

Stochastic Neuroscience

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NOISY OSCILLATORS

Synchronous oscillations occur throughout the central nervous system. Recordings of population activity such as the electroencephalogram (EEG) and local field potential (LFP) often show a strong peak in the power spectrum in certain frequencies. This synchronous activity is sometimes observed across multiple recording sites and over distant brain areas. While local circuitry in the cortex is ideal for the production of local rhythms, the mechanisms for synchronization across different regions are more complex. Furthermore, the rhythms observed in real biological networks are not perfect oscillations. Instead, correlations between cells are often weak and the width of peaks in the power spectrum can also be quite broad. There are many reasons for this imperfect synchronization. Among them are heterogeneity in properties of individual neurons, heterogeneities in the connectivity between cells and their inputs, and finally, intrinsic noise (due, e.g. to channel fluctuations as well as the aforementioned heterogeneities). The goal of this chapter is to analyze the role of noise in synchronizing and desynchronizing coupled oscillators using a particularly simple class of model oscillators.

There is a long history of the study of noise in oscillators, going back to the work of Stratonovich (35; 36) where the interest was on how noise could disrupt oscillatory radio circuits. Our focus in this chapter concerns how noise affects neural oscillators, both in isolation and when coupled to each other. Furthermore, we will mainly consider the behavior when the noise and coupling are small and the oscillators are nearly identical. This allows one to significantly reduce the dimensionality of the problem and treat each oscillator as a single variable coding its phase. In other chapters of this book (notably Longtin), the effects of larger noise will be studied on systems which may not even intrinsically oscillate (coherence resonance).

The overall organization of this chapter is as follows. First we consider the general question of perturbed oscillators and introduce the phase resetting curve. We then look at how correlated noise can serve as a synchronizing signal for uncoupled oscillators. We study how noise can desynchronize coupled oscillators. We first study a pair and then a large network of globally coupled oscillators using population density methods.

1.1 The phase resetting curve & weak perturbations.

1.1.1 Preliminaries.

Many authors (particularly in physics) define an oscillator to be any dynamical system which makes repeated (although not necessarily predictable) transits

through some local region in phase space. For example, chaotic systems are often called oscillators. In this chapter, we confine our attention to systems in which there is an underlying attracting limit cycle, $X_0(t)$ such that $X_0(t+T) = X_0(t)$. We suppose that this satisfies an ordinary differential equation:

$$\frac{dX}{dt} = F(X(t)) \quad (1.1)$$

All autonomously generated limit cycles have an arbitrary phase associated with them. Thus, let us define the phase of the limit cycle to be t modulo T , with $t = 0$ defined as some identifiable point on the cycle. Since our main examples come from neuroscience, the 0 phase, is often defined as the time of the spike. Thus a rhythmically firing neuron produces spikes at multiples of T . Now, suppose that we add to this a possibly noisy, time dependent perturbation, which is “weak” in the sense that it does not destroy the overall shape of the limit cycle. Formally, the limit cycle attractor is a closed orbit in phase space and there is a local tubular neighborhood of the cycle in which all points of this neighborhood are attracted to the limit cycle with a well-defined asymptotic phase. The perturbation should be small enough so as not to leave this neighborhood. In practice, it can be quite large. Since each point in the neighborhood has a well-defined phase, there are curves called *isochrons* which parametrize the phase of every point on the limit cycle (20; 22; 43; 17). Figure 1.1A shows a neighborhood (dashed ellipses) around a limit cycle with the zero phase, $\theta = 0$ defined to be the maximum in the horizontal direction. Phase increases at a constant rate in the counterclockwise direction. The curve passing through $\theta = 0$ is the 0-phase isochron. Any points on this curve will asymptotically approach the unshifted oscillator. Consider a brief (instantaneous) stimulus in the horizontal direction occurring at phase ϕ . The perturbation will cause the dynamics to leave the limit cycle, but, if it is sufficiently small, it will remain in a neighborhood where the asymptotic phase is defined. Figure 1.1A shows that the perturbation moves the limit cycle from its current phase, ϕ to a new phase, $\hat{\phi}$. The mapping from ϕ to $\hat{\phi}$ is called the phase transition curve (PTC). The net change in phase is the phase resetting curve (PRC), $\Delta(\phi) := \hat{\phi} - \phi$. Note that in this example, the change in phase is negative and the time of the next maximum will be delayed. An alternate way to look at the PRC is through the spike (or event) time. Figure 1.1B shows how the PRC is constructed in this manner. The perturbation is given at phase ϕ producing the next spike/event at a time \hat{T} . The PRC is then, $\Delta(\phi) := T - \hat{T}$. As above, in this example, the next spike is delayed so PRC at this value of phase is negative. We should remark that the PRC is often defined in terms of a phase between 0 and 1 or 0 and 2π . In this case, one only needs to divide by the period T and multiply by 2π . We prefer to work using the real time of spike, but it doesn't matter.

In the above geometric example, the perturbation was a horizontal kick; of course, there could also be a vertical kick which would give a PRC in the y -direction. If the kicks are small, then the effects add linearly, so that we can

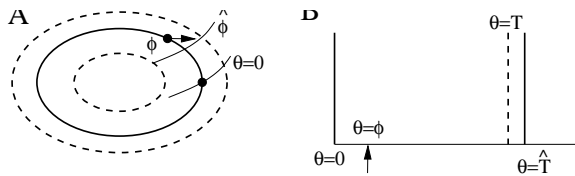


FIG. 1.1. (A) Definition of the phase of an oscillator. Isochrons for $0, \hat{\phi}$ are shown; (B) defining the phase resetting curve.

regard the actual PRC as a vector quantity corresponding to small perturbations in each of the n -directions of an n -dimensional dynamical system. If we parametrize the j^{th} component of the PRC by the amplitude of the perturbation, a_j , where a_j has the dimensions of the given quantity, e.g. voltage for membrane deflections or millimolar for, say, calcium perturbations, then we can define:

$$Z_j(t) = \lim_{a_j \rightarrow 0} \frac{\Delta_j(t, a_j)}{a_j} \quad (1.2)$$

which is called the *adjoint* for the limit cycle; it is also called the infinitesimal PRC. The adjoint is the unique periodic solution to:

$$\frac{dZ}{dt} = -D_X F(X_0(t))^T Z(t) \quad (1.3)$$

such that $Z(t)^T X'_0(t) = 1$. (Here $D_X F(X_0(t))$ is the linearization of $F(X)$ with respect to X evaluated at $X_0(t)$ and $Z(t) := (Z_1(t), \dots, Z_n(t))$.) $Z(t)$ can also be defined geometrically. In figure 1.1A, every point in the dashed region can be assigned an asymptotic phase; let $Q(Y)$ be the asymptotic phase of any point Y in the dashed region. Then, $Z(t) = \nabla_X Q(X_0(t))$; that is, Z is the gradient of the asymptotic phase with respect to the vector field evaluated along the limit cycle. This geometric definition is quite intuitive and matches precisely with equation (1.2), when the reader recalls the definition of the derivative. The advantage of equation (1.3) is that it enables us to calculate $Z(t)$ numerically by solving a linear ODE. Experimentalists measure the PRC in the direct manner illustrated in figure 1.1B; by delivering brief perturbations and measuring the phase shift (32) As we will see in the next sections, the PRC is to limit cycles what the linearization is to fixed points and tells us how the timing of spikes is altered by perturbations.

We close this section with a short discussion on PRCs since they are so important. Figure 1.2 shows some PRCs from a variety of CNS neurons. In each case the zero phase corresponds to the time of the spike. One property which is quite common among neurons is that the PRC vanishes at $0, T$ corresponding to the times of the spikes. Another aspect of PRCs is that for some cells they are strictly non-negative while others have a negative region which always occurs right after the spike. Several authors have noted that these shapes can be

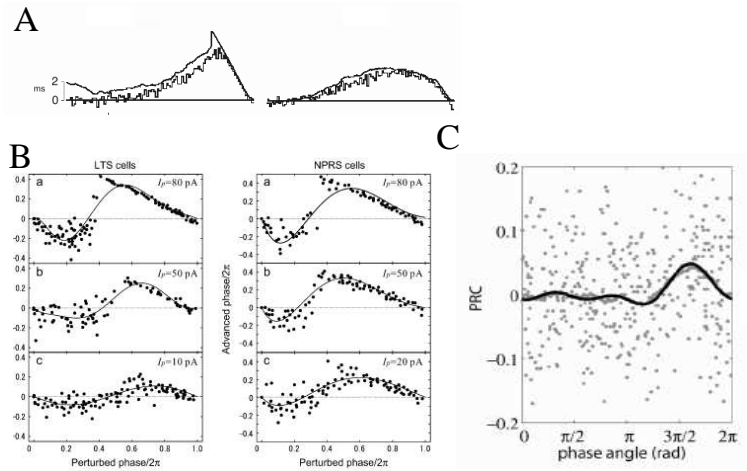


FIG. 1.2. PRCs from different neurons (A) Gutkin et al (18), (B) Tateno et al (39); (C) Galan et al (12). (Note that the axes are either between 0 and 1 or 0 and 2π depending on the conventions of the authors.)

loosely matched to different bifurcations (9; 19; 2). Specifically, the PRC near a saddle-node on a limit cycle (SNIC) (the so-called theta model or quadratic integrate and fire model) has the form $\Delta(t) = K(1 - \cos 2\pi t/T)$ while near a Hopf bifurcation, the PRC has the form $\Delta(t) = K \sin 2\pi t/T$. Thus, in many of the examples we discuss, we will use different variants of these PRCs. In particular, a nice parameterization has the form

$$\Delta(t) = \frac{\sin(t + \alpha) - \sin(\alpha)}{\sqrt{\pi(2 - \cos 2\alpha)}} \quad (1.4)$$

which has an L^2 norm of 1. By varying α , we can smoothly transition from the PRC associated with the Hopf to that associated with the SNIC.

1.1.2 Perturbations.

We now add a small perturbation to equation (1.1):

$$\frac{dX}{dt} = F(X(t)) + \epsilon G(X(t), t). \quad (1.5)$$

Here $0 < \epsilon \ll 1$ is a small parameter. Since the perturbation is small, we expect that solutions will stay close to the stable limit cycle attractor and thus there is a well-defined notion of phase. If we introduce the phase variable, $\theta(t)$ and write $X(t) = X_0(\theta(t)) + Y(t)$ where $Y(t)$ represents coordinates orthogonal to the limit cycle, then

$$X_0'(\theta(t)) \frac{d\theta}{dt} + \frac{dY}{dt} = F(X_0(\theta(t))) + D_X F(\hat{X}(t)) Y(t) + \epsilon G(X_0(\theta) + Y(t), t)$$

where \hat{X} is close to X_0 and X . If we multiply this equation by $Z(t)^T$, we obtain

$$\frac{d\theta}{dt} = 1 + Z(t)^T[-Y'(t) + D_X F(\hat{X}(t))Y(t)] + \epsilon Z(t)^T G(X_0(t) + Y(t), t).$$

(Note that we have used the fact that $Z(t)^T X_0(t)' = 1$.) This is an *exact* equation for the evolution of the phase; it is not an approximation. However, it still involves $Y(t)$ and $\hat{X}(t)$ which are unknown. Note also, that we have not used the smallness of ϵ except to assume that the perturbation remains in a region for which phase is defined. If ϵ is small, $Y(t)$, too, will be of order ϵ and \hat{X} will be close to X_0 . We will exploit this to obtain an approximate equation for the phase. The linear operator, $L(t)Y := -Y' + D_X F(X_0(t))Y$ has a one dimensional nullspace spanned by $X_0'(t)$ and its adjoint (under the usual inner product for periodic systems) has a nullspace spanned by $Z(t)$. Thus, with the approximation $\hat{X} \approx X \approx X_0$, we obtain the self-contained phase model:

$$\frac{d\theta}{dt} = 1 + \epsilon Z(\theta)^T G(X_0(\theta), t). \quad (1.6)$$

This is the main equation of this chapter and we will use it to analyze the effects of noise and coupling of oscillators. We note that in the case of neuronal models, the perturbations are typically only through the somatic membrane potential so that the all but one of the components of G are zero and we can more conveniently write

$$\theta' = 1 + \epsilon \Delta(\theta)g(\theta, t). \quad (1.7)$$

Remarks.

1. If the perturbation is a white noise, then we have to be a bit more careful and make sure we interpret this process correctly since the normal changes of variables that we take need to be adjusted in accordance to the rules of stochastic calculus (33). Thus, if the perturbation is white noise, then the correct version of (1.7) is (40):

$$d\theta = [1 + \epsilon^2 \Delta'(\theta)\Delta(\theta)/2]dt + \epsilon \Delta(\theta)dW(t) \quad (1.8)$$

where $dW(t)$ is a zero mean unit variance Gaussian.

2. The perturbations incorporated in G in equation (1.5) could be the effects of other oscillators to which our example oscillator is coupled via, e.g., synapses or gap junctions. We will consider this in later sections.

1.1.3 Statistics.

In this section, we derive equations for the mean and variance of the interspike interval for noisy oscillators as well as show that the variance of the phase-resetting curve is phase-dependent. We first consider the nonwhite case for which the perturbation is zero mean:

$$\theta' = 1 + \epsilon \Delta(\theta)\xi(t).$$

Here $\xi(t)$ is the “noise.” We look for a solution of the form: $\theta(t) = t + \epsilon\theta_1(t) + \epsilon^2\theta_2(t) + \dots$ and obtain:

$$\theta_1(t) = \int_0^t \Delta(s)\xi(s) ds.$$

Similarly,

$$\theta_2(t) = \int_0^t \int_0^s \Delta'(s)\Delta(s')\xi(s)\xi(s') ds ds'.$$

The unperturbed period is T , so that we want to find the value of t^* such that $\theta(t^*) = T$. Thus, we expect $t^* = T + \epsilon\tau_1 + \epsilon^2\tau_2 + \dots$, which results in

$$\tau_1 = - \int_0^T \Delta(s)\xi(s) ds$$

and

$$\tau_2 = -\Delta(T)\xi(T)\tau_1 - \int_0^T \int_0^s \Delta'(s)\Delta(s')\xi(s)\xi(s') ds ds'.$$

Let $C(t) := \langle \xi(0)\xi(t) \rangle$ be the autocorrelation function for the noisy perturbation (which we assume is stationary with zero mean). We see that the expected period of the oscillation is just

$$\bar{T} = T + \epsilon\langle \tau_1 \rangle + \epsilon^2\langle \tau_2 \rangle.$$

To order ϵ , there is no effect of the signal since the mean of τ_1 is zero. However, there are second order effects:

$$\langle \tau_2 \rangle = \Delta(T) \int_0^T \Delta(s)C(s-T) ds - \int_0^T \int_0^s \Delta'(s)\Delta(s')C(s-s') ds ds'. \quad (1.9)$$

The variance (to order ϵ^2) is

$$\text{var} = \epsilon^2\langle \tau_1^2 \rangle = \epsilon^2 \int_0^T \int_0^T \Delta(s)\Delta(s')C(s-s') ds ds'. \quad (1.10)$$

For a simple low-pass filtered white noise process (Ornstein-Uhlenbeck), $C(t) = \exp(-|t|/\tau)/2$ so that these integrals can be readily evaluated for simple PRCs such as (1.4).

Figure 1.3 shows some numerical as well as analytical results on the effects of the noise color on the statistics of weakly perturbed oscillators. As noted above, there is a weak effect on the mean period of the oscillator for colored noise as seen in figure 1.3A that is well-accounted for by the theoretical expression in equation (1.9). For a purely sinusoidal PRC, there is a “resonance” in the variance as a function of the noise color. That is, the variance has a maximum when the temporal correlations are proportional to the period of the oscillator as seen by the width of the histograms in figure 1.3B. Using equation (1.10), we can make this more explicit by evaluating the double integrals. Figure 1.3C

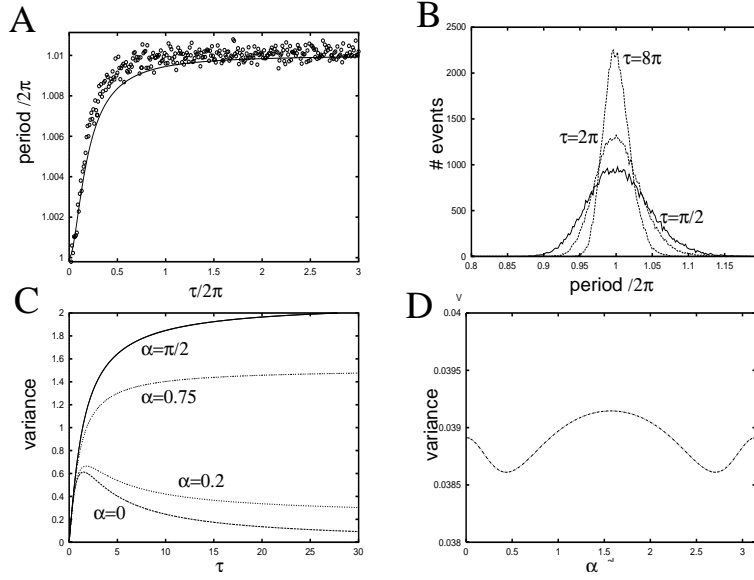


FIG. 1.3. Statistics of a single noisy oscillator as the shape of the PRC varies (α) and the temporal correlation of the noise changes (τ). (A) Mean value of the period for the PRC model, $\Delta(t) = \sin t$ as the correlation time, τ varies for $\epsilon = 0.2$ along with the theoretical value from equation (1.9). (B) Histograms of the period of the oscillator for 10000 firings and different values of τ . (C) Variance from equation (1.10) for different shapes of the PRC (using (1.4)) as a function of the noise color. (D) Variance as a function of α for $\epsilon = 0.2$ and white noise.

clearly shows a resonance in the variance (here we have scaled out ϵ^2) for PRCs that are nearly sinusoidal (cf equation (1.4) with α small). However as the PRC becomes more like the SNIC case, α near to $\pi/2$, this resonance is lost and the variance increases monotonically with the correlation time, τ . We remark that the PRC for the integrate and fire neuron is strictly positive and shows the same monotonic behavior of variance with respect to noise color. The key feature shared by both the SNIC and the integrate-and-fire PRCs is the large 0-mode Fourier component. The pure sinusoidal PRC lacks this component.

The case of white noise is more straightforward and does not require perturbation theory since we can write explicit equations for the mean first passage time, T_1 and second moment, T_2 (33):

$$-1 = [1 + \epsilon^2 \Delta'(t) \Delta(t)] T_1' + (\epsilon^2/2) \Delta(t)^2 T_1'' \quad (1.11)$$

$$-2T_1 = [1 + \epsilon^2 \Delta'(t) \Delta(t)/2] T_2' + (\epsilon^2/2) \Delta(t)^2 T_2''. \quad (1.12)$$

Here we assume that $\Delta(t)$ is 1-periodic. These equations have to be solved with the appropriate boundary conditions, which are found by setting $t = 0$ and

exploiting the fact that $\Delta(0) = 0$, thus, $T_1'(0) = -1, T_1(1) = 0$ and $T_2'(0) = -2T_1(0), T_2(1) = 0$. The mean period is $T_1(0)$ and the variance is $T_2(0) - T_1(0)^2$. Explicit expressions for these quantities could be found (?), but they involve integrals that are not readily evaluated. Instead, we can solve the boundary value problem by shooting or some other technique and compute how the variance depends on shape of the PRC. Figure 1.3D shows this dependence for $\epsilon = 0.2$. The variance remains less than would be the case for a constant PRC ($\text{var}=\epsilon^2 = 0.04$) and is maximal when $\alpha = \pi/2$ corresponding to the SNIC bifurcation.

As a last look at statistics, we can study the effect of noise on the actual calculation of the phase resetting curve. In particular, we consider the following simple model:

$$\frac{d\theta}{dt} = 1 + [\epsilon\xi(t) + \beta\delta(t - \phi)]\Delta(\theta) \quad (1.13)$$

which represents the noise $\xi(t)$ along with a Dirac delta function perturbation for the PRC. Here ϕ is the time of the perturbation and lies between 0 and T , the period. The net gain in phase given $\theta(0) = 0$ is found by evaluating $\theta(T)$. In absence of any stimuli (noise or experimental perturbations), $\theta(T) = T$. For a completely noise-free system, $\theta(T) = T + \beta\Delta(\phi)$ so that the gain (or loss) in phase is just $\theta(T) - T = \beta\Delta(\phi)$ as it should be; the PRC of the noise free system should be proportional to $\Delta(\tau)$. With noise, $\theta(T)$ is a random variable. Using perturbation theory, it is possible to show that the mean value of $\theta(T)$ is the same as the noise-free case, but that the variance is phase-dependent. In fact, we have shown (unpublished work) that for white noise:

$$\text{var}(\phi) = \epsilon^2 \left([1 + \beta\Delta'(\phi)]^2 \int_0^\phi \Delta^2(s) ds + \int_\phi^T \Delta^2(s + \beta\Delta(\phi)) ds \right). \quad (1.14)$$

That is, the variance is phase-dependent. Figure 1.4 shows the phase-dependence of the PRC for two different phase models. Solid lines are equation (1.14) and points are from Monte Carlo simulations of 1000 repetitions of an impulse at each phase point. Phase-dependence of the variance of the PRC was shown experimentally in several papers (28; 32; 18) and Ermentrout and Saunders (10) showed how this phase-dependence had interesting consequences for the synchronization of coupled oscillators. We revisit this point in section 3.

In conclusion, by using PRC theory and perturbation theory, we can study how various types of noise affect the regularity of spiking and how the properties of the PRC and the noise factor into these effects. Furthermore, we have provided an explanation for phase-dependence in the variance of the PRC.

1.2 Noise induced synchrony.

Suppose that we have a population of nearly identical oscillators which are uncoupled but receiving some kind of common input. A well-known example would be independent oscillators receiving common periodic input. E.g., most living organisms contain in internal clock with a period of about 24 hours which is locked

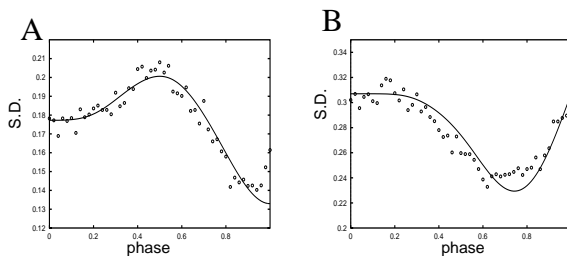


FIG. 1.4. Standard deviation (square root of the variance) of the PRC for (A) $\Delta(t) = \sin 2\pi t$ and (B) $\Delta(t) = 1 - \cos 2\pi t$. Here $\epsilon = 0.1$ and $\beta = 1/(8\pi)$.

to the light-dark cycle as the earth circles the sun. Thus, even though these oscillators are not directly coupled, the periodic drive they receive is sufficient for them to partially synchronize. Of course, the frequency of the periodic drive must match that of the individual oscillators in order for this to work. What is surprising is that the common signal received by the uncoupled oscillators need not be periodic.

Pikovsky and his collaborators were among the first to describe models and theory for the synchronization of dynamical systems to common noisy input (16; ?; 31). These authors look not only at oscillators but also at chaotic systems and other systems with complex dynamics. They have also shown that for strong noise, synchrony is disrupted. Jensen (21) studied an abstract phase model for oscillators receiving a common signal and Ritt (34) analyzed synchronization of a specific model (the theta model) to white noise. In this section, we will use phase response curves once again to explore synchrony when they are uncoupled but receive a common noisy input. The methods described here are close to those of Teramae and Tanaka (40).

Figure 1.5 shows an example of a synchronization due to a common input for two Hodgkin-Huxley oscillators. Voltages are plotted against time in the upper plots and against each other in the three-dimensional plot below. The cells are identical, uncoupled, and start with a phase difference of half a cycle. They are driven by weak white noise and after several cycles, the phase-difference disappears and the oscillators are completely synchronized. This phenomena is not restricted to neural *models*; Galan et al (13) demonstrated that filtered white noise stimuli could synchronize mitral cells in the olfactory bulb. This mechanism is called the Moran effect in ecology (8) and has also been suggested as a means to synchronize intracellular signalling oscillations (44). The goal in this section is to use phase models to study how noise can synchronize uncoupled oscillators. The mechanism for this type of synchronization is closely related to the issue of spike time reliability as first discussed by (5) and popularized by (45) To see the connection, suppose that we apply a constant current to a neuron to induce it to fire repetitively and mark the times of the spike. We repeat this experiment many times and create a histogram of the spike times. In a completely noise-

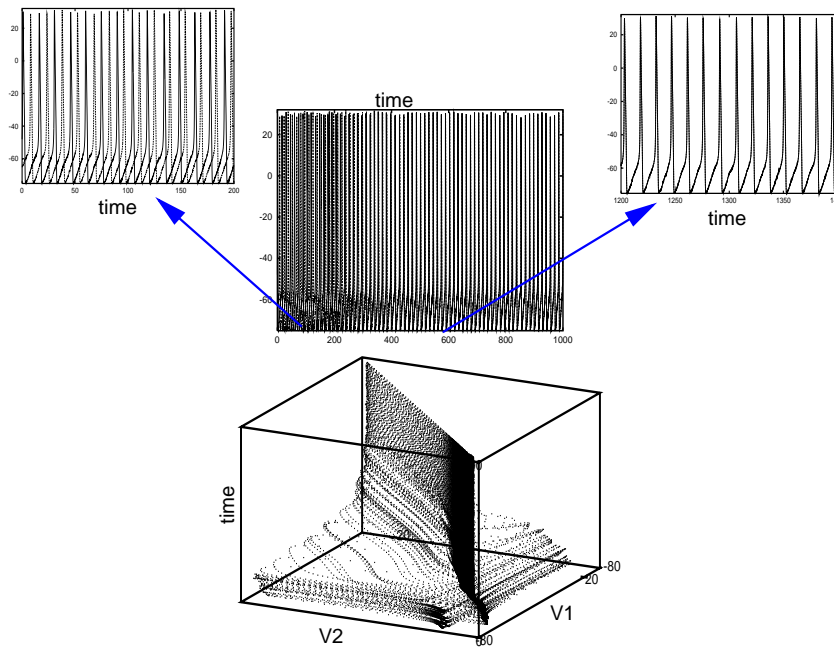


FIG. 1.5. White noise synchronization of two Hodgkin-Huxley oscillators. The oscillators are identical and start at different points in their cycle. Both receive an identical white noise stimulus. Time series and V_1 versus V_2 are shown.

free environment, the spikes will line up perfectly. However, if there is noise and it is uncorrelated from trial to trial, then as time progresses, spikes will occur less and less reliably. In contrast, suppose that in addition to the uncorrelated noise, there is a fast signal (e.g. correlated noise) common to each trial. With this background signal, both of the above experimental groups found that the spike times were considerably more reliable from trial to trial. Figure 1.6 shows an illustration of this effect with the Hodgkin-Huxley equations when there is just extrinsic noise and then when there is an additional signal on top. A single cell model is simulated for 100 trials with uncorrelated noise and starting from identical initial conditions. The right panel has an additional weak frozen white noise signal (it is the same for every trial and plays the role of a stimulus). The histogram of the spike times is much thinner around later spikes when there is a stimulus. The mechanism for reliability and for noise synchronization is the same. If the signal is such that the dynamics is an attractor, then initial data nearby will fall into the attractor induced by this stochastic force. As it is attractive, it is also robust against small enough perturbations, such as extrinsic noise. Brette (3;

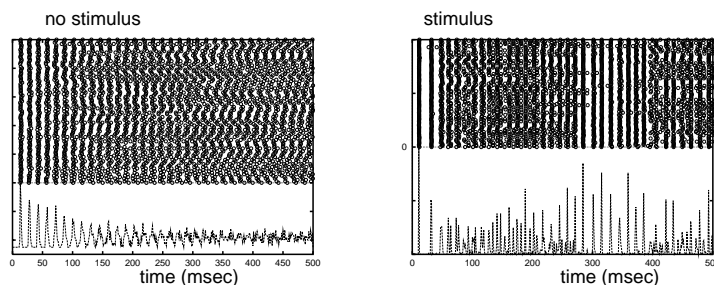


FIG. 1.6. Reliability in the Hodgkin-Huxley model. 100 trials of a constant current injection with uncorrelated noise (amplitude 1) with no stimulus and then with a common white noise stimulus (amplitude=15). Spike times and histograms (below) are shown.

4) analyzed these spike-time attractors for the integrate-and-fire model; Troyer (41) also analyzes these attractors in a context similar to that described here. We will formalize the notion of stability in the next several pages and introduce the so-called Lyapunov exponent.

1.2.1 White noise.

Pikovsky (30) was among the first to analyze synchronization to noise when he studied Poisson inputs. More recently, this work has been extended to white noise and to more general synchronization issues. We will follow Teramae and Tanaka for the white noise case and sketch the analysis for the Poisson case as well. We start with a single oscillator driven by white noise and reduced to a phase model. As our motive is to study neuronal oscillations, we will confine ourselves to the case when white noise appears only in the voltage equation. For any regular perturbations, equation (1.6) is valid, however, when the noise is white, we have to be careful and make the correct change of variables using the Ito stochastic calculus, so that we start with equation (1.8). Solutions to this equation have an invariant density found by solving the steady state Fokker-Planck equation:

$$0 = [(1 + D\Delta'(x)\Delta(x))\rho(x) + D(\Delta(x)^2\rho(x))']'$$

where $D = \epsilon^2/2$ and $\rho(x)$ is the invariant density; that is the probability that $\theta \in [a, b]$ is $\int_a^b \rho(x)dx$. This differential equation must be solved subject to $\rho(x)$ is periodic and $\int_0^T \rho(x) dx = 1$, the normalization. Solutions can be found by integrating or, since D is small, using perturbation theory. For our purposes, the invariant density is close to being uniform when D is small, so that we will approximate $\rho(x)$ by $1/T$. Consider two oscillators driven with the same white noise signal:

$$d\theta_1 = [1 + D\Delta'(\theta_1)\Delta(\theta_1)]dt + \epsilon\Delta(\theta_1)dW \quad (1.15)$$

$$d\theta_2' = [1 + D\Delta'(\theta_2)\Delta(\theta_2)]dt + \epsilon\Delta(\theta_2)dW.$$

We are interested in whether or not they will synchronize. That is, we would like to assess the stability of the state $\theta_2 = \theta_1$. We let $\theta_2 - \theta_1 = y(t)$ and thus study the variational equation which has the form

$$dy = [D\Delta'(\theta)\Delta(\theta)]'ydt + \epsilon\Delta'(\theta)y dW.$$

Here $\theta(t)$ satisfies equation (1.8). This is a linear SDE in $y(t)$ and we would like to solve it. Let $z(t) = \log y(t)$ be a change of variables. Then appealing to Ito's formula, we find that

$$dz = D[(\Delta'(\theta)\Delta(\theta))' - \Delta'(\theta)^2]dt + \epsilon\Delta'(\theta)dW.$$

This is now a standard stochastic equation and we can integrate it to obtain the mean drift in $z(t)$:

$$\lambda := D \lim_{t \rightarrow \infty} \int_0^t [(\Delta'(\theta(s))\Delta(\theta(s)))' - \Delta'(\theta(s))^2] ds.$$

This is the mean rate of growth of $y(t)$ so that if $\lambda < 0$, then $y(t)$ will decay and synchrony will be stable. The quantity, λ is called the Lyapunov exponent and since our system is ergodic, we obtain a simple expression:

$$\lambda = D \int_0^T [(\Delta'(x)\Delta(x))' - \Delta'(x)^2]\rho(x) dx.$$

Using the approximation that $\rho(x) \approx 1/T$ and the periodicity of $\Delta(x)$, we find

$$\lambda = -D \frac{1}{T} \int_0^T \Delta'(x)^2 dx. \quad (1.16)$$

This is the main result on the stability of synchrony with identical white noise stimuli. It was derived by Teramae and Tanaka (40) for the white noise case. What it tells us is that the details of the oscillator are irrelevant, the Lyapunov exponent is always negative for weakly forced oscillators.

As we began this section out by discussing reliability, it is interesting to relate reliability to the magnitude of the Lyapunov exponent. In (14) we show that the reliability (measured as the ratio of the cross correlation of the output and the auto-correlation) is

$$R = \frac{|\lambda|}{|\lambda| + c}$$

where $c \geq 0$ is the magnitude of the extrinsic noise which is uncorrelated between the neurons. Note that if $c = 0$, then reliability is 1, which is perfect. For small λ , reliability decreases which is why we generally want to maximize the magnitude of λ .

1.2.2 Poisson and colored noise.

Pikovsky (30) and others (26) have also studied the case of Poisson inputs. Let θ_n denote the phase of an oscillator right before the n^{th} impulse where the train of impulses obeys some type of distribution. Assume each has an amplitude ϵ and we obtain a model for the phase:

$$\theta_{n+1} = \theta_n + I_n + \epsilon\Delta(\theta_n) \quad \text{mod } T$$

where I_n is the time between impulses. As with the white noise case, it is possible to write an equation for the invariant density. Let $Q(I)$ denote the density function for the intervals, I_n modulo the period, T . (Thus, the support of Q is the interval $[0, T)$.) Then the invariant density for the phase θ , $\rho(x)$ satisfies the linear integral equation:

$$\rho(x) = \int_0^T Q[x - y - \epsilon\Delta(y)]\rho(y) dy.$$

(See (23; 10; 27).) In this case, the Lyapunov exponent satisfies:

$$\lambda_P = \int_0^T \log[1 + \epsilon\Delta'(x)]\rho(x) dx.$$

For ϵ small, $\rho(x)$ is nearly uniform and expanding in ϵ , we find the same expression for λ_P as for the white noise case.

We can use equation (1.6) for colored noise in order to study the stability of synchrony. As in the rest of this section, the single oscillator satisfies

$$\frac{d\theta}{dt} = 1 + \epsilon\Delta(\theta)\xi(t)$$

where $\xi(t)$ is a general process. The variational equation satisfies

$$\frac{dy}{dt} = \epsilon\Delta'(\theta(t))\xi(t)y(t)$$

and the Lyapunov exponent is

$$\lambda_\xi = \epsilon \lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t \Delta'(\theta(s))\xi(s) ds.$$

Using perturbation theory, as above, $\theta(t) = t + \epsilon \int_0^t \Delta(s)\xi(s) ds$ can be substituted into the equation for λ_ξ and obtain:

$$\lambda_\xi = \lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t \Delta''(s) \int_0^s \Delta(s')C(s-s') ds' ds \quad (1.17)$$

where $C(t)$ is once again the autocorrelation of the common noise. For low pass filtered noise and $\Delta(t)$ as in equation (1.4), we obtain:

$$\lambda_\xi = -\epsilon^2 \frac{1}{2\pi(2 - \cos 2\alpha)} \frac{\tau}{1 + \tau^2}.$$

This shows that the Lyapunov exponent shows “resonance” with respect to the PRC shape. For this model, the minimum occurs when $\tau = 1$. Figure 1.7A shows

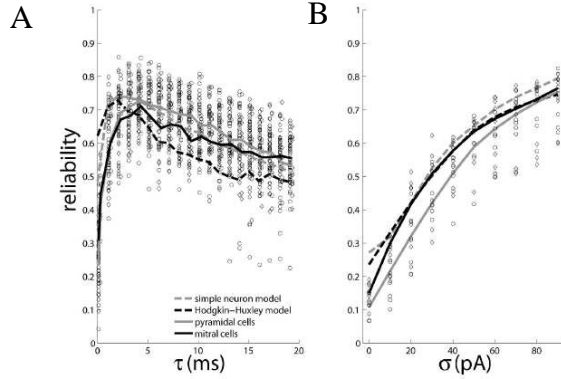


FIG. 1.7. Reliability of real and model neurons (from (14)). (A) Reliability is a nonmonotonic function of the correlation time of the signal for both real (mitral and pyramidal neurons) and model neurons. (B) Reliability increases monotonically with signal amplitude.

an experimental verification of the dependence of reliability on the correlation time of the signal, $\xi(t)$. Since reliability is a monotonic function of the Liapunov exponent, this shows that the above calculations hold in realistic settings for both real and model neurons. Reliability is also a monotonic function of the noise amplitude for a given correlation time as can be seen from 1.7B.

1.2.3 Heterogeneity and extrinsic noise.

In figure 1.5, we showed that perfectly correlated noise produces a perfectly synchronized state. How does this change in the presence of heterogeneities or in uncorrelated noise. Nakao et al (27) consider the white noise problem when there is a mixture of identical and uncorrelated noise. We can generalize that slightly to study the case when there is additionally heterogeneity in the natural frequencies of the oscillators. The generalization of equation (1.15) is

$$\begin{aligned} d\theta_1 &= [1 - \hat{\mu}/2 + (\epsilon^2/2)\Delta'(\theta_1)\Delta(\theta_1)]dt + \epsilon\Delta(\theta_1)(\sqrt{q}dW + \sqrt{1-q}dW_1) \\ d\theta_2 &= [1 + \hat{\mu}/2 + (\epsilon^2/2)\Delta'(\theta_2)\Delta(\theta_2)]dt + \epsilon\Delta(\theta_2)(\sqrt{q}dW + \sqrt{1-q}dW_2). \end{aligned}$$

where $\hat{\mu}$ is the difference in natural frequency and q is the fraction of shared noise. When $q = 1$, $\hat{\mu} = 0$, then the oscillators receive identical noise and have no intrinsic differences, in short, equation (1.15). Nakao et al develop an equation for the probability density function for the phase-difference, $\theta_2 - \theta_1$ for small ϵ when $\hat{\mu} = 0$. If we rescale $\hat{\mu} = \epsilon^2\mu$, then we can generalize their result and obtain the following equation for the density of the phase differences:

$$\left[\left(1 - c \frac{h(x)}{h(0)}\right) \rho(x) \right]' = K + \mu \rho(x) \quad (1.18)$$

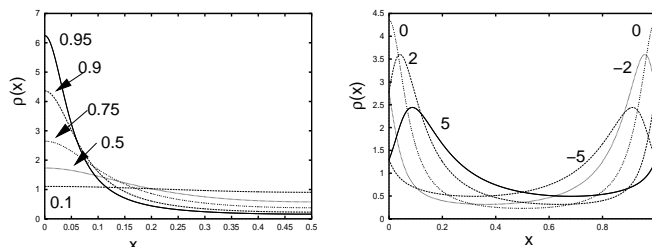


FIG. 1.8. The effect of heterogeneity on noise-induced synchrony. (A) Identical oscillators ($\mu = 0$) as the correlation, c varies. As the density is symmetric, only $x \leq 0.5$ is shown. $\Delta(x) = \sin 2\pi x$. (B) $c = 0.9$ and the frequency difference, μ between the oscillators varies.

where, $c = 2q/(1 + q)$ is the correlation,

$$h(x) := \int_0^T \Delta(x+y)\Delta(y) dy$$

and K is an arbitrary constant chosen so that $\rho(x)$ is periodic. An almost identical equation was derived by (26) for Poisson inputs. Integrating this equation over one period and using the normalization and periodicity, it is clear that $K = -\mu/T$. When $\mu = 0$, then the density of the phase differences is just

$$\rho(x) = \frac{N}{1 - ch(x)/h(0)}$$

with N a normalization constant. As $c \rightarrow 1$, this density approaches a delta function. The definition of $h(x)$ implies it is an even function so that in general, the density is symmetric around 0 and has a peak at 0. One could integrate (1.18) to get the general solution for different values of μ , but the formulae are not particularly insightful. Instead, we simply solve the resulting boundary value problem numerically. Figure 1.8 shows the effects of the two kinds of heterogeneity on the phase difference between oscillators. For $c = 0$ and weak noise, the density is flat. As c increases, the density becomes more and more highly peaked. (11; 26) showed that the degree of this sharpening depends a great deal on the shape of the PRC. However, the general shape of the distribution and the general trends are identical. Nakao et al showed more complex forms for the density when the noise in equation (1.5) was not simply additive. Figure 1.8B fixes the correlation at 90% and varies μ the difference in frequencies. For $\mu < 0$, oscillator 1 is faster than oscillator 2 and the density of $\theta_2 - \theta_1$ is skewed to the right as expected. For $\mu > 0$, the skew is opposite and oscillator 2 tends to lead oscillator 1. This is exactly what one would expect and is similar for coupled oscillators (see below).

In conclusion, in this section, we have shown that noise can induce synchronization between uncoupled oscillators when there are correlations. The rate and

degree of synchronization depends on the properties of the noise as well as the amount of the correlation. Understanding of this process can be reduced to the analysis of several integrals and the solutions to some linear boundary-value problems.

1.3 Pairs of oscillators

In the remainder of this chapter, we review the effects of coupling between oscillators. We start with weak coupling with noise and use this to discuss how noise has mild effects on coupling. Then we turn to pulse coupling with stronger noise.

1.3.1 Weak coupling.

As in the previous chapters, we begin with equation (1.6) which is the general equation for the effects of perturbations on an oscillator. We now split the perturbations into two parts, those that come from extrinsic noise and those that arise from coupling to other oscillators. That is, we write $G(X(t), t) = K_j(X_j(t), X_k(t)) + R_j(X_j(t), t)$ where $X_j(t)$ are the state variables for oscillators $j = 1, 2$ and K_j is the coupling and R_j is the noisy perturbation. Each oscillator obeys exactly the same dynamics, equation (1.1), when $\epsilon = 0$. While we could do this more generally, it is simpler to split the perturbations into the coupling and noise parts. From the point of view of neural applications, this makes sense as well. Finally, we will assume the noise is white and that the amplitude of the noise is such that the variance of the noise and the strength of the coupling match. Thus, we take the coupling strength to be ϵ and the noise strength to be $\sqrt{\epsilon}\sigma$, where $\sigma = O(1)$, so that they match. We thus obtain

$$d\theta_j = [1 + \epsilon(\Delta(\theta_j)B_j(\theta_j, \theta_k) + \sigma^2 \Delta'(\theta_j)/2)]dt + \sqrt{\epsilon}\Delta(\theta_j)dW_j. \quad (1.19)$$

The term, B_j represents the voltage component of the coupling, which will generally be some type of synaptic interaction between neurons either electrical or chemical. We will not go through all the different cases and how the time courses of synapses and their position as well as the shape of the PRC effect the way neurons interact. This, in itself, is a topic for an entire book or at least a lengthy chapter. Our main goal in this chapter is to see how noise affects the interactions and not what the interactions themselves do. Furthermore, in this section, all noise is uncorrelated. (However, the interactions between correlated noise and coupling are fascinating and the subject of some current research.) We let $\theta_j = t + \psi_j$ be a change of variables and this leads to:

$$d\psi_j = \epsilon\Delta(t + \psi_j)[B_j(t + \psi_j, t + \psi_k) + \sigma^2 \Delta'(t + \psi_j)/2]dt + \sqrt{\epsilon}\Delta(t + \psi_j)dW_j.$$

We average this equation over t to obtain an effective coupling equation:

$$d\psi_j = \epsilon H_j(\psi_k - \psi_j)dt + \sqrt{\epsilon} \|\Delta\|_2 dW_j \quad (1.20)$$

where

$$H_j(\phi) := \frac{1}{T} \int_0^T \Delta(t) B_j(t, t + \phi) dt$$

and $\|\Delta\|_2$ is the L_2 -norm of the PRC. We take this to be 1 without loss of generality. We can now drop the ϵ as we can rescale time. Finally, we let $\phi = \psi_2 - \psi_1 = \theta_2 - \theta_1$ and have now reduced the initially $2n$ -dimensional noisy dynamical system to a single scalar stochastic differential equation:

$$d\phi = [H_2(-\phi) - H_1(\phi)]dt + \sigma dW \tag{1.21}$$

where dW is a white noise process. (We use the fact that the difference between two uncorrelated Gaussian processes is also Gaussian.) This Langevin equation is readily solved and the stationary density function for the phase-difference, $\rho(\phi)$ satisfies:

$$K = -[H_2(-\phi) - H_1(\phi)]\rho(\phi) + \frac{\sigma^2}{2}\rho'(\phi)$$

where K is a constant chosen so the solutions are periodic and the density function ρ has a unit integral. At this point, it is convenient to rewrite the drift term. Suppose that the coupling between oscillators is identical (symmetric) and that the only difference in the two oscillators is in their natural frequencies (as in the previous section). We write

$$H_2(-\phi) - H_1(\phi) := -q(\phi) + \mu$$

where $q(\phi)$ is twice the odd part of the coupling function and μ is the difference in natural frequencies.

For simplicity, we assume that the period is 1. Without noise, the dynamics reduces to

$$\frac{d\phi}{dt} = -q(\phi) + \mu.$$

Since q is an odd periodic function, it always has zeros at $\phi = 0$ and at $\phi = 1/2$ corresponding to the synchronous and anti-phase solutions respectively. Thus, when $\mu = 0$, there are at least two phase-locked fixed points, synchrony and anti-phase. If $q'(0) > 0$ then synchrony is stable and if $q'(1/2) > 0$, anti-phase is stable. For small values of μ , the fixed points persist and are near 0 or 1/2. However, any continuous periodic function is bounded, so that for sufficiently large values of μ , there will be no fixed point and thus no phase-locked solutions. The noise-free system no longer has a steady state. However, the phase difference does have an invariant density:

$$\rho(\phi) = \frac{N}{\mu - q(\phi)}$$

where N is a normalization constant. Note that this is only valid when $\mu - q(\phi)$ has no zeros; otherwise the oscillators will phase-lock and the density is a sum of Dirac delta functions.

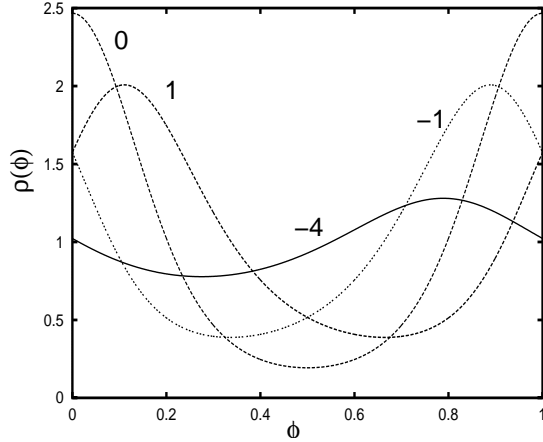


FIG. 1.9. Probability density function for the phase-difference between a pair of oscillators when $\sigma = 0.5$ and $q(\phi) = \sin 2\pi\phi$ for different degrees of heterogeneity, μ .

If $q(\phi)$ is odd (as will be the case with symmetric coupling between identical oscillators) and there are no frequency difference, $\mu = 0$, then we can write down a closed form solution for the probability distribution in the presence of noise:

$$\rho(\phi) = N \exp \left[\frac{-2Q(\phi)}{\sigma^2} \right]$$

where $Q(\phi) = \int_0^\phi q(s) ds$. Since q is odd, Q is periodic. Here N is just a normalization constant. Stable roots of $q(\phi)$ (that is, where $q'(\phi) > 0$) correspond to local maxima in density function and unstable roots correspond to local minima. With heterogeneity, the peak of the density function is shifted as would be expected from the noise-free case. That is, if oscillator 1 is faster than oscillator 2, then $\mu < 0$ and the noise-free phase-locked value of ϕ is negative, thus, the peak of the density function in the presence of noise is shifted to the left. Figure 1.9 shows how heterogeneity both moves the peak and makes the distribution more uniform.

1.3.2 Correlations.

Neuroscientists cannot generally measure phase-differences between two coupled neurons. However, they can measure the correlation between spike trains of neurons. Pfeuty et al (2005) showed that there is a relationship between the spike train cross correlogram and the density function. Suppose that each time $\theta_j(t)$ crosses zero modulo the period, we will say that a spike has occurred. We break continuous time into a discrete set of bins of width w and let $S_j(t)$ be $1/w$ if

there is a spike the bin corresponding to t and zero otherwise. The normalized cross correlation is

$$C(t_2 - t_1) := \frac{\langle S_1(t_1)S_2(t_2) \rangle}{\langle S_1(t) \rangle \langle S_2(t) \rangle}.$$

Here $\langle S(t) \rangle$ is the average of $S(t)$. Pfeuty et al (29) show that as w gets small,

$$C(\tau) \approx \rho(\tau).$$

Thus, there is simple relationship between the cross-correlation (to lowest order) and the density function of the phase-difference.

1.3.3 Pulse coupling.

In the above parts of this section, we considered additive noise merged with weak coupling of oscillators. However, in an earlier part of this chapter, we also showed that the phase resetting curve is subject to uncertainty in the form of phase-dependent noise. Thus, consider two neurons which are coupled via phase resetting curves (in the sense of Goel and Ermentrout (15)):

$$\theta_j' = \omega + \sum_n B(\theta_j, z_j) \delta(t - t_n^k).$$

Here t_n^k are the times that oscillator k fires (crosses 0 modulo its period). $B(\theta, z)$ is the phase resetting curve parametrized by a random variable, z taken from some distribution. Recall from equation (1.14) that the PRC can have phase-dependent variance, so this model might incorporate this variance. If we consider two identical mutually coupled cells, the phase, ϕ of cell 2 at the moment cell 1 fires satisfies

$$\phi_{n+1} = G(G(\phi_n, z_n))$$

where $G(x, z) = 1 - x - B(x, z)$ (see for example, (15; 10)). Here we have assumed a period of 1. Let us write $B(x, z) = \epsilon \Delta(x) + zR(x)$ so that there is possibly phase-dependent noise, R and a deterministic coupling via the PRC, $\epsilon \Delta(x)$. As in section 2.2, we can use the theory of stochastic maps to derive an equation for the invariant density:

$$P(x) = \int_{-\infty}^{\infty} \frac{Q([x + y + \epsilon \Delta(y)]/R(y))}{R(y)} P(y) dy, \quad (1.22)$$

where $Q(z)$ is the density of the variable z defined on the real line. We seek solutions to this equation when $P(x + 1) = P(x)$. Notice that we can wrap the line up as an bi-infinite sum over the unit interval using the periodicity of $\Delta(x)$, but for the purposes of analysis, it is much easier to keep the integral over R . If $R(x) = 1 + \epsilon r(x)$ and ϵ is small, it is possible to write a formula for the invariant

density, $P(x)$ in a perturbation expansion in ϵ . For example, if $r(x) = 0$ and $\Delta(x) = b_1 \sin 2\pi x$, then

$$P(x) \approx 1 - \epsilon 2\pi b_1 \frac{q_1}{1 - q_1} \cos 2\pi x$$

where $q_n = \int_{-\infty}^{\infty} Q(x) \cos 2\pi x \, dx$. The shape of $P(x)$ is not surprising. If $b_1 > 0$, then there is a peak at $x = 1/2$, corresponding to antiphase oscillations while for $b_1 < 0$, the peak is at synchrony. Suppose that the noise amplitude is now phase-dependent and suppose the coupling tends to push the oscillators toward the antiphase solution ($x = 1/2$). Let $R(x)$ be such that the variance is minimal near $x = 0, 1$ and maximal near $x = 1/2$. Then, for strong enough noise, one might expect that the antiphase state might become unstable. That is, even though the deterministic dynamics push the oscillators toward antiphase, the PRC is so noisy near that state that the oscillators cannot remain there. Figure 1.10 shows an example of this. We take $\Delta(x) = b \sin 2\pi x$ and $R(x) = 1 + c \cos 2\pi x$, with $b = 0.05$ so that the deterministic system has a stable antiphase solutions and $c = -0.4$ so that the PRC is noisiest at $x = 1/2$. For low values of noise, $\sigma = 0.1$, Monte-Carlo simulations show a peak at $x = 1/2$ as predicted from the deterministic dynamics. However, for $\sigma = 0.35$, the histogram of phases shows peaks at $0, 1$ corresponding to synchrony. Using the ϵ small approximation for the invariant density, we find that

$$P(x) = 1 - 2\pi\epsilon \frac{q_1}{1 - q_1} (b + \pi\sigma^2 c) \cos 2\pi x.$$

Whether the peak is at $1/2$ or $0, 1$ depends only on the sign of $b + \pi\sigma^2 c$. Thus, there will be a change in the peak if b, c have opposite signs and the noise is large enough. For our case, the critical value of σ is about 0.25 . Figure 1.10B shows the stationary solutions to equation (1.22) as a function of σ for $\epsilon = 1$ via a color code. The switch from a peak at $x = 1/2$ to $x = 0, 1$ is evident.

In conclusion, we have shown that for pulse coupling, noise can have a qualitative effect on the steady state phase distribution if there is phase-dependent variance in the PRC. For weak coupling, uncorrelated noise does not have more than a quantitative effect on the behavior of coupled pairs of oscillators. As expected, the phase-differences between the oscillators stay close to the noise-free case in the sense that stable locked states correspond to peaks in the probability density. What is interesting is that the peaks remain in the presence of heterogeneities for case in which the deterministic dynamics do not have phase-locked solutions. (E.g., figure 1.9, $\mu = -4$.) Interactions between correlated noise and coupling is the subject of some of our recent research and should prove to be interesting.

1.4 Networks of oscillators.

We close this chapter with a sketch of the kinds of analysis that can be done with large systems of coupled oscillators in the presence of noise and possibly

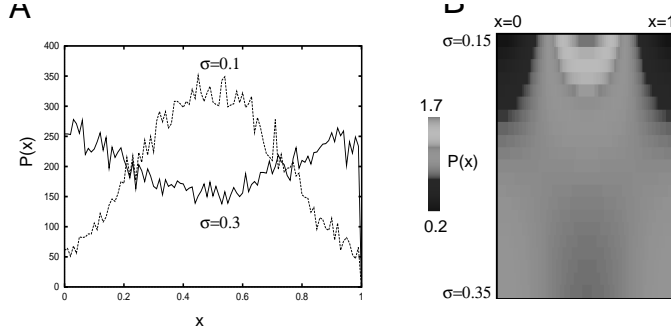


FIG. 1.10. Noise-induced bifurcation in a system with phase-dependent variance. $\Delta(x) = b \sin 2\pi x$, $R(x) = (1 + c \cos 2\pi x)$ with $b = 0.05$, $c = -0.25$, $\epsilon = 1$ for different values of σ . (A) Monte Carlo simulation of phase equations with 20000 spikes. (B) Steady state density as σ increases from 0.15 to 0.35. Peak in middle disappears while a pair of peaks appears at synchrony.

heterogeneities. Kuramoto (22) and later Strogatz (37), Crawford (7), and more recently, Buice and Chow (6) have studied the behavior of globally coupled oscillators in the presence of heterogeneities and noise. (6) consider finite size effects, while the others are interested in the infinite size limit. As the latter case is considerably easier to understand and analyze, we only consider this. A very extensive review of the analysis of the Kuramoto model and its generalizations can be found in Acebron et al (1). Here, we sketch the population density approach (37).

Consider the generalization of equation (1.20) after we have averaged and rescaled time:

$$d\psi_j = \left(\omega_j + \frac{1}{N} \sum_{k=1}^N H(\psi_k - \psi_j) \right) dt + \sigma dW_j(t) \quad (1.23)$$

where we assume that all oscillators are symmetrically coupled to each other and that they all have independent noise. As it will be notationally easier, we assume that the period of H is 2π . Kuramoto studies the case in which $\sigma = 0$ and $H(\phi) = \sin \phi$ as well as the case of no heterogeneity but nonzero noise. The review paper (1) references dozens of papers on the analysis of the Kuramoto model and its descendants. As $N \rightarrow \infty$, the ansatz of the population density method is that there is a function, $P(\theta, \omega, t)$ describing the probability of finding the oscillator with natural frequency, ω at phase θ at time t . A nice history of this method and its development are found in (38; 37). The sum in equation (1.23) is an average over the other phases and as $N \rightarrow \infty$ can be written in terms of the density function P as

$$\lim_{N \rightarrow \infty} \frac{1}{N} \sum_{k=1}^N H(\phi_k - \phi_j) = \int_{-\infty}^{\infty} \int_0^{2\pi} g(\omega) H(\phi - \phi_j) P(\phi, \omega, t) d\phi d\omega := J(\phi_j, t) \quad (1.24)$$

where $g(\omega)$ is the distribution of the frequencies, ω_j . With this calculation, the density satisfies:

$$\frac{\partial P}{\partial t} = -\frac{\partial}{\partial \theta} [J(\theta, t) P(\theta, \omega, t)] + D \frac{\partial^2 P}{\partial \theta^2}, \quad (1.25)$$

where $D = \sigma^2/2$. This equation is a nonlinear, integro-partial differential equation. Unlike the Fokker-Planck equations we previously encountered, the flux, J is a function of the probability which involves a convolution (so it is nonlocal). As with most nonlinear equations, there are very few methods for solving them. Here, we will perform a linear stability analysis to get a handle on the types of patterns which are possible. We will not perform a complete bifurcation analysis for the general case, but provide the normal forms for the case with just noise and no heterogeneities. As noise is the main topic of this book and this chapter, we treat D as a parameter. In the original Kuramoto analysis, there is no noise and the bifurcation parameter is the amplitude of the coupling. Another possible parameter is the “spread” of the natural frequencies, ω_j (the variance of the distribution, $g(\omega)$ where defined). Normalization requires that

$$\int_{-\infty}^{\infty} \int_0^{2\pi} g(\omega) P(\phi, \omega, t) d\phi d\omega = 1.$$

A trivial solution to equation (1.25) is $P(\theta, \omega, t) = 1/(2\pi)$. Our strategy is to linearize around this trivial fixed point. This state corresponds to the completely asynchronous state with the oscillators effectively uncoupled and a uniform probability of finding them in any state. (As a contrast, suppose that there is no heterogeneity and no noise. The perfectly synchronous state is $P(\theta, \omega, t) = \delta(\theta - \Omega t)$ where Ω is the “ensemble” frequency, $\Omega = \omega_0 + H(0)$ with ω_0 the uncoupled frequency of each oscillator.)

We write $P = 1/(2\pi) + r(\theta, \omega, t)$ and write the linear terms for r :

$$\frac{\partial r}{\partial t} = D \frac{\partial^2 r}{\partial \theta^2} - \frac{\partial}{\partial \theta} (\omega + H_0) r + \frac{1}{2\pi} \int_{-\infty}^{\infty} \int_0^{2\pi} g(\omega) H'(\phi - \theta) r(\phi, \omega, t) d\phi d\omega,$$

where H_0 is the average value of H . This is a linear problem which is homogeneous in θ, t but not in ω . The former homogeneity implies that $r(\theta, \omega, t) = \exp(\lambda t + in\theta) f_n(\omega)$ where f_n is an unknown function of ω and n is an integer. If, $\Re \lambda < 0$ for all n then the asynchronous state is asymptotically stable. We plug this function into the linearization and we find:

$$\lambda f_n(\omega) = -D n^2 f_n - i(\omega + H_0) n f_n + h_n \bar{f}_n \quad (1.26)$$

where

$$\bar{f}_n = \int_{-\infty}^{\infty} g(\omega) f_n(\omega) d\omega$$

and

$$h_n = \frac{1}{2\pi} \int_0^{2\pi} H'(\phi) \exp(in\phi) d\phi.$$

Note that h_n is the n^{th} Fourier coefficient of the derivative of the H function. We can solve equation (1.26) for $f_n(\omega)$:

$$f_n(\omega) = \frac{h_n \bar{f}_n}{\lambda + Dn^2 + in(H_0 + \omega)}.$$

We plug this into the definition of \bar{f}_n to obtain:

$$\bar{f}_n = \bar{f}_n \int_{-\infty}^{\infty} \frac{g(\omega) h_n}{\lambda + Dn^2 + in(H_0 + \omega)} d\omega.$$

This equation has a nontrivial solution for \bar{f}_n if and only if

$$1 = \int_{-\infty}^{\infty} \frac{g(\omega) h_n}{\lambda + Dn^2 + in(H_0 + \omega)} d\omega := \Gamma(\lambda). \quad (1.27)$$

Equation (1.27) is the eigenvalue equation that must be solved and the values of λ determine stability. The simplest scenario and the only one which we solve here is when all oscillators are identical and $g(\omega)$ is a Dirac delta function at ω_0 . In this case, the integral is easy to evaluate and we find after trivial algebra:

$$\lambda = h_n - Dn^2 - i(\omega_0 + H_0)n. \quad (1.28)$$

There is always a zero eigenvalue ($n = 0$) corresponding to translation invariance of the phases. For $n \neq 0$, since h_n are bounded, for sufficient noise, D , $\Re\lambda$ is negative and the asynchronous state is asymptotically stable. (When there is heterogeneity and no noise, the spectral equation is extremely subtle and the analysis complex. As there is always noise in neural systems, we make life easy by assuming $D > 0$.) Suppose that we write

$$H(\phi) = H_0 + \sum_{n=1}^{\infty} a_n \cos n\phi + b_n \sin n\phi.$$

Then

$$h_n = -ina_n/2 + nb_n/2$$

thus, the real part of λ is

$$\Re\lambda = -Dn^2 + nb_n/2.$$

The only terms in H which can destabilize the asynchronous state are those for which the Fourier sine coefficients are positive. The critical value of noise is thus

$$D^* = \max_{n>0} \frac{b_n}{2n}$$

Figure 1.11 shows an example of the application of this analysis to a simulation of 400 globally coupled oscillators. Here $H(\phi) = 0.25 \cos \phi - 0.5 \sin \phi + \sin 2\phi$. The critical value of D predicted is $1/4$ corresponding to $\sigma = 1/\sqrt{2}$. We let the simulation run to steady state with $\sigma = 0.8$ (above criticality) and then changed σ to 0.6 which is below the critical value. Figure 1.11A shows a space-time plot of the 400 oscillators as a function of time. Their phases relative to oscillator 1 are plotted in a color code over a time window including the decrease of the noise amplitude. The color coding shows that after the noise is reduced, oscillators are divided into roughly two clusters (pink and blue) corresponding to a 0 and π phase-differences. This is a two cluster state. We introduce so-called “order parameters”, which quantify the degree of synchrony between the oscillators:

$$\text{OP}_n := \frac{1}{N} \sqrt{\left(\sum_{j=1}^N \cos n\theta_j \right)^2 + \left(\sum_{j=1}^N \sin n\theta_j \right)^2}.$$

These pick out the Fourier coefficients of the invariant density, $P(\theta, \omega, t)$ and vanish when the oscillators are asynchronous. If $D < b_n/n$, we expect OP_n to grow. Figure 1.11B shows the abrupt change in OP_2 as predicted from the infinite N theory. Figure 1.11C shows histograms at the high and low noise levels for one time slice of the 400 oscillators. There are two clear peaks in the low noise case as predicted from the linear analysis.

A natural, next approach to the equation is to do a full nonlinear bifurcation analysis. This was done in chapter 5 of Kuramoto. The first step is to subtract off the constant frequency and the constant Fourier term of H . Thus, we reduce (1.25) to the following nonlinear equation:

$$\frac{\partial P}{\partial t} = -\frac{\partial}{\partial \theta} \int_0^{2\pi} H(\phi - \theta) P(\theta, t) P(\phi, t) d\phi + D \frac{\partial^2 P}{\partial \theta^2}.$$

Letting m denote the critical wave number, the normal form for the bifurcation has the form:

$$z_t = z[m^2(D^* - D) + \gamma_2 z \bar{z}]$$

where

$$\gamma_2 = -\frac{m\pi^2}{2} \left(\frac{b_m^2 + a_m^2 + a_m a_{2m} - b_m b_{2m} + i(a_{2m} b_m + a_m b_{2m})}{2b_m - b_{2m} + i(a_{2m} - a_m)} \right)$$

and

$$H(\phi) = \sum_n a_n \cos n\phi + b_n \sin n\phi.$$

The bifurcation is supercritical if the real part of γ_2 is negative. Note that if H contains only odd periodic terms then

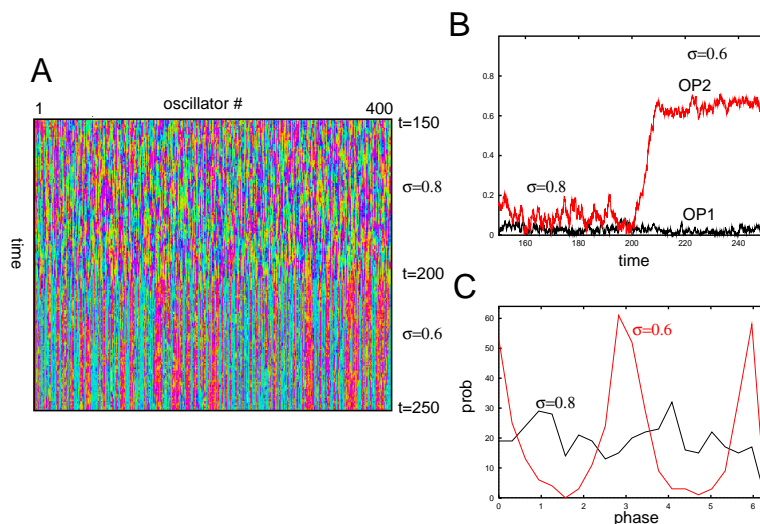


FIG. 1.11. Example of the destabilization of the asynchronous state as the noise is reduced leading to a two-cluster solution. ($H(\phi) = 0.25 \cos \phi - 0.5 \sin \phi + \sin 2\phi$, $\sigma^* = 1/\sqrt{2} \approx 0.707$). (A) Space-time plot of the phases relative to oscillator 1. At $t = 200$, the noise is abruptly reduced from $\sigma = 0.8$ to $D = 0.6$. The emergence of a two-cluster state (turquoise/red) is apparent. (B) Order parameters $OP_{1,2}$ showing the two-cluster instability. (C) Histogram of the relative phases during two different points in the simulation corresponding to the two different levels of noise.

$$\gamma_2 = -\frac{mb_m\pi^2}{2} \frac{b_m - b_{2m}}{2b_m - b_{2m}}.$$

Note that the denominator is always positive since $b_m/m > b_{2m}/(2m)$ by hypothesis. For the case illustrated in figure 1.11, the bifurcation is supercritical.

In conclusion, we have used the methods of Kuramoto to analyze the effects of noise and coupling on a large population of coupled neurons and shown that only the odd Fourier components of the interaction function contribute to synchronization.

1.5 Summary.

Noise interacts with oscillators in complex ways. Correlated noise can act to synchronize uncoupled oscillators. Using perturbation theory and the method of phase reduction, it is possible to reduce the analysis of these high-dimensional systems to simple phase models. Coupled oscillators can be similarly reduced and the effects of noise on them also analyzed. Methods include using population

density equations, Fokker-Planck equations, and the analysis of linear integral operators. There are many unanswered questions such as what happens with larger noise and how interactions between internal dynamics and correlated inputs change the ability to synchronize.

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