FAST COMMUNICATION

RELIABILITY OF LAYERED NEURAL OSCILLATOR NETWORKS[*]

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Abstract. We study the *reliability* of large networks of pulse-coupled oscillators in response to fluctuating stimuli. Reliability means that a stimulus elicits essentially identical responses upon repeated presentations. We view the problem on two scales: *neuronal reliability*, which concerns the repeatability of spike times of individual oscillators embedded within a network, and *pooled-response reliability*, which addresses the repeatability of the total output from the network. We find that individual embedded oscillators can be reliable or unreliable depending on network conditions, whereas pooled responses of sufficiently large networks are mostly reliable.

Key words. Neural network dynamics, coupled oscillators, random dynamical systems.

AMS subject classifications. 92B20, 82C32, 34C15, 37H99.

1. Introduction

Many complex, nonlinear systems are usefully viewed as networks composed of simpler systems; familiar examples include the electrical power grid, genetic circuitry, and the nervous system [32]. A basic question about a network's response to external forcing is its *reliability* [29, 35]: if a network is driven multiple times by the same fluctuating signal, how similar will its responses be across trials? Reliability affects the predictability of the response and is often desirable in engineered systems. It also impacts a system's ability to process or transmit information. While the dynamics of networks has received much recent attention [8, 21, 11, 22, 16, 36, 3, 6, 4], our understanding of the reliability of networks remains incomplete.

From a physical perspective, networks receiving external stimuli can be viewed as driven dynamical systems. For large networks, these dynamical systems have many degrees of freedom, making a statistical approach desirable. In this paper, we show that the theory of *random dynamical systems* provides a useful framework for studying the reliability of large networks driven by rapidly fluctuating stimuli [1, 5].

The dynamics of networks depend strongly on their constituents, type of coupling, etc. We focus here on *neural oscillator networks.* Reliability is of particular interest in neuroscience, as it impacts the precision of neural codes based on temporal patterns of spikes [7, 18, 26, 27, 24]. Experimental and theoretical studies have concluded that reliability is typical for single neurons [7, 18, 34, 28, 20, 39, 23, 25]. However, for networks of neurons, behavior ranging from reliable to highly unreliable is seen in theoretical studies [16, 36, 3, 6, 4, 33].

What network mechanisms determine the degree of reliability? Here, we identify the conditions for reliability in certain idealized models of *layered* neural oscillator networks. See figure 1.1. Such layered architectures model a system with an input stimulus that arrives at one part of a network and is then transmitted elsewhere – as occurs, e.g., in all sensory processing in neuroscience [31, 9]. Our study combines qualitative theory with numerical simulations.
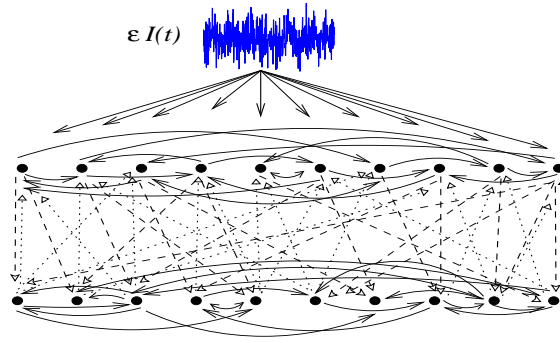
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FIG. 1.1. *Two-layer network with $N = 20$.*

2. Model details

Individual neurons are modeled as phase oscillators or "Theta neurons"; this is a common model for neurons in intrinsically active, "mean-driven" firing regimes and also characterizes more general oscillators near saddle-node bifurcations on limit cycles [38, 10]. We study pulse-coupled networks described by equations of the form

$$\dot{\theta}_i = \omega_i + z(\theta_i) \left[\sum_{j \neq i} a_{ji} \, g(\theta_j) + \epsilon_i I(t) \right], \tag{2.1}$$

$i = 1, \ldots N$, where $N \gg 1$ (see e.g. [38]). The variables θ_i are the states of the neurons, i.e. they are angles parametrized by $[0, 1]$ with periodic boundary conditions. The ω_i are intrinsic frequencies, and the a_{ji} are synaptic coupling strengths, mediated by a smooth function $g \geq 0$ with $\int_0^1 g(\theta) \, d\theta = 1$ and $g(\theta) > 0$ for $\theta \in (-\frac{1}{20}, \frac{1}{20})$.[1] That is to say, neuron j "spikes" when $\theta_j = 0$, exciting or inhibiting neuron i depending on whether $a_{ji} > 0$ or $a_{ji} < 0$ ($a_{ji} = 0$ means neuron i does not receive direct input from neuron j). The phase response curve is given by $z(\theta) = \frac{1}{2\pi}[1 - \cos(2\pi\theta)]$. The stimulus is represented by $I(t)$, which we take to be "frozen", or *quenched* white noise; we have found numerically that adding low-frequency components to $I(t)$ does not substantially change our results.

We now explain how the parameters ω_i, a_{ji} and ϵ_i in equation (2.1) are chosen. In a reliability study of a fixed network, these parameters remain frozen, as does $I(t)$, and each *trial* corresponds to a randomly-chosen initial condition in the system defined by (2.1).

To incorporate some of the heterogeneity that occurs biologically, we assume some variability in the ω_i and the a_{ji}. Specifically, the ω_i are drawn randomly and independently from the uniform distribution on the interval $[1 - \frac{1}{2}\rho, 1 + \frac{1}{2}\rho]$, so that they have mean 1 and can vary up to ρ between neurons. (The a_{ji} are discussed below.) Simulations indicate that for ρ in the range $5 - 30\%$, the exact value of ρ has little impact on the overall trends reported below; we set $\rho = 20\%$ in what follows.

We study the two network structures introduced above:

Single-layer networks. We set $\epsilon_i \equiv \epsilon$ for all i, so that all neurons receive the same input $I(t)$ at the same amplitude ϵ. For the cases shown here, we assume a 20% connectivity with mean synaptic strength a, i.e., each neuron receives input from $\kappa = 0.2 \, N$ other

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[1]Specifically, we set $g(\theta) \propto (1 - 400 \cdot \theta^2)^3$ for $|\theta| \leq \frac{1}{20}$.

neurons (chosen randomly in simulations); results remain largely unchanged for κ/N in the range $10-30\%$, characterizing sparse networks. The nonzero a_{ji} are drawn independently and uniformly from $[0.9a, 1.1a]$; as is the case for the ω_i, the results are not sensitive to the specific level of heterogeneity. The two main network parameters are thus ϵ and a.

Two-layer networks. We add a second, randomly connected layer downstream of the first. That is, neurons in the network form two layers, each containing $\frac{N}{2}$ neurons. For all neurons i in Layer 1, we set $\epsilon_i \equiv \epsilon$. We set $\epsilon_i \equiv 0$ for Layer 2. Each neuron receives connections from $\kappa = 0.2\,N$ other neurons, with $\frac{\kappa}{2}$ from its own layer and $\frac{\kappa}{2}$ from the other layer. Intra-layer connections within Layer 1 (respectively Layer 2) have mean strength a_1 (respectively a_2). For inter-layer connections, Layer $1 \rightarrow 2$ connections have mean strength a_{ff}, while Layer $2 \rightarrow 1$ connections have mean strength a_{fb}. (Here, "ff" and "fb" refer to "feedforward" and "feedback".) Specific, heterogeneous coupling constants are randomly chosen to lie within 1 ± 0.1 of their mean values, as before. The main system parameters here are ϵ, a_1, a_2, a_{ff}, and a_{fb}.

3. Neuronal reliability

This refers to the repeatability of spike times from trial to trial for *individual neurons* within a network when the same stimulus $I(t)$ is presented over multiple trials. Figure 3.1 shows raster plots for two arbitrarily chosen neurons drawn from two different networks. The top panel shows repeatable spike times; this is our definition of neuronal reliability. The bottom shows unreliability: spike times persistently differ from trial to trial. The latter cannot happen for single Theta neurons *in isolation*, as they are always reliable [34, 28].
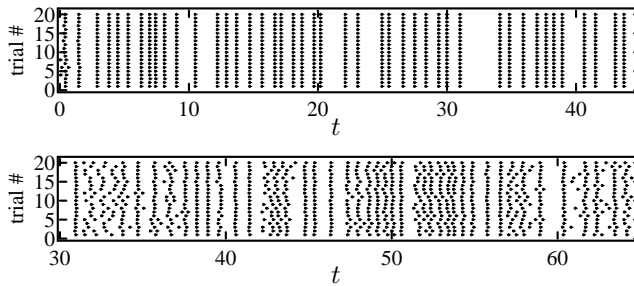

FIG. 3.1. *Raster plots of single oscillators drawn randomly from two different networks. Spike times are recorded for 20 trials. We set $\epsilon = 2.5$ and $N = 100$ in both numerical simulations. Top: Single-layer model, $A = 1$; $\lambda_{\max} = -0.57$. Bottom: Two-layer, $A_{\mathrm{ff}} = 2.8, A_{\mathrm{fb}} = 2.5, A_1 = A_2 = 1$; $\lambda_{\max} = 0.53$.*

(A) Mathematical dichotomy. Neuronal reliability is closely related to stability properties of the dynamical system defined by equation (2.1) [34, 28, 20, 39, 23, 25, 16, 36, 3, 6, 4]. Recall that *Lyapunov exponents* measure the rates of divergence of nearby orbits. These numbers make sense for deterministic as well as random dynamical systems. For the latter, under mild assumptions they are independent of initial condition or realization of Brownian path (see [1, 5]). Let $\lambda_{\max}$ denote the largest Lyapunov exponent of (2.1). The following are known mathematical facts [13, 14]. If $\lambda_{\max} < 0$, then regardless of the state of the network at the onset of the stimulus, all trajectories coalesce into a small region of phase space; this scenario, referred to as a *random sink*, corresponds to entrainment to the stimulus. Conversely, if $\lambda_{\max} > 0$, the

trajectories organize themselves around a complicated object called a *random strange attractor*. This means that at any given time, the network may be in many different states depending on its initial condition. *In this paper, we equate $\lambda_{max} < 0$ with neuronal reliability and $\lambda_{max} > 0$ with neuronal unreliability.*

Our challenge here is to understand network reliability in terms of the system parameters introduced above. Measuring reliability using a single quantity, λ_{max}, has the advantage that large parts of the landscape can be seen at a glance, as in figure 3.2.[2]

(B) Highly different responses of single- and multi-layer networks. Without going into details, one sees readily from figure 3.2 that λ_{max} is largely positive for the two-layer system (right), whereas λ_{max} tends to be negative for the single-layer (left).

Single-layer networks. We find that it is fruitful to view λ_{max} as a function of the quantity $A = \kappa a$, which has the following interpretation. Focus on an arbitrary neuron, say neuron i. In the limit $N \to \infty$, one would expect each of its κ presynaptic neighbors to spike once per unit time ($\omega \approx 1$) with average strength a. A mean-field argument suggests that the average impact of one kick on the phase of neuron i is $a\bar{z}$, where $\bar{z}$ is the average value of $z(\theta_i)$ at the arrival times of incoming spikes. That is, when $N \gg 1$, we expect neurons to be pushed (forwards if $A > 0$ and backwards if $A < 0$) by $A\bar{z}$ of a cycle per unit time. (This assumes that the mean spike rate is $\approx \langle \omega_i \rangle = 1$, as is the case here.) If the dynamics were to approach a meaningful limit as $N \to \infty$, it is necessary to stabilize the total synaptic input received by a typical neuron. So $A = \kappa a$ is a natural scaling parameter.
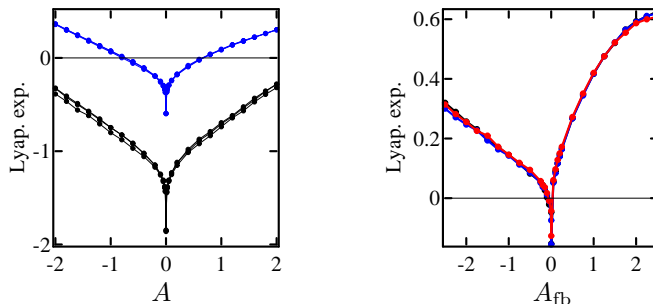

FIG. 3.2. *Lyapunov exponents λ_{max}. Left: Single-layer, $N = 100$, $\epsilon = 1.5$ (top curve), 2.5 (bottom curve). Right: Two-layer, $N = 100$, $A_{ff} = 2.8, A_1 = |A_2| = 1$ (with $sign(A_2) = sign(A_{fb})$), $\epsilon = 2.5$. Three realizations of network graphs are used in each case with their plots superimposed.*

Figure 3.2 (left) shows the basic relationship between λ_{max}, A, and ϵ (the stimulus amplitude). Plots for $1.5 < \epsilon < 2.5$ interpolate between the two curves in a straightforward way. When $A = 0$, i.e., when the oscillators are uncoupled, we have $\lambda_{max} < 0$ as expected. When $A \neq 0$, λ_{max} can be positive or negative. Notice that (i) it increases with $|A|$ for fixed ϵ (the sign of A matters little), and (ii) it decreases with ϵ for fixed A. Item (ii) is due to the entraining effects of the stimulus; (i) suggests that the couplings here are intrinsically destabilizing.

We find that single-layer networks remain reliable even for large coupling strengths. For example, figure 3.2 (left) shows that λ_{max} can be negative even for

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[2]We compute λ_{max} by solving the variational equation for the SDE (2.1) using the Euler scheme.
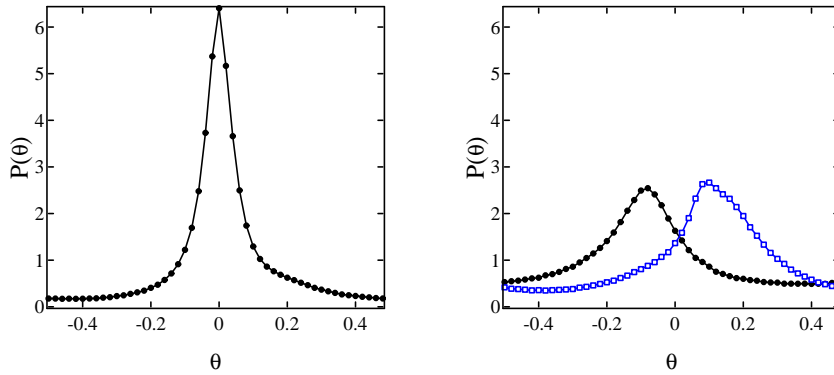
FIG. 3.3. *Phase distributions of neurons at the instant they receive an* incoming *spike.* Left: *Single-layer, $A=1.8$; all spikes.* Right: *Two-layer, $A_{\mathrm{ff}}=2.8$, $A_{\mathrm{fb}}=0.8$, $A_1=A_2=1$; for inter-layer spikes only – right peak for phases of Layer 1 neurons, left peak for Layer 2.*

$|A|\approx 2$, despite the fact that if we (somewhat naively) neglect correlations between neurons, then $\bar{z}\approx\int_0^1 z(\theta)\,d\theta=\frac{1}{2\pi}$ and each spike would shift the receiving neuron's phase by $\approx 1/3$ of a cycle. Why is the network so reliable? This can be explained by the entraining effects of the stimulus, which causes all neurons to spike at roughly the same time (see figure 3.3, left). Because $z(\theta)=z'(\theta)=0$ when $\theta=0$, near-synchrony means that $z(\theta)$ is typically quite small when a spike arrives, so that the *effective* total coupling strength $A\bar{z}$ is considerably smaller than $\frac{A}{2\pi}$, due to the strong correlation between neurons. (Greater heterogeneity leads to less synchrony and, as a result, less reliability. We have found numerically, however, that reliability is very robust: e.g., for $A=1$ and $\epsilon=2.5$, single-layer networks remain reliable at $\rho=60\%$, with $\lambda_{\max}\approx-0.2$.)

We also find that the value of $\lambda_{\max}$ depends strongly on A and ϵ but only weakly on the specific connection graph and the exact values of N, κ, and a. Figure 3.2 (left) shows that different (random) realizations of networks with the same (N,κ,a) produce very similar values of $\lambda_{\max}$. Further simulations have shown that $\lambda_{\max}$ does not vary appreciably for combinations of (κ,a) giving the same A, and the overall dependence of $\lambda_{\max}$ on A and ϵ remains the same over a broad range of N ($40\leq N\leq 1000$). See [15] for details. The reliability profile seen here is thus characteristic of single-layer networks for a broad range of parameters.

Two-layer networks. We again express $\lambda_{\max}$ in terms of A_1, A_2, A_{ff}, and A_{fb}, defined to be $\frac{\kappa}{2}=0.1\,N$ times a_1, a_2, a_{ff}, and a_{fb}, respectively. The interpretations are as before, e.g., A_{ff} is the total synaptic input per unit time received by each neuron in Layer 2 from Layer 1.

Figure 3.2 (right) shows $\lambda_{\max}$ as a function of A_{fb} with $A_{\mathrm{ff}}=2.8$, $A_1=A_2=\pm 1$ (we give A_1 and A_2 the same signs as A_{ff} and A_{fb}, respectively, as each neuron is usually either excitatory or inhibitory), and $\epsilon=2.5$. At $A_{\mathrm{fb}}=0$, the system is definitively reliable. As $|A_{\mathrm{fb}}|$ increases, however, *we find that the two-layer network loses its reliability almost immediately*, even before $|A_{\mathrm{fb}}|\approx\frac{1}{10}A_{\mathrm{ff}}$; this instability occurs in two-layer networks with any appreciable feedback for a wide range of A_{ff} and ϵ. This very surprising fact is also partially explained by the phase distributions of Layer 1 and Layer 2 neurons at the instants when they receive inputs from the other layer (see figure 3.3, right). The distributions are more spread out than in the single-layer case;

moreover, their peaks are centered away from $\theta = 0$, leading to a value of $\bar{z}$ more than double that of the single-layer case. This shift and broadening of the phase distribution can be predicted from reduced two-neuron models, based on the fact that neurons are largely synchronized within a given layer [15]. Thus at the same numerical values, A_{ff} and A_{fb} in the two-layer model are far more destabilizing than A in the single-layer. See also [2, 17, 37].

We expect the ideas above, i.e., the tendency to synchronize within each layer, the dominant effects of inter-layer interactions, and the extreme sensitivity of network reliability to feedback from downstream layers, to extend to multi-layer systems.

4. Reliability of pooled responses

Finally, we ask: how is the reliability of individual oscillators reflected in the bulk output of a network? A function representing this total synaptic output (cf. [19, 30, 12])

$$S(t) = \sum_{T_i < t} f(t - T_i) ; \quad f(t) = \tau^{-1} e^{-t/\tau},$$

where f is a postsynaptic current and $\tau \approx \frac{1}{15}$; for neurons with natural frequency ≈ 10 Hz, this value of τ corresponds to ≈ 7 ms. *Pooled-response reliability* describes how repeatable $S(t)$ is in response to $I(t)$. Clearly, neuronal reliability implies pooled-response reliability. On the other hand, one would expect individual neurons to be more volatile than the network as a whole.
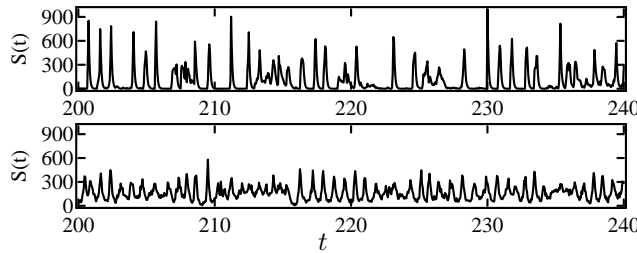

FIG. 4.1. *The bulk synaptic output function $S(t)$; one trial each for the two sets of parameters in figure 3.1.*

Two time courses for $S(t)$ are shown in figure 4.1. The first is for a reliable single-layer system; tall, well-defined spikes are generated when the system is in partial synchrony. The second is for an unreliable, 2-layer model. Here the floor of $S(t)$ is strictly positive, i.e., some neurons in the system are spiking at nearly all times, consistent with the broader phase distributions in figure 3.3 (right).

For each t, we measure the repeatability of $S(t)$ by its time-dependent, cross-trials variance $V(t)$. This information can be distilled further to give a single number $\bar{V}$ by time averaging $V(t)$; note that $\bar{V} = 0$ when $\lambda_{\text{max}} < 0$ and $\bar{V} > 0$ when $\lambda_{\text{max}} > 0$. Our main finding is that $\bar{V}/N^2$, which measures the variability of $S(t)$ across different trials (appropriately scaled as N increases), is a decreasing function of N; see figure 4.2 (left). Thus, it is apparent that due to averaging effects, the total synaptic outputs of sufficiently large networks tend to be reliable, even as individual neurons behave unreliably. We note that because of the highly correlated dynamics of the neurons, this averaging phenomenon is beyond the reach of known ergodic theorems.
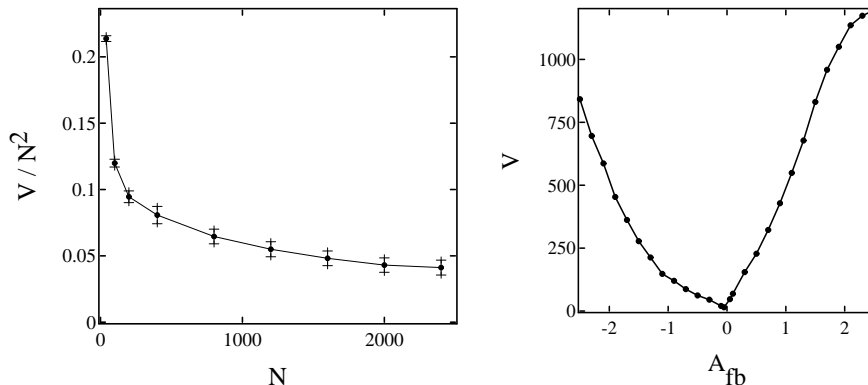
FIG. 4.2. *Mean cross-trial variances $\bar{V}$. Left: $\bar{V}/N^2$ as function of N for $A_{\mathrm{ff}} = 2.8, A_{\mathrm{fb}} = 2.5$. Right: $\bar{V}$ as function of A_{fb}. The setup is identical to that in figure 3.2 (right); $N = 100$.*

Next, we fix N. As parameters are varied, we find strong correlation between $\lambda_{\max}$ and $\bar{V}$; compare Figs. 3.2 (right) and 4.2 (right). This confirms that the two different ways of measuring unreliability we have proposed are in good qualitative agreement.

Conclusion. We have carried out a systematic study of stimulus-response reliability for layered networks of neural oscillators, and have identified simple but prototypical ways in which this reliability depends on network structure and parameters. Our findings, all of which are new in the present context and are consistent with results of earlier studies of different models, are of a very basic nature and thus are likely to shed light on situations beyond those considered here.

(1) *On the neuronal level, single-layer networks remain reliable for high connection strengths, due to a tendency to synchronize. For networks with downstream layers, by contrast, recurrent connections are strongly destabilizing.* In general, individual neurons can behave reliably or unreliably as a result of the competition between entrainment to the stimulus or upstream layer and the perturbative effects of inter-layer interactions.

(2) *Pooled responses of large enough networks are mostly reliable* even when individual neurons within it are not. In a fixed-size network, they have similar reliability properties as individual neurons but with lower volatility. As the network size increases, the volatility of pooled responses decreases.

REFERENCES

[1] L. Arnold, *Random Dynamical Systems*, Springer, New York, 2003.
[2] Y. Aviel, C. Mehring, M. Abeles, and D. Horn, *On embedding synfire chains in a balanced network*, Neural Comp., 15, 1321–1340, 2003.
[3] A. Banerjee, *On the sensitive dependence on initial conditions of the dynamics of networks of spiking neurons*, J. Comput. Neurosci., 20, 321–348, 2006.

[4] A. Banerjee, P. Seriès, and A. Pouget, *Dynamical constraints on using precise spike timing to compute in recurrent cortical networks*, Neural Computation, 20, 974–993, 2008.

[5] P.H. Baxendale, *Stability and equilibrium properties of stochastic flows of diffeomorphisms*, Progr. Probab., Birkhauser, 27, 3–35, 1992.

[6] M. Bazhenov, N. Rulkov, J. Fellous, and I. Timofeev, *Role of network dynamics in shaping spike timing reliability*, Phys. Rev. E, 72, 041903, 2005.

[7] H.L. Bryant and J.P. Segundo, *Spike initiation by transmembrane current: a white-noise analysis*, J. Phys., 260, 279–314, 1976.

[8] M.A. Buice and C.C. Chow, *Correlations, fluctuations, and stability of a finite-size network of coupled oscillators*, Phys. Rev. E, 76, 2007.

[9] E. Douglas and K. Martin, *Neuronal circuits of the neocortex*, Annu. Rev. Neurosci., 27, 419–451, 2004.

[10] G.B. Ermentrout, *Type I membranes, phase resetting curves, and synchrony*, Neural Comp., 8, 979–1001, 1996.

[11] J.G. Restrepo, E. Ott, and B. R. Hunt, *Emergence of coherence in complex networks of heterogeneous dynamical systems*, Phys. Rev. Lett., 96, 254103, 2006.

[12] B. Knight, *Dynamics of encoding in neuron populations: Some general mathematical features*, Neural Comp., 12, 473–518, 2000.

[13] Y. Le Jan, *Équilibre statistique pour les produits de difféomorphismes aléatoires indépendants*, Ann. Inst. H. Poincaré Probab. Statist., 23(1), 111–120, 1987.

[14] F. Ledrappier and L.S. Young, *Entropy formula for random transformations*, Probab. Th. and Rel. Fields, 80, 217–240, 1988.

[15] K.K. Lin, E. Shea-Brown and L.S. Young, *Spike-time reliability of layered neural oscillator networks*, submitted, 2008.

[16] K.K. Lin, E. Shea-Brown, and L.S. Young, *Reliability of coupled oscillators*, J. Nonlin. Sci., to appear.

[17] V. Litvak, H. Sompolinsky, I. Segev, and M. Abeles, *On the transmission of rate code in long feedforward networks with excitatory-inhibitory balance*, J. Neurosci., 23, 2003.

[18] Z. Mainen and T. Sejnowski, *Reliability of spike timing in neocortical neurons*, Science, 268, 1503–1506, 1995.

[19] M. Mazurek and M. Shadlen, *Limits to the temporal fidelity of cortical spike rate signals*, Nature Neurosci., 5, 463–471, 2002.

[20] H. Nakao, K. Arai, K. Nagai, Y. Tsubo, and Y. Kuramoto, *Synchrony of limit-cycle oscillators induced by random external impulses*, Physical Review E, 72, 026220, 1–13, 2005.

[21] J. Gómez-Gardeñes, Y. Moreno, and A. Arenas, *Synchronizability determined by coupling strengths and topology on complex networks*, Phys. Rev. Lett., 98, 066106, 2007.

[22] T. Nishikawa, Y.C. Lai, and F. Hoppensteadt, *Heterogeneity in oscillator networks: are smaller worlds easier to synchronize?* Phys. Rev. Lett., 91, 2003.

[23] K. Pakdaman and D. Mestivier, *External noise synchronizes forced oscillators*, Phys. Rev. E, 64, 030901–030904, 2001.

[24] D. Perkel and T. Bullock, *Neural coding*, Neurosci. Res. Program Bull., 6, 221–344, 1968.

[25] A. Pikovsky, M. Rosenblum, and J. Kurths, *Synchronization: A Universal Concept in Nonlinear Sciences*, Cambridge University Press, Cambridge, 2001.

[26] M.I. Rabinovich, P. Varona, A.I. Selverston and H.D.I. Abarbanel, *Dynamical principles in neuroscience*, Rev. Mod. Phys., 78, 2006.

[27] F. Rieke, D. Warland, R. de Ruyter van Steveninck and W. Bialek, *Spikes: Exploring the Neural Code*, MIT Press, Cambridge, MA, 1996.

[28] J. Ritt, *Evaluation of entrainment of a nonlinear neural oscillator to white noise*, Phys. Rev. E, 68, 041915–041921, 2003.

[29] F. Sagués, J.M. Sancho and J. García-Ojalvo, *Spatiotemporal order out of noise*, Rev. Mod. Phys., 79, 2007.

[30] M.N. Shadlen and W.T. Newsome, *The variable discharge of cortical neurons: implications for connectivity, computation, and information coding*, J. Neurosci., 18, 3870–3896, 1998.

[31] G. Shepard, *The Synaptic Organization of the Brain*, Oxford Univ. Press, 2004.

[32] S. Strogatz, *Exploring complex networks*, Nature, 410, 268–276, 2001.

[33] J. Teramae and T. Fukai, *Reliability of temporal coding on pulse-coupled networks of oscillators*, arXiv:0708.0862v1 [nlin.AO], 2007.

[34] J. Teramae and D. Tanaka, *Robustness of the noise-induced phase synchronization in a general class of limit cycle oscillators*, Phys. Rev. Lett., 93, 204103–204106, 2004.

[35] A. R. Uchida, R. McAllister, and R. Roy, *Consistency of nonlinear system response to complex drive signals*, Phys. Rev. Lett., 93, 2004.

[36] C. van Vreeswijk and H. Sompolinsky, *Chaos in neuronal networks with balanced excitatory*

and inhibitory activity, Science, 274, 1724–1726, 1996.

[37] T. Vogels and L. Abbott, *Signal propagation and logic gating in networks of integrate-and-fire neurons*, J. Neurosci., 25, 10786–10795, 2005.

[38] A. Winfree, *The Geometry of Biological Time*, Springer, New York, 2001.

[39] C. Zhou and J. Kurths, *Noise-induced synchronization and coherence resonance of a Hodgkin-Huxley model of thermally sensitive neurons*, Chaos, 13, 401–409, 2003.