantage of easy comparison of waveforms across pass bands by shortening the length of the segment displayed inversely in proportion to the center frequency of each pass band. After filtering, the Hilbert transform was applied to calculate the analytic signal for each pass band at each time step (MATLAB 7.4.0, rev 2007a). The analytic power was given by the sum of squares of the real part (the ECoG) and imaginary part (the Hilbert transform). The analytic phase was given by the arctangent of the ratio of the imaginary part to the real part. After unwrapping, the analytic phase differences were calculated for each step by subtracting the preceding value of phase. The difference in radians was divided by the digitizing step in s to give the analytic “instantaneous” frequency in radians/s. These components of the analytic signal were plotted as time series, and distributions of values were displayed in histograms.

3. Results

Figures 1 and 2 compare the simulated and experimental waveforms in fixed 2 s segments. A. The unfiltered raw signals were dominated by the power in the low frequencies. C. The fluctuations in the filtered signals showed intermittent variations in phase and amplitude, here illustrated for the gamma band. Self-similarity of the oscillations in the four frequency bands was demonstrated by display in segments: 2 s of gamma, 4 s of beta, 8 s of alpha, and 16 s of theta (Table 1). B. The analytic frequency showed segments of low rates of change between extremes of frequency modulation in both higher and lower directions. D. The extremes in frequency coincided with instances in which the analytic power approached zero. The same patterns appeared in all four frequency ranges for the simulated ECoG and experimental ECoG of the expectant state in rabbits and in the human subject at rest, with the sampling interval set respectively at 2 ms (Nyquist frequency = 250 Hz) and 5 ms (Nyquist frequency = 100 Hz).

Figures 3 and 4 compare \log_{10} analytic power in the gamma and theta bands for simulated and experimental filtered ECoG. A and C show the time series; B and D show the histograms in log-log format. The lower traces below the analytic power show the analytic frequency on the representative channel and trial, in order to show the tight

coupling of null spikes with extremes of analytic frequency. The display time duration was proportionate inversely to the center frequency. Similar forms were observed for the intervening alpha and beta bands in both the rabbit and human ECoG and in the simulated data at 2 ms and 5 ms sampling intervals.

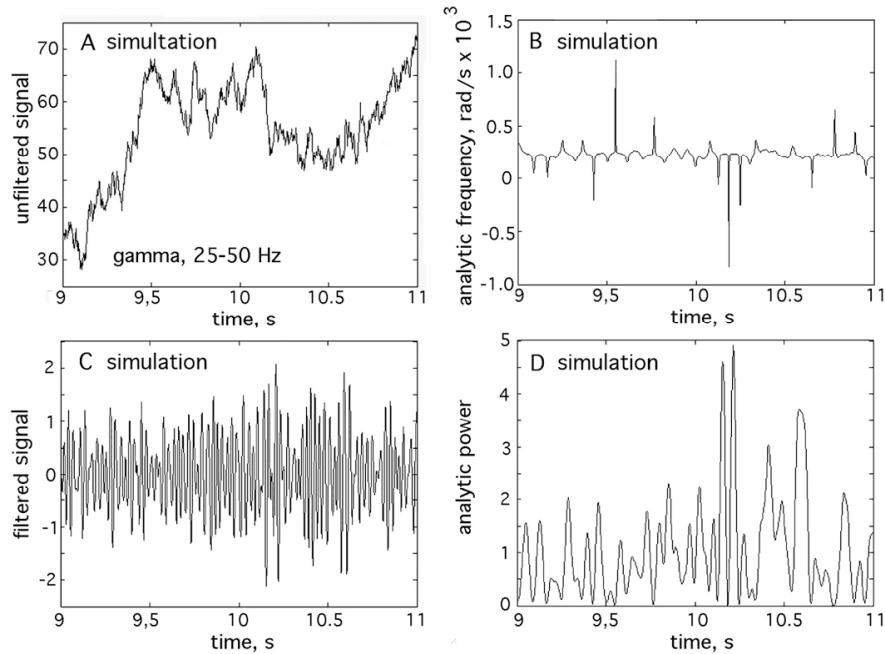


Fig. 1. A. Brown noise giving a PSD with a slope of -2 ($1/f^2$). C. Noise filtered in the low gamma range, 25-50 Hz. B. Analytic frequency. D. Analytic power.

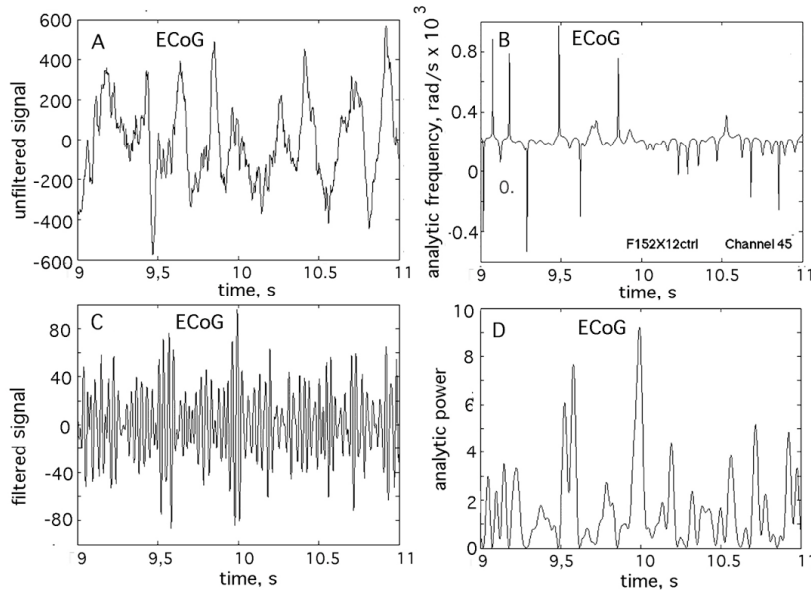


Fig. 2. A. ECoG recorded with analog pass band 0.1-100 Hz and digitized at 2 ms steps. C. Signal filtered in the low gamma range, 25-250 Hz. B. Analytic frequency. D. Analytic power.

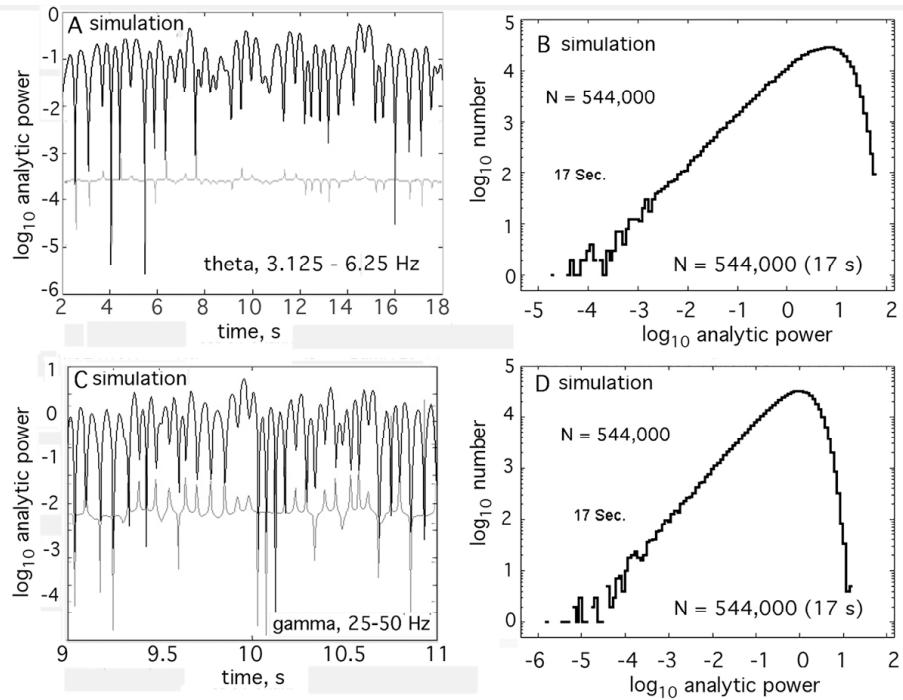


Fig. 3. Simulated log₁₀ analytic power of representative channel with analytic frequency in lower trace: simulated theta (A), simulated gamma (C). B, D, Distribution of analytic power in log₁₀ scales..

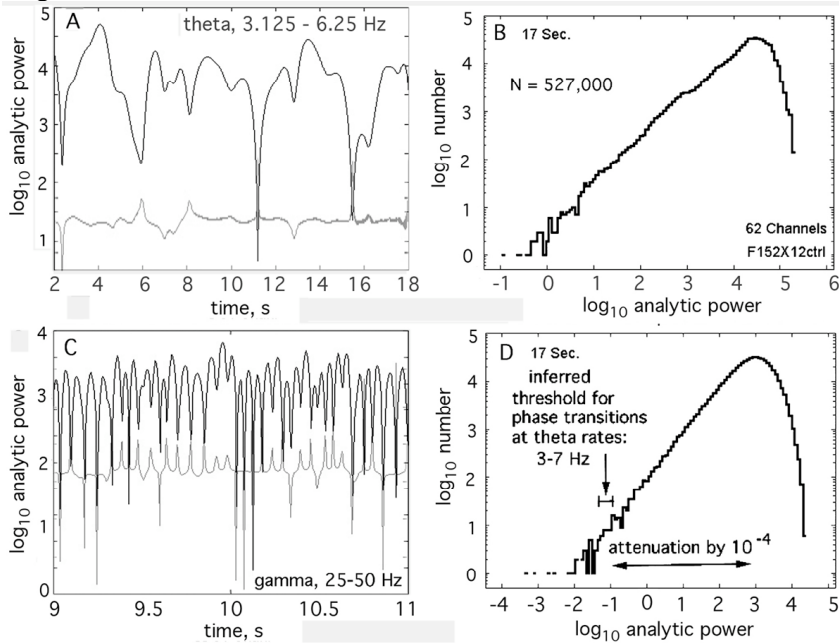


Fig. 4. Observed log₁₀ analytic power of representative channel with analytic frequency in lower trace: ECoG theta (A), ECoG gamma (C). B, D, Distribution of analytic power in log₁₀ scales.

4. Discussion

Prior studies using these human and rabbit data have shown that brains at rest or in expectancy of a conditioned stimulus often generate ECoG with power-law PSD having a slope near -2. Here we have shown that, in the absence of spectral peaks deviating significantly from the “1/f” form, the effect of band pass filtering the ECoG is to generate sequences of null spikes in the analytic power. The analytic phase and frequency at and near the cusps of these downward spikes are essentially undefined and takes widely varying values. As expected for a power-law PSD, the patterns from analytic power distribution are self-similar over the range of frequencies tested, when the spectral widths and temporal windows are scaled inversely with the center frequency of each pass band. The demonstration is based on dividing the spectra in orders of powers of 2 (Wilson, 1983). The form of the distribution is invariant with the order of the FIR filter set at 500. In the distributions of analytic power for both the simulated and experimental ECoG the minimal values were lower and the variance of analytic frequency was higher with sampling at 2 ms than at 5 ms, indicating that in an underlying continuous process the analytic power may very closely approach zero.

The present model for the simulation postulates that mutual excitation among excitatory neurons generates self-stabilized background axonal action potentials that resemble white noise, and that cumulative summation by dendrites gives the ECoG that resembles brown noise (Freeman, 2006). The background activity is stabilized by refractory periods, not by inhibition (Freeman, 1974). The role of inhibitory feedback is to generate oscillations, with gamma frequencies resulting from local feedback with shorter delays and beta frequencies coming from longer feedback pathways giving longer delays. This simple model suffices to simulate the null spike amplitudes and coordinated analytic phase differences (CAPD). It does not suffice to simulate the variations in the slopes of the spectra with sleep and seizure (Freeman et al., 2006), nor does it simulate the distributions of time intervals between null spikes in the theta range, as shown by the differences between traces in Fig. 3. A and Fig. 4, A.

Evidence reviewed elsewhere (Freeman, 2007; Freeman and Vitiello, 2008) indicates that the role of the null spikes in perception is to reduce the background activity in selected pass bands, so that under the impact of a conditioned stimulus activating a Hebbian nerve cell assembly for that stimulus, the sensory cortex may transit to an appropriate basin of attraction (Freeman, 2005). If so, the new evidence presented here indicates that there may be a threshold for the reduction in background noise that might be a prerequisite for a phase transition.

In prior studies with these subjects (Barrie, Freeman and Lenhart, 1996) the repetition intervals between the frames with gamma carrier frequencies that were classifiable with respect to conditioned stimuli were in the range of the upper theta band (5-7 Hz) [Freeman, 2006]. Those intervals in 17 s would give 85-119 null spikes. If the formation of each classifiable frame required a null spike, then the threshold for reduction in power would be roughly 10^{-4} from the modal value of power (Fig. 4, D). Alternatively, since the interval between null spikes depends on the width of the pass band, the observed repetition rates in ECoG may reflect a relatively fixed width of the pass band despite wide variation in the center frequency (Freeman, 2005).

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