School of Mathematical Sciences

G14TNS Theoretical Neuroscience

Phase Response Curves

It is common practice in neuroscience to characterize a neuronal oscillator in terms of its phase response to a perturbation. This gives rise to the notion of a so-called phase response curve (PRC). Consider a dynamical system $\dot{z} = F(z)$ with a T-periodic solution $Z(t) = Z(t+T)$ and introduce an infinitesimal perturbation Δz_0 to the trajectory $Z(t)$ at time $t = 0$. This perturbation evolves according to the linearised equation of motion:

$$\frac{d\Delta z}{dt} = DF(Z(t))\Delta z, \qquad \Delta z(0) = \Delta z_0. \tag{1}$$

Here $DF(Z)$ denotes the Jacobian of F evaluated along Z. Introducing a time-independent phase shift $\Delta\theta$ as $\theta(Z(t)+\Delta z(t)) - \theta(Z(t))$, we have to first order in Δz that

$$\Delta\theta = \langle Q(t), \Delta z(t)\rangle, \tag{2}$$

where $\langle \cdot, \cdot \rangle$ defines the standard inner product, and $Q = \nabla_Z \theta$ is the gradient of θ evaluated at $Z(t)$. Taking the time-derivative of (2) gives

$$\left\langle \frac{dQ}{dt}, \Delta z \right\rangle = -\left\langle Q, \frac{d\Delta z}{dt} \right\rangle = -\langle Q, DF(Z)\Delta z\rangle = -\left\langle DF^T(Z)Q, \Delta z\right\rangle. \tag{3}$$

Since the above equation must hold for arbitrary perturbations, we see that the gradient $Q = \nabla_Z \theta$ satisfies the linear equation

$$\frac{dQ}{dt} = D(t)Q, \qquad D(t) = -DF^T(Z(t)), \tag{4}$$

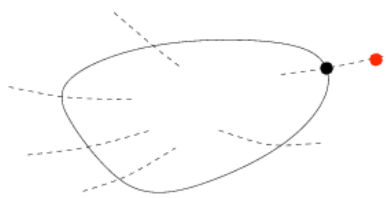
subject to the conditions $\nabla_{Z(0)}\theta \cdot F(Z(0)) = 1/T$ and $Q(t) = Q(t+T)$. The first condition simply guarantees that $\dot{\theta} = 1/T$ (at any point on the periodic orbit), and the second enforces periodicity. The (vector) PRC R, is related to Q according to the simple scaling $R = QT$. In general equation (4) must be solved numerically to obtain the PRC, say, using the *adjoint* routine in XPP.

Isochronal coordinates

Consider a limit cycle oscillation. Let $x(t)$ and $x'(t)$ be trajectories on and off the limit cycle respectively. If

$$\lim_{t\to\infty} d(x(t), x'(t)) = 0$$

where d is the distance function, then $x(t)$ and $x'(t)$ are said to have the same *latent phase* Φ. The locus of all points with the same latent phase Φ is called an **isochron**.



Isochrons as leaves of the stable manifold of a hyperbolic limit cycle.

An example - supercritical Hopf bifurcation

$$\dot{x} = \mu x - \omega y - (x^2 + y^2)x,$$
$$\dot{y} = \omega x + \mu y - (x^2 + y^2)y.$$

In polar coordinates

$$\dot{r} = \mu r - r^3, \qquad \dot{\theta} = \omega,$$

and we see that there is a supercritical Hopf bifurcation giving rise, for $\mu > 0$, to a stable limit cycle of radius $\sqrt{\mu}$ and frequency $\omega = 1/T$. The limit cycle takes the explicit form

$$(x, y) = \sqrt{\mu}(\cos(\omega t), \sin(\omega t)).$$

Setting $Q = (q_1, q_2)$ the normalisation condition $Q \cdot F = 1/T$ (valid for any time) gives:

$$q_1 \left(\mu x - \omega y - x r^2\right)\Big|_{r=\sqrt{\mu}} + q_2 \left(\omega x + \mu y - y r^2\right)\Big|_{r=\sqrt{\mu}} = \omega,$$

yielding

$$-q_1 y + q_2 x = 1.$$

Now since Q is the gradient of a level set ($\theta =$ constant) it must be orthogonal to the isochrons at the limit cycle. For the problem here it is easy to check that these are simply radial lines. Hence $(x, y) \cdot (q_1, q_2) = 0$ giving

$$q_1 x + q_2 y = 0.$$

Solving the above two equations for q_1 and q_2 gives

$$(q_1, q_2) = (-y/(x^2 + y^2), x/(x^2 + y^2)),$$

which we may write as a function of the phase $\theta \in [0, 1)$ along the limit cycle as

$$(q_1, q_2) = (-\sin(2\pi\theta), \cos(2\pi\theta))/\sqrt{\mu}.$$