# Pseudospectra and turbulence in a neural network

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## Abstract

The implementation of central pattern generators in spiking neurons requires that those neurons be capable of developing stable phase-locked patterns for regular breathing and locomotion. Previously, eigenvalue analysis has been used to develop a criterion for stability of phase-locked patterns in a ring of pulse-coupled oscillators (Dror et al 1999). In this work, I use the mathematical technique of pseudospectra to show that this criterion is incomplete - it fails in the limit of large numbers of neurons and relatively steep slopes of the phase-resetting curve. Specifically, the Jacobian matrix governing transition from one cycle to the next is nonnormal, so there is substantial transient divergence from the phase-locked solution before the network stabilizes. Even worse, I show that in the presence of noise, the phase-locked solution becomes progressively less likely as the number of neurons in the network increases.

## Introduction

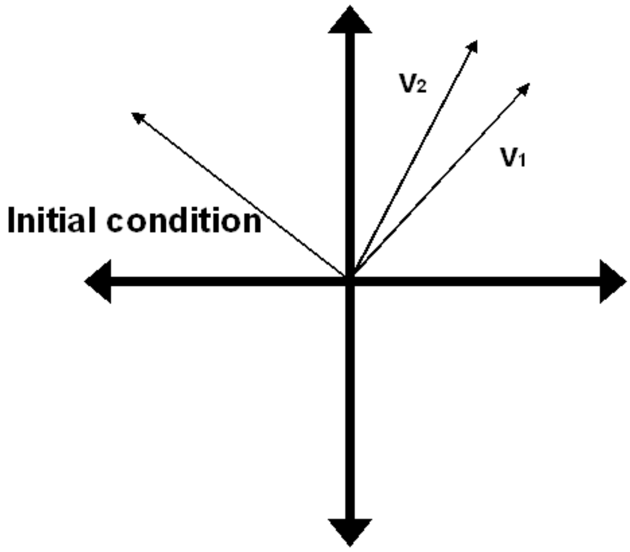
It has recently been recognized that eigenvalue stability analysis of nonnormal matrices does not take into account transient effects and may fail entirely in the presence of noise (Trefethen and Embree 2005). Pseudoeigenvalue analysis can help reconcile predictions from eigenvalue stability analysis with these transient effects, and has been applied to diverse fields, including hydrodynamics (Trefethen et al 1990), numerical analysis, and, recently, neuroscience (Goldman 2009; Murphy and Miller 2009). However, no one has applied the technique to synchronization in a network of neurons - a framework within which stability of patterns in the presence of noise is an essential requirement for successful function.

In order to develop an intuition for how transient effects can emerge that are not described by eigenvalue analysis, we turn to a version of an argument given in Murphy and Miller (2009; Supplementary material). The simplest definition of a nonnormal matrix is that it is a matrix for which the eigenvalue expansion:

$A = S\Lambda S^{-1}$

yields a set of eigenvectors (the columns of **S**) which are not orthogonal. In the extreme case given in Figure 1, we can see how the vector of initial conditions is represented poorly by the two eigenvectors, **v1** and **v2**, which must both have large magnitude. Now, consider what happens when one of these eigenvectors, **v1**, decays much more rapidly than **v2**, but both eventually decay to zero. That is, **v1** has a more negative (continuous time) or smaller (discrete time) eigenvalue.

We can see that for some k, then, that $\mathbf{A}^k$***Initial condition vector** increases before it decays to zero - that is the transient to which I referred earlier.




$$\mathbf{A}^k * \mathbf{v_1} = \lambda_1^k * \mathbf{v_1}$$
$$\mathbf{A}^k * \mathbf{v_2} = \lambda_2^k * \mathbf{v_2}$$

**Figure 1 - Explanatory figure showing how having non-orthogonal eigenvectors leads to transient phenomena. V1 and V2 are the two eigenvectors. Since they are not orthogonal, they must be very large and opposite sign to represent the initial condition - if the corresponding eigenvalues both decay but at different rates (for example, if they are 0.9 and 0.1, respectively), transient growth will be seen.**

To see the connection between nonnormality and the behavior of systems in the presence of noise, we must consider the meaning of the term pseudospectra. There are many equivalent definitions of pseudospectra - for our purpose, we will use the following definition:

> Definition 1: For a matrix A, the epsilon-pseudospectra refers to the set of points in the complex plane which could be eigenvalues of the matrix A+E, where the norm of E is less than epsilon.

We can think of the perturbation matrix **E** in physical terms as the noise that is present in addition to the idealized system **A**. If the epsilon-pseudospectra protrudes into the region of the complex plane that defines instability (the real part is greater than 0 for the continuous time case, or 1 for the discrete case), then our system will be unstable in the presence of noise of magnitude epsilon.

In hydrodynamics, the concept of turbulence can be modelled as the regime in which the eigenvalues (for a continuous time system) of the Navier-Stokes equations are greater than zero. Transition to turbulence from laminar flow therefore occurs at some particular Reynolds number. However, experimental observations of fluid dynamics showed that transition to turbulent flow occurs at Reynolds numbers for which stability is predicted by eigenvalue analysis. Trefethen et al (1990) resolved this contradiction using pseudospectral analysis by showing that the pseudoeigenvalues of the hydrodynamic system grow into the turbulent regime even when the eigenvalues predict stability. Therefore, in an experimental situation where some amount of noise is present, the real system is pushed into the turbulent regime for large Reynolds numbers.

The present work is essentially a mapping of the synchronization of pulse-coupled oscillators onto this hydrodynamics problem, where laminar flow corresponds to phase-locking and turbulence corresponds to irregular and unstable phase relationships between neurons. The eigenvalue analysis that I wish to call into question is the idea of Dror et al that a mathematical criterion for synchronization can be derived from eigenvalue analysis. There does not exist a clear correlate of the disagreement between experiment and theory, since no one has built a ring of tens or hundreds of neurons. However, the very lack of existence of such a ring may be precisely the experimental observation that disagrees with the theory - why do central pattern generators always consist of a few neurons in a ring if a larger ring is equally good at phase-locking? The best studied example of a larger ensemble (on the order of tens to hundreds) of neurons creating a central pattern generator is the pre-Botzinger cells that drive respiration - intriguingly, they use a recurrent architecture and not a ring architecture (Schwab et al 2008).

# Results

Dror et al (1999) give an explicit Jacobian matrix which describes the evolution of the difference between the relative phase for N neurons on a ring. In order to test whether there was some dynamics of this system that were not described by the eigenvalues, I first decided to plot the pseudoeigenvalues for a ring of 10 neurons (Figure 2a) using the freely available Matlab package EigTool (http://web.comlab.ox.ac.uk/pseudospectra/eigtool/). If the matrix were normal, the pseudospectra would be a set of concentric circles around the eigenvalues (black dots in Figure 2a). The real part of all eigenvalues is less than 1, confirming prior results showing that this matrix must be stable in the limit as time goes to infinity.

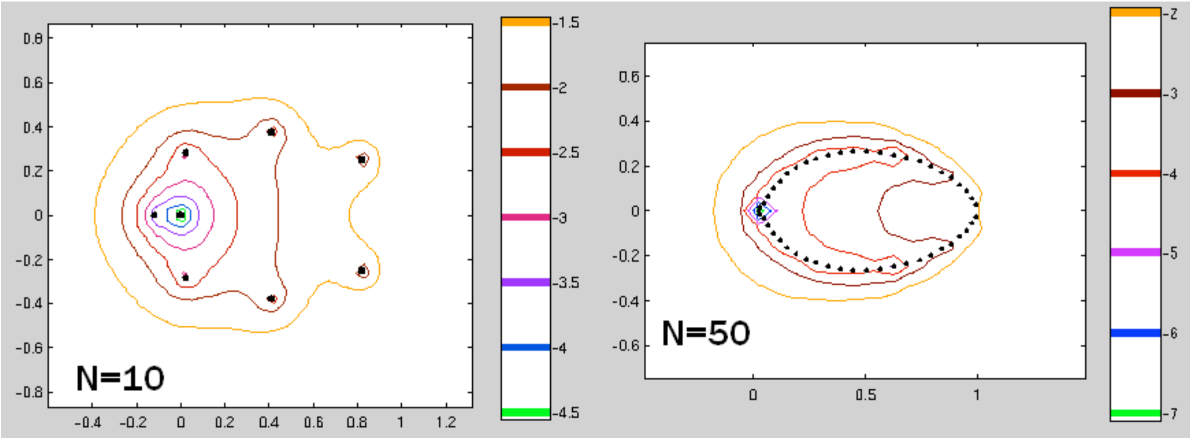



**Figure 2 Borders of pseudospectra for a ring of pulse coupled oscillators with phase resetting curve of slope 0.7.**

Figure 2b shows the corresponding matrix for N=50 neurons in a ring - it is clear from this figure that the pseudoeigenvalues for epsilon = $10^{-2}$ protrude into the part of the complex plane corresponding to instability (real part greater than 1). After noticing that the pseudospectral radius (area encompassed by the set of pseudospectra) appears to increase as a function of the number of neurons in the ring, I decided to plot the power bound (largest transient value of the norm of the matrix **A**, see Trefethen and Embree 2005 for discussion) of **A** as a function of the number of neurons in the ring (Figure 2). The power bound increases monotonically with N, and also with the slope of the phase resetting curve (m, Dror et al 1999).

If the power bound of the matrix grows with increasing N, then the time it takes the matrix to eventually decay to the stable phase-locked solution ought to increase as well. I observed just such a relationship in my numerical experiments, shown in Figure 3 for the same N=10 and N=50 rings shown in Figure 2. To generate these plots, I simply started with an initial vector of times relative to the phase-locked solution, and plotted the individual traces for the iterated matrix ($\mathbf{A}^k$) times a random initial conditions vector. Each color, then, represents a different neuron oscillating relative to its steady-state solution before eventually decaying. In physical terms, k represents a single iteration of the central pattern generator - 100 iterations, for a ring of 10 neurons, each with a period on the order of seconds, is on the order of tens of minutes.

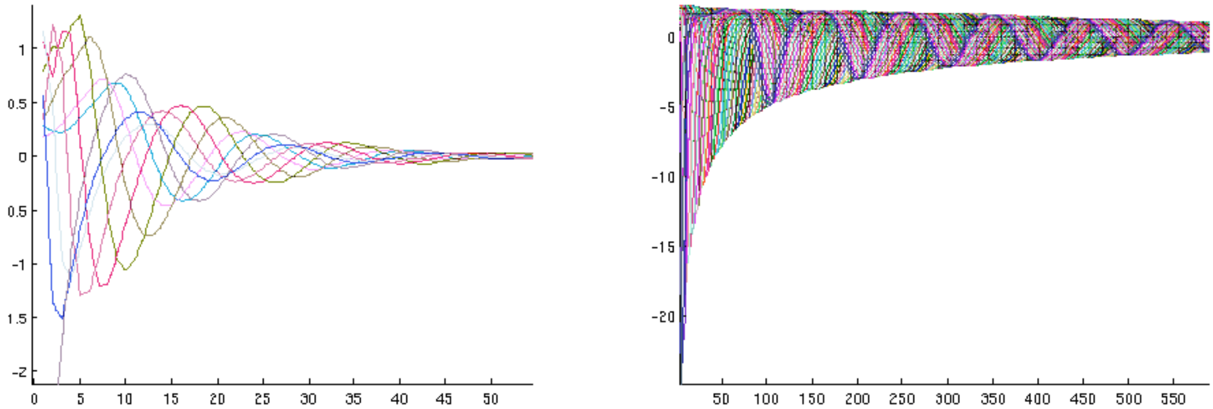


**Figure 3 - x-axis shows iterations (k), y-axis shows relative phase (deviation from steady state phase-locking) for N=10 (left) and N=50 (right) ring of pulse-coupled oscillators. The trajectory of each neuron's relative phase shows the transient growth and oscillatory activity before eventually decaying to 0.**

Presumably, a central pattern generator which took this long to settle down to a stable rhythm would be of limited adaptive utility. Actually, the problem with large rings of neurons is much worse, since the notions of transience and turbulence in the presence of noise are intimately related by the concept of nonnormality. The more nonnormal a matrix is, the less orthogonal its eigenvectors are, and the more likely to experience transient effects it is. At the same token, this will also lead to larger and more irregular sets of pseudoeigenvalues around the originally stable eigenvalues, so the system is more likely to experience turbulence when perturbed with noise (see definition 1).

Figure 4 demonstrates the close link between these concepts: I iterated the matrix **A** as in Figure 2, only this time I have added a Gaussian distributed random matrix **E** to **A** on each iteration [e.g., randn(N,N) in Matlab]. Example traces for the N=50 matrix are shown in 4a, b, and c for increasing values of the norm of **E**. The noise is apparent in Figure 4b, but it represents small perturbations from steady state which decay quickly. Figure 4c shows a qualitatively different pattern of activity - now the perturbations occasionally become amplified, leading to spikes of very large magnitude in the trace. What occurred when the norm of the perturbation matrix **E** went from $10^{-3}$ to $10^{-2}$ to cause this qualitatively different behavior? This behavior is predicted in Figure 2b, where the pseudospectra for N=50 neurons is plotted - the epsilon=$10^{-2}$ pseudospectra is the smallest plotted set that protrudes into the part of the complex plane corresponding to turbulence in the ring (real part greater than 1).

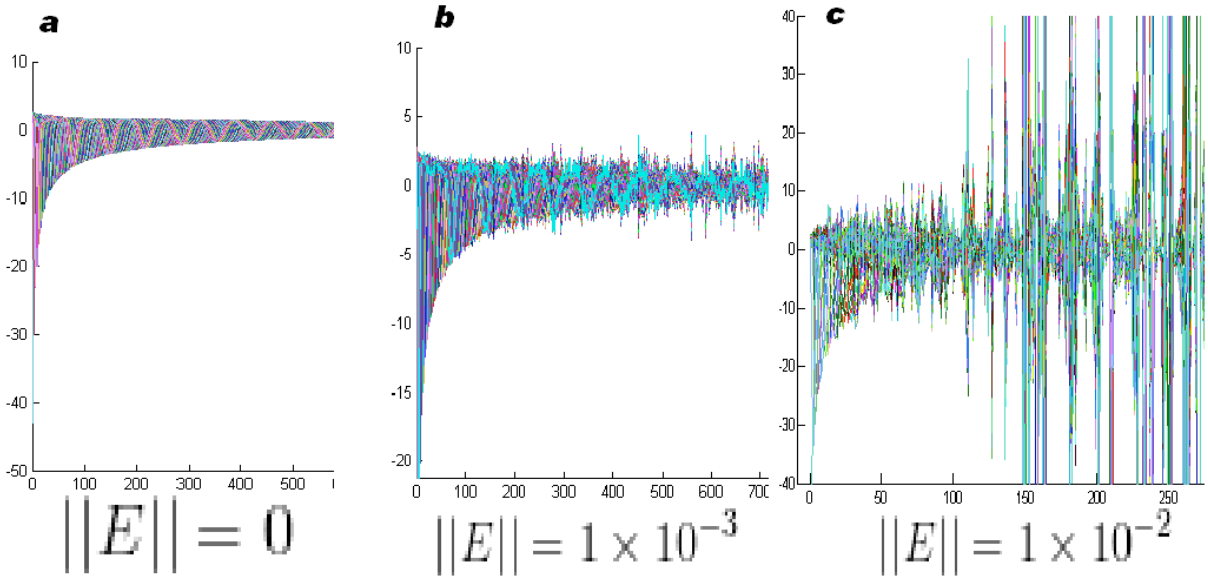



**Figure 4 - Matrix iterations times a random initial conditions vector as in Figure 3b for the N=50 ring, except that a random matrix with 2-norm as written is added to A on each iteration.**

In order to quantify the relationship between the slope of the phase resetting curve, the number of neurons, and the departure from normality, I calculated the largest transient observed for every ring between 3 and 100 at four slopes of the phase-resetting curve. Figure 5 shows that after 5 neurons, transient activity increases with the slope of the phase resetting curve. For all values of the phase resetting curve, the transient size increases with the number of neurons.

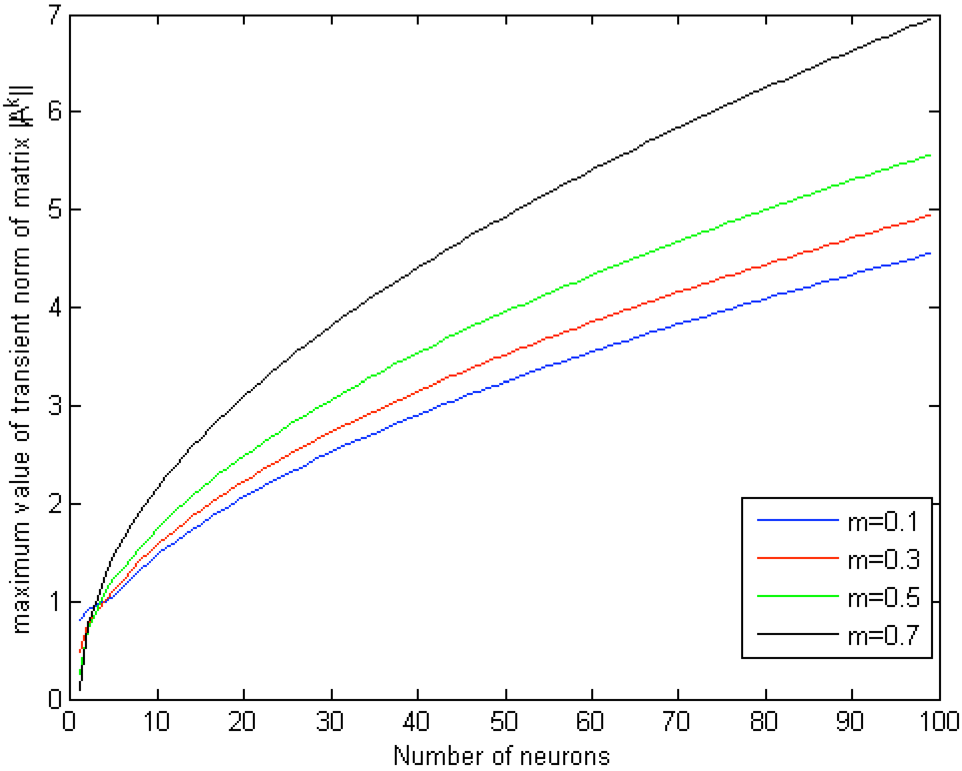



**Figure 5 - What is the correlate of the Reynolds number for pulse-coupled oscillators? Greater slope of the phase resetting curve and number of neurons on the ring both lead to greater departure from normality.**

Finally, I implemented a ring of Hodgkin-Huxley neurons with unidirectional inhibitory synapses (conductance was determined by an alpha function, which produced a roughly linear phase resetting curve with m=0.68). In the absence of noise, the ring phase-locked quickly (Figure 6a,b), even for a N=50 neurons. However, in the presence of an equal amount of noise, there was a substantial difference between smaller and larger rings. Examples from N=3 and N=10 neurons (Figure 6c,d) underscore this point - the N=10 neuron ring never relaxes to the hypothetically stable phase-locked solution. It is difficult to formulate the amount of noise in terms of the "epsilon" that it would correspond to, so I cannot confirm the very precise predictions of Figure 4 which relate pseudospectra to turbulence. However, Figure 6 is in qualitative agreement with the notion that larger rings of neurons will be less likely to phase lock in the presence of noise.

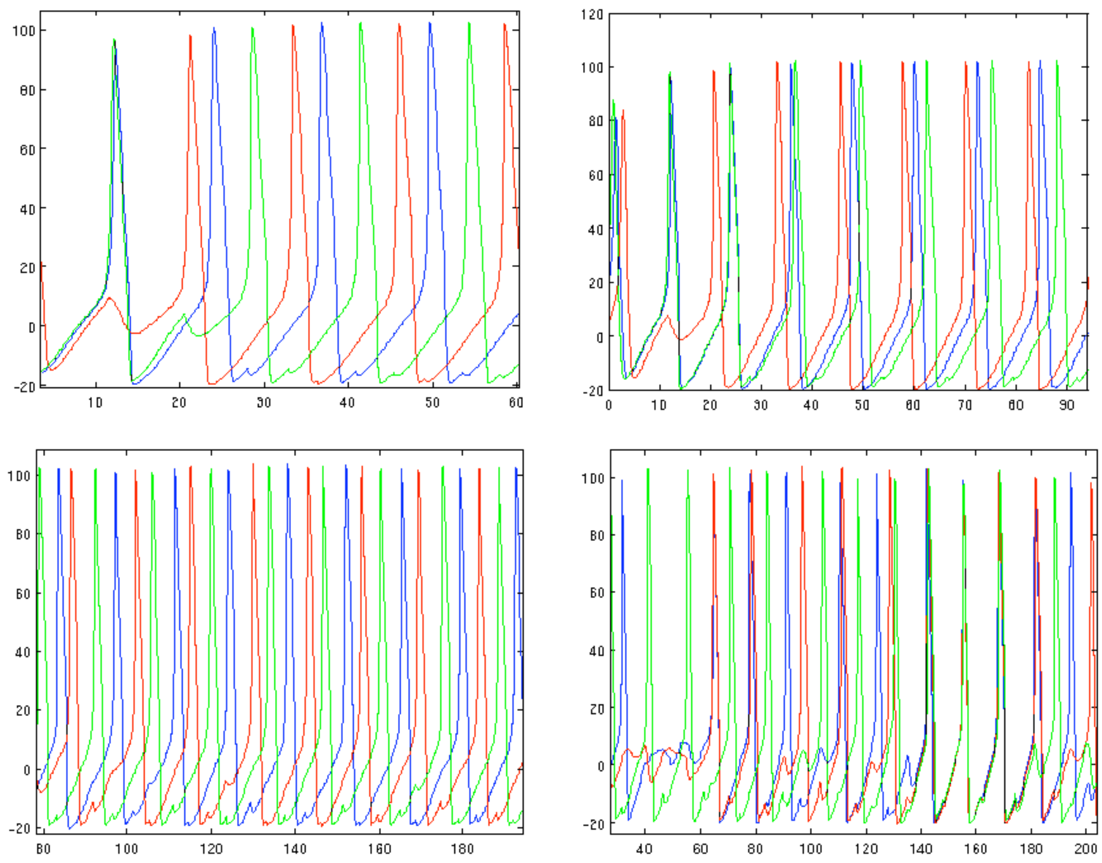


**Figure 6 - milliseconds vs. millivolts for neurons 1, 2, and 3 in a ring of (a, upper left) N=3, (b, upper right) N=50, (c, lower left) N=3, or (d,lower right) N=10 neurons. Upper traces (a,b) are in the absence of noise, lower traces (c,d) are in the presence of noise).**

# Discussion

This work represents the first application of the theory of pseudospectra to neurons with precise timing. I have used this technique to show how large rings of neurons are likely to be turbulent in the presence of noise, thus resolving a contradiction between theoretical predictions that larger networks should be equally stable and the lack of long central pattern generator loops in biological systems.

The work of Goldman (2009) and Murphy and Miller (2009) has shown how pseudospectral analysis can explain the persistence of activity in recurrent networks for time periods much longer than the time constants of the individual neurons in the network. These authors used an alternative to the eigenvalue decomposition, the Schur decomposition, to show how recurrent connectivity can actually hide fundamentally feedforward mechanisms in recurrent networks. However, these authors worked with rate-coding neurons, and did not attempt to study synchronization phenomena.

It would be interesting to apply the Schur decomposition to a large, recurrent network of phase-coupled oscillators - this might provide an explanation for how pre-Botzinger cells function as the central pattern generators for breathing despite not having an orderly ring architecture like the networks described here. Large rings, while mathematically tractable, are unlikely to robustly phase-lock in the presence of noise. It may therefore be possible to derive a unified theory relating connectivity to synchronization in central pattern generators despite superficial dissimilarities in organization using the framework developed here. This might have further implications for the stability of higher-level oscillatory patterns in cortex (Yuste et al 2005).

# References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