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I. INTRODUCTION

It is well-known that various forms of stochastic resonance occur in neural tissue, both in vitro and in living brains[1]. An unsolved macro-problem is to what extent noise facilitates, or is necessary, for the functioning of various computational tasks accomplished by the brain in giving rise to perception, cognition, and behaviour[1]. This presentation describes the context for three important problems within this arena: To what extent may the oscillatory behavior of individual neurons, or linked populations of neurons, best be characterized as noise-driven quasicycles or as noisy limit cycles? What role(s) does neural noise play in the synchronization of, and information transmission between, neural populations located far from one another in the brain? To what extent do noise-driven quasipatterns arise in the brain and affect its overall functioning?

II. NOISY LIMIT CYCLES OR NOISE-DRIVEN QUASICYCLES?

An influential model of the interactions between populations of excitatory and inhibitory neurons in brains (Fig. 1) is

$$\tau_E dV_E(t) = \Bigg[-V_E(t) + g\Big[a_E\Big(S_{EE}V_E(t) - S_{EI}V_I(t) - \theta_E + P_E(t)\Big)\Big]\Bigg] dt + \sigma_E dW_E(t), \tag{1}$$

$$\tau_I dV_I(t) = \Bigg[-V_I(t) + g\Big[a_I\Big(-S_{II}V_I(t) + S_{IE}V_E(t) - \theta_I\Big)\Big]\Bigg] dt + \sigma_I dW_I(t), \tag{2}$$

where $V_E(t), V_I(t)$ are voltages of excitatory and inhibitory neuron populations, respectively, $S_{EE}, S_{II}, S_{EI}, S_{IE}$ are synaptic efficacies, τ_E, τ_I are time constants, g is a threshold function, $a_E, a_I, \theta_E, \theta_I$ are constants, $P_E(t)$ is input current, and $W_E(t), W_I(t)$ are standard Brownian motions. This model is similar to some models of individual neurons, e.g., the Morris-Lecar neuron, where a pair of differential equations models fast and slow processes within the neuron[2]. When $g(x) = (1 + e^{-x})^{-1}$ and $\sigma = 0$, this model yields deterministic limit cycles with a characteristic frequency, i.e., neural oscillations[3]. When $\sigma > 0$ the limit cycle is noisy[4], and for very large σ the noise obscures the limit cycle and there is no oscillation apparent. If we take $g = 1, a_E = a_I = 1, \theta_E = \theta_I = 0$, and $P(t) = 0$, then the system exhibits a damped oscillation that goes to a fixed point with a rate depending on the synaptic efficiacies and the time constants. If we take $\sigma > 0$, however, then the system exhibits quasicycles, that is, the noise drives the system away from the fixed point and we see what appear to be noisy oscillations about that point at a mean frequency determined by the various synaptic efficacies and time constants[5]. Thus, in the limit cycle version of the model, noise is a nuisance that obscures the inherent oscillations that may, or may not, play a significant role in information processing in the brain. In the quasicycle version of the model, however, noise is an essential driving force without which neurons or neuron populations would not exhibit oscillations, or any other interesting behaviour, at all. This is a quinessential example of what McDonnell and Ward[1] called 'stochastic facilitation.' Although much theoretical work has been done on the limit cycle model, and some is beginning on the quasicycle version (e.g.,[4–6]), it is unknown which model best captures the characteristics of oscillatory neural activity in the brain, or indeed whether both models capture neural oscillations at particular scales. There are some reasons to believe that quasicycles dominate at intermediate scales in the brain[5] but much more information is needed. There exist some methods that may differentiate between noisy limit cycles and quasicycles[7] but these have yet to be applied to a wide range of neural data at many scales.

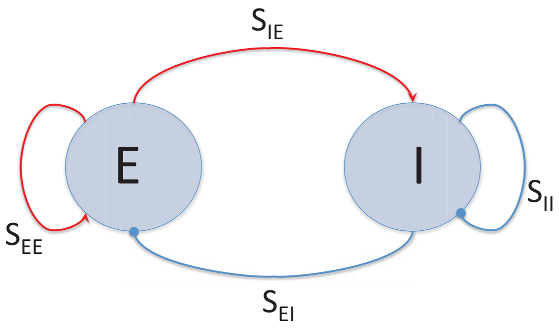

FIG. 1. Typical arrangement of an excitatory (E) and inhibitory (I) neuron pair. S_{EE}, S_{II}, S_{EI}, S_{IE} refer to the synaptic efficacies of the connections; see equations (1), (2).

III. NOISE IN SYNCHRONIZATION AND INFORMATION TRANSMISSION?

Noise is known to facilitate neural synchronization, both through studies of models[8] and through experiment[9]. Interestingly, even when deterministic versions of the Wilson-Cowan equations are studied, noise is added to the simulation process in order to 'accelerate' the process[10]. Importantly, both limit cycle[10] and quasicycle[11] models of neural interactions exhibit Kuramoto-type synchronization, indicating that for local neural populations at least, noise could be deeply involved in neural synchronization, and thus could play an important role in information transmission in the brain. This is because oscillatory synchronization of neural populations has been seen as an important mechanism for improving information transmission between those populations[12].

There is considerable controversy about the role of neural oscillations in the brain, however. And there have been no direct experiments to our knowledge on the effect of variations in neural noise levels on any information-transmission related neural computational tasks. Moreover, if quasicycles dominate at the scale of interregional information transmission, then there is likely an optimal noise level involved, both for the maintenance of the quasicycles themselves and for the synchronization between sets of quasicycles. It is unknown whether such a noise level would be the same for both functions, or whether different noise sources and levels (synaptic noise for synchronization and ion channel noise for quasicycles?) would be required.

Finally, it is possible that information can be transmitted between brain regions through a multiplexing-demultiplexing process that depends on an oscillatory modulation of noisy firing-rate population codes[13]. It is unknown whether such a scheme requires stochasticity (noise) or whether it would work better without any noise at all.

IV. NOISE-DRIVEN QUASIPATTERNS?

Stochastic differential equation models of neural systems, like the stochastic equations 1 and 2, describe only fluctuating temporal oscillations. But several large scale models of the brain, when simulated, have indicated that spatial patterns of temporal oscillations can occur, e.g.[14]. Recently mathematical methods have been developed to derive temporal and spatial patterns (indexed by frequency ω and by wave number k)[15] from a system of stochastic partial differential equations. Power spectra, as in Fig. 2, indicate the existence of temporal-spatial quasipatterns (Turing patterns) occurring on a lattice. , as in Potentially such a system could be extended to describe the types of noise-driven quasipatterns seen in other models and in the brain itself, providing an account of the generation and consequences of such noise-driven quasipatterns. This is yet to be be accomplished.

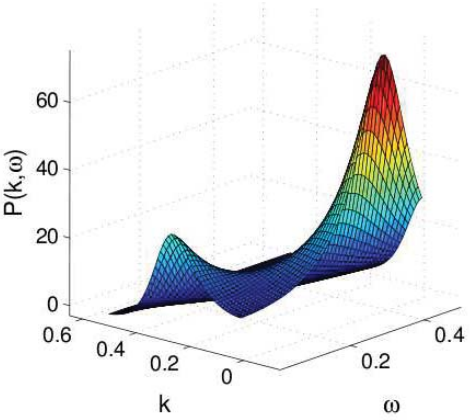

FIG. 2. Power spectrum showing spatial-temporal stochastic patterns. Reprinted with permission from[16].

ACKNOWLEDGMENTS

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