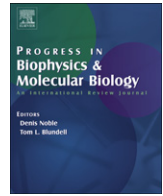




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Original Research

Macroscopic entrainment of periodically forced oscillatory ensembles

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ABSTRACT

Large-amplitude oscillations of macroscopic neuronal signals, such as local field potentials and electroencephalography or magnetoencephalography signals, are commonly considered as being generated by a population of mutually synchronized neurons. In a computational study in generic networks of phase oscillators and bursting neurons, however, we show that this common belief may be wrong if the neuronal population receives an external rhythmic input. The latter may stem from another neuronal population or an external, e.g., sensory or electrical, source. In that case the population field potential may be entrained by the rhythmic input, whereas the individual neurons are phase desynchronized both mutually and with their field potential. Intriguingly, the corresponding large-amplitude oscillations of the population mean field are generated by pairwise desynchronized neurons oscillating at frequencies shifted far away from the frequency of the macroscopic field potential.

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1. Introduction

Large-amplitude LFP, EEG or MEG oscillations are considered to be generated by a large population of neurons firing in synchrony (Elul, 1972; Singer, 1993; Hämäläinen et al., 1993; Bressler, 1995; Pfurtscheller and da Silva, 1999; Nunez et al., 2001). In contrast, an uncorrelated firing of neurons is averaged out, so that the corresponding LFP, EEG or MEG signal becomes indistinguishable from the noisy background. Accordingly, these signals are used to assess collective neuronal dynamics (Gray and Singer, 1989). As a rule of thumb, the larger the amplitude of an LFP, EEG or MEG oscillation, the stronger the synchronization of the generating neuronal population is expected to be (Elul, 1972; Singer, 1993; Hämäläinen et al., 1993; Bressler, 1995; Pfurtscheller and da Silva, 1999; Nunez et al., 2001). This paradigm has led to the commonly accepted notion of EEG/MEG (de)synchronization, which is solely based on the magnitude of the spectral peak of the EEG/MEG signal, i.e., the amplitude of the corresponding frequency component of the measured macroscopic signal (Singer, 1993; Klimesch, 1996; Pfurtscheller and da Silva, 1999).

Numerous theoretical and experimental studies have focused on how the above mentioned macroscopic observables relate to the

underlying neuronal activity under both physiological and pathological conditions. Mathematically, the interdependence between population mean field and collective dynamics of individual oscillators, e.g., oscillatory neurons, has been studied for an ensemble of globally coupled phase oscillators by Kuramoto (Kuramoto, 1984), see also Tass (1999), Strogatz (2000), Acebron et al. (2005). It has been shown that the onset of synchronization among the oscillators results in a large-amplitude oscillation of the population mean field, whereas the mean field of a desynchronized population exhibits statistical fluctuations of the order $1/\sqrt{N}$, where N is the number of the oscillators in the ensemble (Pikovsky and Ruffo, 1999). In the synchronized regime the large-amplitude mean field coherently oscillates with the mutually synchronized oscillators, which are phase-locked to the mean field. Experimentally, the temporal correlation between the firing of the individual neurons and the prominent oscillations of the population field potential has successfully been demonstrated in several studies in the intact brain (Buzsaki et al., 1983; Eckhorn et al., 1988; Gray and Singer, 1989; Engel et al., 1990; Murthy and Fetz, 1992; Bragin et al., 1995) as well in neurological disorders (Levy et al., 2002; Kuehn et al., 2005; Weinberger et al., 2006).

In several studies, however, it has been found that the individual neurons are not very tightly correlated with LFP oscillations (Murthy and Fetz, 1992). In some cases the correlation is even absent (Engel et al., 1990), or LFP oscillations exhibit either “overlapping” or “mixed” relationships with the simultaneously recorded discharges of individual neurons (Donoghue et al., 1998). In the latter case, the pronounced LFP oscillations coincide with periods of

Abbreviations: EEG, electroencephalography; MEG, magnetoencephalography; LFP, local field potential; DBS, deep brain stimulation.

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suppressed neuronal firing. The firing of the individual neurons, although there might be a statistically revealed phase preference to the large-amplitude LFP oscillations, need not strictly follow the phase dynamics of the population field (Denker et al., 2007). Furthermore, it has experimentally been shown that the hippocampal electroencephalographic theta rhythm clearly shows a gradual and systematic phase shift with respect to the recorded activity of the individual place cells (O'Keefe and Recce, 1993; Skaggs et al., 1996; Kamondi et al., 1998; Buzsaki and Draguhn, 2004). The variety of different findings indicates that the phase relation between the firing of the individual neurons and the large-amplitude oscillations of the population field potential generated by these neurons requires further examination. In particular, the question still remains open, whether the large-amplitude oscillations of the population LFP can be considered as a reliable measure for the synchronization among the individual neurons. A clarification of the mechanism of the generation of the macroscopic field potentials by the underlying individual neurons is thus of great importance (Elul, 1972; Buzsaki et al., 1983; da Silva, 1991).

In this paper we computationally address the above question for a basic setup: a population of interacting neurons receiving an external periodic input. This scenario represents or approximates different fundamental situations. Rhythmic input may originate from other neuronal populations in the context of bottom-up or top-down streams of information processing (Ullman, 1995; Engel et al., 2001) mediated, e.g., by thalamic and intra-cortical signal inflow via thalamo-cortical and cortico-cortical functional loops (Mumford, 1991, 1992; Steriade, 2001). On the other hand the source of the external periodic driving may be located outside the body. For instance, a fundamental type of external driving comes from the 24-hour light-dark cycle, which entrains intrinsically oscillatory neurons in the suprachiasmatic nucleus (SCN) and leads to circadian rhythms (Welsh et al., 1995; Liu et al., 1997; Yamaguchi et al., 2003). Another example comes from stereotaxic neurosurgery. Recently it has been suggested to use an external low-frequency electrical stimulation for functional target point localization for depth electrode implantation for deep brain stimulation (DBS) in Parkinson's disease (Barnikol et al., 2008). The goal of this method is to provoke and periodically entrain tremor in patients, in whom tremor vanishes intraoperatively, e.g., due to general anaesthesia or due to an insertional effect (Maltete et al., 2004; Yousif and Liu, 2007), so that the standard methods become inapplicable.

It is commonly assumed that a common rhythmic or periodic input, either excitatory or inhibitory, strongly enforces mutual synchronization with zero phase shift between neurons, as revealed by many cross-correlation studies (Gerstein and Perkel, 1972; Michalski et al., 1983; Ts'o et al., 1986; Gochin et al., 1991; Nelson et al., 1992; Cobb et al., 1995). In this paper we demonstrate that the situation is, in fact, considerably more involved. We show that a periodic driving of intermediate strength causes quite surprising effects over a wide parameter range. As expected, the population mean field may get entrained by the periodic forcing, so that it oscillates at the frequency of the external periodic force. Intriguingly, the single neurons behave totally different. They oscillate at frequencies which significantly deviate from the frequency of the large-amplitude population mean field. The single neurons are not mutually synchronized. In other words, their mutual phase differences are not bounded. So, the single neurons are neither locked to the population mean field nor to each other. Nevertheless, due to a dynamic, intermittent regrouping of coincidentally firing neurons a large-amplitude population mean field arises, the classical hallmark of neuronal synchronization.

Our study shows that, in case of a periodically driven neuronal population, from a large-amplitude population mean field, e.g., LFP, we cannot conclude that the single neurons are mutually

synchronized. Our results may contribute to a more sophisticated view on the relationship between neuronal dynamics on the macrolevel (as assessed by EEG, MEG and LFP) and neuronal dynamics on the microlevel (i.e., single neuron). In particular, our results may contribute to an improvement of low-frequency stimulation techniques used for stereotaxic target point diagnosis for DBS electrodes.

2. Material and methods: models

Since the phenomena investigated in this paper strongly relate to the phase dynamics of interacting and forced oscillators, e.g., oscillatory neurons, it is reasonable to consider an ensemble of interacting simple phase oscillators, where the phases are naturally defined and calculated. For our computational analysis we use the famous and generic Kuramoto system of globally coupled phase oscillators with periodic forcing. In addition, we verify our results with a neuronal ensemble of interacting FitzHugh-Rinzel bursting neurons receiving a periodic common synaptic input.

2.1. Phase ensemble

Ensembles of phase oscillators have widely been used to model basic synchronization properties of interacting oscillators with periodic forcing, for example, concerning the entrainment of circadian oscillators (Kori and Mikhailov, 2004, 2006). Ensembles of coupled oscillators with periodic driving have also been used to model neocortical brain activity in the paradigmatic finger-tapping Julliard experiment with an external acoustic pacing (Frank et al., 2000). There, the phase dynamics of oscillatory components of the measured encephalographic signals were approximated by the behavior of the mean field of weakly coupled and forced phase oscillators.

The Kuramoto model of N globally coupled phase oscillators (Kuramoto, 1984) with an additional term of the periodic force reads (Sakaguchi, 1988; Antonsen et al., 2008; Ott and Antonsen, 2008; Childs and Strogatz, 2008)

$$\dot{\psi}_j = 2\pi\omega_j + \frac{C}{N} \sum_{i=1}^N \sin(\psi_i - \psi_j) + K \sin(2\pi\Omega_f t - \psi_j), \quad (1)$$

where ω_j , $j = 1, 2, \dots, N$, are the natural frequencies of the oscillators, and C is the strength of the global coupling. Ω_f and K are the frequency and the strength of the periodic forcing, respectively. The global coupling tends to minimize the pairwise phase differences between oscillators, thus, promoting an in-phase synchronization in the ensemble and equalizing the individual frequencies. The external forcing on the other hand attracts the oscillator phases to the phase of the stimulation signal and forces the oscillators to rotate at the driving frequency. In the forcing-free regime ($K=0$) system (1) is known to demonstrate a transition to synchronization as the coupling strength increases (Kuramoto, 1984; Tass, 1999; Strogatz, 2000; Acebron et al., 2005). In the limit $N \rightarrow \infty$ a macroscopic fraction of the oscillators spontaneously synchronize, i.e., they start to rotate with the same frequency, if the coupling strength exceeds the synchronization threshold $C_{cr} = 4/g(\omega_0)$.¹ Here, $g(\cdot)$ is a unimodal symmetric distribution density of the natural frequencies ω_j , and $\omega_0 = N^{-1} \sum_{j=1}^N \omega_j$ is its mean value. In what follows the natural frequencies will be Gaussian distributed around the mean $\omega_0 = 2.5$ Hz with the standard deviation $\sigma_0 = 0.02$.

¹ Since the angular natural frequencies in model (1) are taken in the form $\tilde{\omega}_j = 2\pi\omega_j$, the original Kuramoto synchronization threshold $C_{cr} = 2/\pi g(\omega_0)$ (Kuramoto 1984, Tass 1999, Strogatz 2000, Acebron et al., 2005) attains the form $C_{cr} = 4/g(\omega_0)$, where $\tilde{g}(\cdot)$ and $g(\cdot)$ are the unimodal symmetric distribution densities of $\tilde{\omega}_j$ and ω_j , respectively, and $\tilde{\omega}_0$ and ω_0 are the corresponding mean values.

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