A GENERALIZED MATHEMATICAL MODEL OF BIOLOGICAL OSCILLATORS

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Abstract: Biological rhythms such as circadian rhythms, biochemical rhythms and neural oscillators are based on the mathematical model of the theory of harmonic oscillators. These are solutions of certain second-order differential equations. They can also be viewed as spherical harmonics on the circle in the two-dimensional Euclidean space. The spherical harmonics on (n-1)-spheres and, more generally, the Stiefel harmonics can represent oscillatory phenomena, and we expect that they can serve as models for more complex biological rhythms.

Key Words: Biological Oscillators, Spherical Harmonics, Stiefel Harmonics.

The work of many researchers suggests the existence of endogenous oscillators in living systems and daily cycles of biological phenomena are controlled by such oscillators. Circadian rhythms are observed in the eclosion of the fruit fly *Drosophila pseudoobscura*, in cell population growth such as in cultures of *Euglena gracilis*, in the rate at which various biochemical reactions proceed at various times of the day, and in periodically firing neurons in the nervous system of various animals (see [1]). Even though biological oscillators are nonlinear systems, their linear approximation is the basic differential equation of a harmonic oscillator which is the motion of a small ball with a mass m suspended from a spring with constant $k > 0$. If $Y(t)$ denotes the position of the ball and $V(t)$ denotes its velocity at time t, then we have a differential equation

$$(1) \qquad \frac{md^2Y}{dt^2} + kY = 0, \qquad Y(t_0) = Y_0,\ V(t_0) = V_0.$$

This gives the solution: $Y(t) = A\cos[(k/m)^{1/2}t + \Phi]$, where $A\cos\Phi = Y_0$, $A\sin\Phi = -(m/k)^{1/2}V_0$. Let us consider a harmonic homogeneous polynomial P of degree *l* in two variables, x and y, i.e., $\Delta P = 0$, where $\Delta = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$. Then the Laplacian can be expressed in polar coordinates as

$$(2) \qquad \Delta = \frac{\partial^2}{\partial r^2} + \frac{1}{r}\frac{\partial}{\partial r} + \frac{1}{r^2}\frac{\partial^2}{\partial \theta^2}.$$

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If $S_1 = \{(x, y) \varepsilon R^2 \mid x^2 + y^2 = 1\}$ denotes the unit circle, then clearly P is uniquely determined on the circle. In terms of polar coordinates, we can write $P(x,y) = P(r \cos\theta, r \sin\theta) = r^l Y(\theta)$, where $Y(\theta)$ is a function on S_1. From Eq. (2),

$$\Delta P = \left(\frac{\partial^2}{\partial r^2} + \frac{1}{r}\frac{\partial}{\partial r} + \frac{1}{r^2}\frac{\partial^2}{\partial \theta^2}\right) r^l Y(\theta) = \left(l(l-1) + l + \frac{\partial^2}{\partial \theta^2}\right) r^{l-2} Y(\theta). \tag{3}$$

Since Y depends only on θ, we obtain $\frac{\partial^2}{\partial \theta^2} Y(\theta) + l^2 Y(\theta) = 0$ which, by a simple change of variables, is reduced to Eq. (1). For a harmonic homogeneous polynomial P of degree l in the variable $X = (x, y, z)$,

then $\Delta P = 0$, where the Laplacian $\Delta = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2} + \frac{\partial^2}{\partial z^2}$.

Let $S_2 = \{(x, y, z) \varepsilon R^3 \mid r = \|X\| = (x^2 + y^2 + z^2)^{1/2} = 1\}$ denote the unit sphere in the three-dimensional Euclidean space and express X in spherical coordinates as $x = r \cos\varphi \sin\theta$, $y = r \sin\varphi \sin\theta$, $z = r \cos\theta$, $0 \le \varphi < 2\pi$, $0 < \theta < \pi$. In spherical coordinates

$$\Delta = \frac{\partial^2}{\partial r^2} + \frac{2}{r}\frac{\partial}{\partial r} + \frac{1}{r^2}\Delta_{S_2}, \quad \Delta_{S_2} = \frac{1}{\sin\theta}\frac{\partial}{\partial \theta}\left(\sin\theta \frac{\partial}{\partial \theta}\right) + \frac{1}{\sin^2\theta}\frac{\partial^2}{\partial \varphi^2}, \tag{4}$$

where Δs_2 is called the Laplace-Beltrami operator. Then $P(r, \varphi, \theta) = r^l Y(\varphi, \theta)$ and

$$\begin{aligned} 0 = \Delta P(r, \varphi, \theta) &= \left(\frac{\partial^2}{\partial r^2} + \frac{2}{r}\frac{\partial}{\partial r} + \frac{1}{r^2}\Delta_{S_2}\right) r^l Y(\varphi, \theta) \\ &= \left(l(l-1) + 2l + \Delta_{S_2}\right) r^{l-2} Y(\varphi, \theta). \end{aligned}$$

Since Y depends only on φ and θ, we have $\Delta s_2 Y = -l(l + 1)Y$, Y can be determined as eigenvectors of the Laplace-Beltrami operator. The solutions are called spherical harmonics of degree l. The spherical harmonics of degree l form a vector space H^l ofdimension $2l + 1$. An orthonormal basis for H^l (see [2]) can

be given by Y_m^l (φ, θ), $-l \le m \le 1$, where

$$(5) \qquad Y_m^l(\varphi,\theta) = \frac{1}{\sqrt{2\pi}} e^{im\varphi} P_m^l(\theta) \text{ and for } m \geq 0,$$
$$P_{-m}^l(\theta) = P_m^l(\theta) = \frac{N_m^l}{2^l l!} \sin^m\theta \frac{d^{l+m}\sin^{2l}\theta}{d(\cos\theta)^{l+m}},$$

where $N_m^l = \{[(l - m)!/(l + m)!][(2l + 1)/2]\}^{1/2}$ is a normalization factor. In general (see [3]) for $X = (x_1, \dots , x_n)$, we express X in spherical coordinates. Then the Laplacian $\Delta = \frac{1}{r^{n-1}}\frac{\partial}{\partial r}\left(r^{n-1}\frac{\partial}{\partial r}\right) + \frac{1}{r^2}\Delta s_{n-1}$, where $S_{n-1} = \{X \varepsilon R^n \mid \|X\| = 1\}$ is the unit sphere in the n-dimensional Euclidean space, and the Laplace-Beltrami operator is given by

$$\Delta_{S_{n-1}} = \frac{1}{\sin^{n-2}\theta_{n-1}} \frac{\partial}{\partial\theta_{n-1}} \left(\sin^{n-2}\theta_{n-1} \frac{\partial}{\partial\theta_{n-1}}\right) + \cdots$$
$$(6) \qquad + \frac{1}{\sin^2\theta_{n-1} \cdots \sin^2\theta_2} \frac{\partial^2}{\partial\theta_1^2}.$$

If P is a harmonic homogeneous polynomial of degree *1*, then

$\Delta P(r,\theta_1, \dots , \theta_{n-1}) = [(n - 1)l + l(l - 1) + \Delta s_{n-1}]r^{l-2}Y(\theta_1, \dots , \theta_{n-1}) = 0.$

This implies that $\Delta s_{n-1}Y = - l(l + n - 2)Y$, i.e., Y is an eigenfunction for the Laplace-Beltrami operator Δs_{n-1}. These functions are the generalized “harmonic oscillators” which can be used as a mathematical model for biological oscillators.

In connection with the spherical harmonics, let us consider the following problem: “*Determine all continuous functions f:* $R^n \to R$ *such that for all* $X \varepsilon R^n$ *and* $\rho > 0$*, we have*

$$(7) \qquad f(X) = \frac{1}{|S_{n-1}|} \int_{S_{n-1}} f(X + \rho Y)\, d\omega(Y),$$

where $d\omega(Y)$ *is the surface area element, and* $|S_{n-1}|$ *is the surface area of the sphere*.” For example for S_2, $d\omega(Y) = \sin\theta\, d\varphi\, d\theta$ and $|S_2| = 4\pi$. Eq. (7) says that *f* has the Mean Value Property. The solution to this problem follows from the famous Gauss’s Lemma which states *that f has the Mean Value Property if and only if f is harmonic, i.e.,* $\Delta f = 0$. Now if $M_n(R)$ denotes the space of all in n x n

in matrices over R and if R^T denote the transpose of the matrix R, let $SO(n) = \{R \varepsilon M_n(R) \mid R^T = R^{-1}, \det(R) = 1\}$ denote the group of all rotations in the n-dimensional Euclidean space. Then SO(n) acts on functions on R^n as follows: $(L(R)f)(X) := f(R^TX)$. It is easy to show that $\Delta L(R)f = L(R)\,\Delta f$ and $\Delta s_{n-1} L(R)Y = L(R)\,\Delta s_{n-1} Y$ for all $R \varepsilon SO(n)$ and for all spherical harmonics Y. This means that spherical harmonics are invariant under rotations. In physics, one says that the rotations form a group of symmetry for the system of spherical harmonics.
Spherical harmonics can be further generalized to Stiefel harmonics as follows (see [4]). Consider the vector space $P(R^{n\,x\,k})$ of all polynomial functions on R^{nxk} $k \geq 2n$. For $X = (x_{rs}) \varepsilon R^{nxk}$, let $\Delta_{ij} = \sum_{s=1}^{k} \frac{\partial^2}{\partial x_{is} \partial x_{js}}$, $1 \leq i, j \leq k$. Then a polynomial function $P \varepsilon \mathbf{P}(R^{nxk})$ is said to be rotational harmonic if $\Delta_{ij}P = 0$, for all i, j = 1, ... , k. Let $\mathbf{H}(R^{nxk})$ denote the space of all rotational harmonics, and let $S^{nxk} = \{X \varepsilon R^{nxk} \mid XX^T = I_n\}$ denote the Stiefel manifold. Then we have the following

Theorem. *The space $H^r(R^{nxk})$ of all rotational harmonic homogeneous polynomials of degree r is spanned by all polynomials $f^{\,r}$ where $f(X) = \sum_{ij} a_{ij}x_{ij}$ with $A = (a_{ij}) \varepsilon C^{nxk}$, $AA^T = 0$ and i = 1, ... ,n; j = 1, ... , k. The restriction mapping $f \rightarrow f \mid S^{nxk}$ $(f \varepsilon \mathbf{H}(R^{nxk}))$ is an isomorphism; i.e., a one-to-one and onto linear map.*

The restriction of the rotational harmonics to the Stiefel manifold are called Stiefel harmonics, and the rotations SO(*k*) form a group of symmetry for the system of Stiefel harmonics. A similar notion of symplectic Stiefel harmonics is also studied in [5].

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