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Modeling the electrical field created by mass neural activity

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ABSTRACT

Gamma oscillations of large scale electrical activity are used in electrophysiological studies as markers for neural activity and functional processes in the cortex, yet the nature of this mass neural phenomenon and its relation to the evoked response potentials (ERP) are still not well understood. Many studies associated the gamma oscillations with oscillators around the 40 Hz frequency, yet recent studies have shown that gamma frequencies may be part of a broadband phenomenon ranging from 30 Hz up to 250 Hz. In this study we have examined the possibility that a simple model, based on available neurophysiological parameters, involving an increase in asynchronous (Poisson distributed) neural firing may be sufficient to generate the observed gamma power increases. Our simulation shows a roughly linear increase in gamma power as a function of the aggregated firing rate of the neural population, while the influence of the synchronization level within the neurons on the gamma power is limited. Our model supports the viewpoint that the broadband gamma response is mainly driven by the summed, asynchronous, activity of the neural population. We show that the time frequency spectrogram of the stimulus response can be reconstructed by combining two different phenomena—the broadband gamma power increase due to local processing and the more spatially distributed event related desynchronization (ERD). Our model thus raises the possibility that the broadband gamma response is closely linked to the aggregate population firing rate of the recorded neurons.

1. Introduction

Most of the electro-physiological research on the human brain is based on the electro-magnetic fields created by the activity of large populations of neurons. Thus, non-invasive EEG studies are largely based on analyzing the event related potential (ERP) which mainly reveals activity in low frequencies (<30 Hz). Over the last decade MEG, local field recordings in behaving primates as well as invasive local field potential (LFP) recordings, conducted in epileptic patients for clinical purposes, have indicated that the signal power in the gamma frequency range (30–70 Hz) increases during a variety of cognitive tasks (Buzsaki & Draguhn, 2004; Crone et al., 1998; Fries, Neuenschwander, Engel, Goebel, & Singer, 2001; Lachaux et al., 2005; Scherberger, Jarvis, & Andersen, 2005; Singer, 1999; Tallon-Baudry, Bertrand, Henaff, Isnard, & Fischer, 2005; Womelsdorf et al., 2007).

Although most studies of gamma frequencies initially emphasized oscillators around 40 Hz (Fries, Roelfsema, Engel, Konig & Singer, 1997; Singer, 1999), recent studies have suggested that the functional activation of the cortex is perhaps more consistently associated with a broadband increase in signal power at a wide spectrum of high frequencies, starting from 30 Hz and extending up to 250 Hz and beyond (Crone, Sinai, & Korzeniewska, 2006; Miller, Sorensen, Ojemann, & den Nijs, 2009), and it was proposed (Manning, Jacobs, Fried, & Kahana, 2009; Mukamel et al., 2005; Nir et al., 2007; Ray & JHR, 2011) that the broadband power increase is directly linked to the average population firing rate. These broadband responses have been observed in a variety of functional domains, including motor (Crone et al., 1998; Miller et al., 2007), auditory (Mukamel et al., 2005; Nir et al., 2007; Trautner et al., 2006) and visual (Fisch et al., 2009; Lachaux et al., 2005; Tallon-Baudry et al., 2005).

It is generally accepted that synaptic currents are the major contributors to the LFP (Mitzdorf, 1985) ; however, the relationship of the two mass neural phenomena of ERP and gamma oscillations to the firing/synaptic activity of the neural population remains unclear. There are many studies suggesting that this mass neural activity is driven mainly by the level of synchrony in the population and the average firing rate of the population (Fries, Nikolic, & Singer, 2007; Manning et al., 2009; Ray, Crone, Niebur, Franaszczuk, & Hsiao, 2008). Here, using a quantitative model, we examined whether a simple model of asynchronous firing activity could account for the gamma responses and evoked responses

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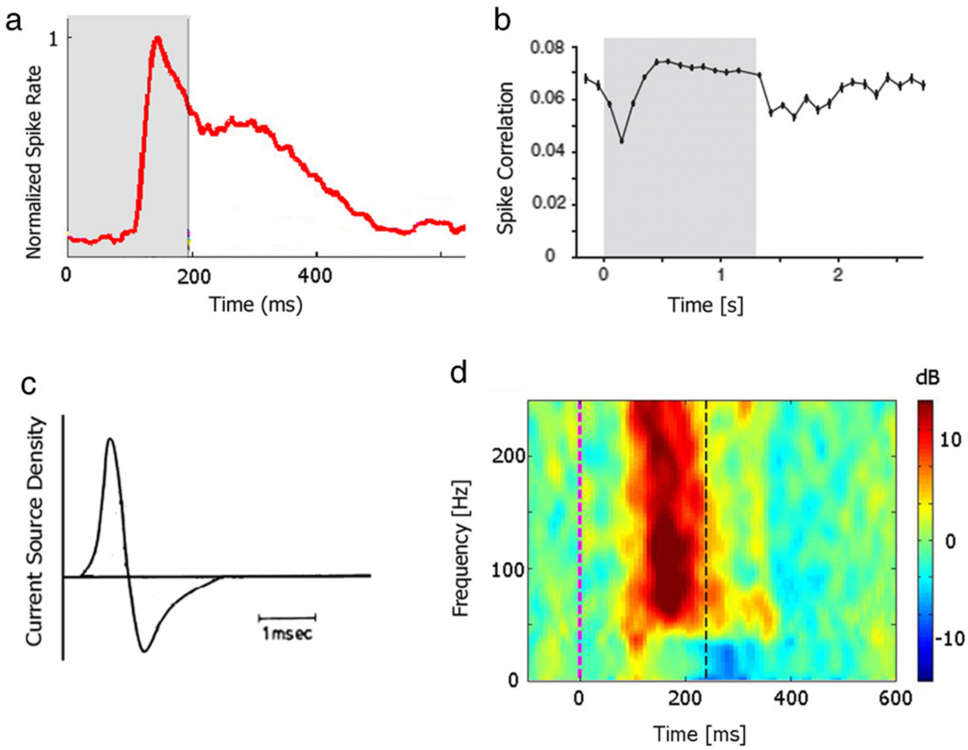

Fig. 1. Data from electrophysiological studies used in the simulation. (a) Firing rate scheme of neurons in monkey's visual cortex, average single-unit responses to face stimulus, obtained by averaging single-unit responses from all visually responsive neurons recorded in face selective cortex patch from supplementary material of Tsao et al. (2006). (b) Neurons synchronization, recorded from a monkey's visual cortex with 60 channels electrode array (Smith & Kohn, 2008), shade background marks stimulus on. (c) Current source density profile (solid line) of EPSP (Mitzdorf, 1985). (d) Spectrogram of ECoG signal recorded from human high order visual cortex (Privman et al., 2010), magenta vertical line — stimulus on, black — stimulus off. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

recorded using ECOG in the human visual system (Fisch et al., 2009; Privman et al., 2007).

One of the strongest phenomena in EGoC recording is the event related desynchronization (ERD) (Crone et al., 1998). It is commonly agreed that the ERD phenomenon is generated by thalamo-cortical circuits where the processing of the visual input blocks the Alpha oscillations in the thalamo-cortical circuits (Pfurtscheller & Lopes da Silva, 1999). It was proposed (Miller et al., 2008) that the ECoG signal could be simulated by superposition of the ERD phenomenon on the broadband gamma power increase.

While it is commonly accepted that the evoked response and gamma power are driven by neuronal activity, we have recently used intracranial ECoG recordings to demonstrate that these signals may be dissociated. Thus, under paradigms of rapid sequential presentation of picture stimuli ("double pulse" paradigm) we found that one visual stimulus suppresses the evoked response of the second stimulus yet the gamma response remains unaffected (Privman et al., 2010).

In the present study we show how a straightforward quantitative simulation of neural activity at the synapses level can generate ECoG response patterns that are compatible with experimentally derived responses. The results of our simulation replicate the broadband nature of the Gamma response, and unlike previous models, indicate that the gamma response can be generated by an increase in asynchronous firing rates even in the absence of precise temporal synchronization.

2. Simulation methods and electrophysiological data

The task of simulating the electrical field sampled by the ECoG electrode requires modeling of extremely large numbers (in the order of magnitude of 10**6 cells and 10**9 synapses) for various configurations of the inter-neuron connections. Following the common approach, we use a simplified statistical model of the networks/ neurons/ synapses behavior based mainly on electrophysiological studies in mammals and humans and results from analytical detailed simulations of relatively small neural networks. It is commonly agreed that the main generator of LFP are the post synaptic currents (Logothetis, 2003; Mitzdorf, 1985), our approach in this simulation was first to simulate the neurons spikes scheme (see 2.1) and then to calculate per simulated spike the synaptic activity in the neuron's axonal synapses and the upstream dendrites derived from this spike (see 2.3). Our model was based on experimentally derived parameters of neuronal firing, electrical spread and ECoG responses.

2.1. Neuron firing scheme in response to stimulus

It is generally accepted that spike trains of cortical neurons can be described as random Poisson processes (Bair, Koch, Newsome, & Britten, 1994; Softky & Koch, 1993; Tolhurst, Movshon, & Dean, 1983) where the firing rate changes according to the cortical state. We have used single unit recording data from "face patches" of the visual cortex of monkeys (Tsao, Freiwald, Tootell, & Livingstone, 2006, see Fig. 1(a)) to estimate firing rates of face selective neurons as a function of the latency from stimulus onset. For our basic simulated neuron, we used a baseline firing rate of 3 Hz; a 20 ms burst of 40 Hz at 170 ms latency from stimulus onset; followed by intermediate firing of 20 Hz for 100 ms; and then back to a baseline firing rate.

2.2. Neurons contribution to the electrical field

The ECoG recordings simulated in the present study were obtained from electrodes of 2 mm in diameter placed under the