CHAPTER FOUR

GLOBAL ELECTROCORTICAL ACTIVITY

4.1 LINEAR MODEL

An important aspect of electroencephalogram is its close correlation with cognition and behavior (e.g. Walter, Kado, Rhodes, Adey 1967; Berkhout, Walter, Adey 1969; Gevins, Zeitlin, Doyle, Yingling, Schaffer, Callaway, Yeager 1979). If cortical cells are viewed as information processing networks, then electrocortical waves might be viewed as statistical shifts in average local depolarization, influencing the transition probability of local network elements, thus baising the logical properties of the networks. If we are able to determine the laws of motion of these waves and their internal mechanisms of control, we shall be a step ahead toward an overall understanding of brain information processing.

Wright and Kydd (1984) developed a linear model for global electrocortical activity and its control by lateral hypothalamus. They proposed that the properties of the electrocortical waves be clearly distinguished from the microscopic and nonlinear interactions which underlie them. The gross waves may be represented as linear, and subject to a specific form of control by certain sub-cortical pathways. From the linearity assumption it immediately follows (*i*) that the waves are subject to the *superposition principle*, (*ii*) that with given boundary conditions the gross electrocortical activity will exhibit resonant modes of fixed natural frequency, and (*iii*) that at each point in the system there is a specific dispersion relation, giving phase velocity for each wavelength.

The lateral hypothalamus is chosen as the focal point in these studies because (Wright, Kydd 1984)

(a) It is one of number of fiber pathways well placed to exert controlling influences in the brain, being made up of numerous pathways ascending and descending from telencephalon to brainstem (Olds 1956a; Nauta, Karten 1970).

(b) Lesion of this pathway leads to the sensorimotor neglect syndrome - an in attention syndrome not accounted for by sensory loss, or motor paralysis (Marshall, Turner, Teitelbaum 1971; Turner 1973; Wright, Craggs 1979).

(c) Stimulation of the lateral hypothalamus exerts strong effects on motivation and attention, as manifested by the intracranial self-stimulation phenomena (Olds 1956b, 1961; Olds, Peretz 1960; Rolls 1971, 1974; Wauquier, Rolls 1976).

(d) The electrocortical power spectra obtained in sensorimotor neglect and intracranial self-stimulation appear to show reciprocal changes in power at each frequency, when each is compared to a resting control state (Wright, Craggs, 1979). The converse nature of these effects reduces the chance that either represents immediate, or later developing, artifactual events, and suggests that opposite shifts along a continuum are induced by these manipulations.

(e) Sensorimotor neglect and intracranial self-stimulation appear to depend upon lesion, or stimulation respectively, of all, or subgroups of cells within the mesoencephalic dopaminergic group (Ljungberg, Ungerstedt 1976; Wise 1978; Wise, Bozarth 1981)

Therefore we see that the lateral hypothalamus exerts important control functions upon telencephalic activity.

Consider the cerebral cortex as a mesh of highly interconnected voltage (or current) sources, equivalent to segments of dendritic trees. The telencephalon constitutes a comparatively closed, highly interlinked system. The entire system may be regarded as driven both by input sensory signals, and active neuronal firing.

Let the potential of a segment of a dendritic tree, $\varphi_i(t)$ be represented by

$$\ddot{\varphi}_i + D_i(t)\,\dot{\varphi}_i + N_i^2(t)\,\varphi_i = 0 \tag{4.1}$$

The Roman index i which runs from 1 to n denotes the number of dendritic trees considered in the model. The equation is inhomogeneous and can, therefore, be fitted to any oscillatory source when $D_i(t)$ and $N_i(t)$ are free parameters. These parameters are analogous to a damping coefficient and a natural frequency.

A mass of unit sources coupled to each other may be similarly represented by (j runs from 1 to n subject to the condition that $i \neq j$)

$$\ddot{\varphi}_i + D_i(t)\,\dot{\varphi}_i + N_i^2(t)\,\varphi_i = \sum_j K_i^j(t)\,\varphi_j \tag{4.2}$$

where $D_i(t)$, $N_i(t)$, $K_i^j(t)$ are again free parameters. These parameters may be given physiological meaning under the following assumptions.

(i) All N_i (D_i, K_i^j) have a finite variance σ_N (σ_D, σ_K)

about a mean <N>, (<D>, <K>). No particular type of distribution for $N_i(t)$, $D_i(t)$, $K_i^j(t)$ is assumed.

(*ii*) All $N_i(t)$, $D_i(t)$, $K_i^j(t)$ are stochastically independent, as each represents processes being perturbed by very complicated nonlinearities in the interactions of the linked oscillatory sources, with diverse input signals.

Under the above listed assumptions regarding the parameters, the *Central Limit Theorem of Cramer* applies as n tends to be a large number. This is a very reasonable assumption. All $N_i(t)$, $D_i(t)$, $K_i^j(t)$ may, therefore, be replaced by <N>, <D>, <K> The model system is equivalent to a linear, time-invariant system while these values remain unchanged.

Eq. (4.2) may be put in another form by defining new variables. Let $z_1 = \varphi_1$, $z_2 = \dot{z}_1 = \dot{\varphi}_1$, $z_3 = \varphi_2$, $z_4 = \dot{z}_3 = \dot{\varphi}_2$ to $z_{m-1} = \varphi_n$, $z_m = \dot{z}_{m-1} = \dot{\varphi}_n$; $m = 2n$. In matrix representation

$$d\mathcal{Z}/dt = \mathcal{A}\,\mathcal{Z} \tag{4.3}$$

where $\mathcal{Z} = [z_k]$; $k = 1,2,\dots,m$ is an m x 1 column vector and $\mathcal{A}$ is the state transition matrix given by

$$\mathcal{A} = \left[\begin{array}{cccccccccc}
0 & 1 & 0 & 0 & 0 & 0 & \cdots & 0 & 0 \\
-N_1^2 & -D_1 & K_1^2 & 0 & K_1^3 & 0 & \cdots & K_1^n & 0 \\
0 & 0 & 0 & 1 & 0 & 0 & \cdots & 0 & 0 \\
K_2^1 & 0 & -N_2^2 & -D_2 & K_2^3 & 0 & \cdots & K_2^n & 0 \\
0 & 0 & 0 & 0 & 0 & 1 & \cdots & 0 & 0 \\
K_3^1 & 0 & K_3^2 & 0 & -N_3^2 & -D_3 & \cdots & K_3^n & 0 \\
\cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\
\cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\
\cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\
0 & 0 & 0 & 0 & 0 & 0 & \cdots & 0 & 1 \\
K_n^1 & 0 & K_n^2 & 0 & K_n^3 & 0 & \cdots & -N_n^2 & -D_n
\end{array}\right] \tag{4.4}$$

The elements in Wright and Kydd's state transition matrix donot all have the same dimensions. $-(N_1)^2$ has units of $(\text{time})^{-2}$ whereas $-D_1$ has units of $(\text{time})^{-1}$. In the next chapter we shall rewrite the system of equations (3.3) so that all the elements of $\mathcal{A}$ are dimensionless.

4.2 COVARIANT MODEL

The model of Wright and Kydd (1984) described above rests on drastic simplifications. It bypasses issues of cell-to-cell coupling, details of anatomy etc. Moreover, it does not take into account of the magnetic fields which are generated when there is a motion of charges.

We start with the model of Wright and Kydd (1984), but write the equation for the potential of a segment of a dendritic tree in the comoving frame of the signal (Kamal, Siddiqui, Husain 1989a). The comoving frame is fixed to the potential wavefront in the dendrite. When this equation is transformed into the laboratory frame a magnetic vector potential appears along with electrostatic potential.

Essential theoretical features of this model, somewhat modified from Wright, Kydd, Lees (1984), may be summarized as:

(a) Electrocortical activity reflect the transformed spatial average of cortical potentials (Elul 1972).

(b) The telencephalon is assumed to be a linear wave medium with regard to the gross wave potentials although the underlying microscopic interactions may be extremely nonlinear.

(c) Closed and constant boundary conditions lead the linear waves to generate activity at a large number of resonant modes, each associated with a constant natural frequency. These are interdependent properties for time-invariant linear systems (Kuo 1982; Feynman, Leighton, Sands 1963).

(d) The values for the natural modes of the resonant frequencies are clustered about certain central values (Cramer's Central Limit Theorem).

(e) Ascending inhibitory systems act partly to damp resonant activity and partly as a source of noise like driving signals.

(f) An electrical potential in a comoving frame of the signal transforms as four-potential in the laboratory frame.

Let us introduce a four-potential whose components are A^{μ}; $\mu = 0,1,2,3$. It can be represented as

$$\mathbf{A} = \begin{pmatrix} \varphi \\ \mathbf{A} \end{pmatrix} \tag{4.5}$$

In the subsequent discussion the subscript μ is dropped. The four-vector $\mathbf{A}$ will be written as simply A. In the comoving frame of the signal passing through a segment of the dendritic tree, the electrical potential can be represented as

$$\ddot{\varphi}_i + D_i(\tau)\, \dot{\varphi}_i + N_i^{2}(\tau)\, \varphi_i = 0 \tag{4.6}$$

τ is time in the comoving frame of the signal. A mass of unit sources coupled to each other may be similarly represented by

$$(4.7) \qquad \ddot{\varphi}_i + D_i(\tau)\,\dot{\varphi}_i + N_i^2(\tau)\,\varphi_i = \sum_j K_i^j(\tau)\,\varphi_j$$

There is no summation over repeated Roman indices. However, repeated Greek indices denote summation. In matrix form the above equation can be written as

$$(4.8) \qquad \ddot{\phi}_i + \mathcal{D}_i(\tau)\,\dot{\phi}_i + \mathcal{N}_i^2(\tau)\,\phi_i = \sum_j \mathcal{K}_i^j(\tau)\,\phi_j$$

where $\mathcal{D}_i(\tau)$, $\mathcal{N}_i(\tau)$ and $\mathcal{K}_i^j(\tau)$ are 4 x 4 matrices. The only nonzero entries are at the intersection of first row and first column; which are $D_i(\tau)$, $N_i(\tau)$ and $K_i^j(\tau)$ respectively. ϕ_i is a 4 x 1 column vector with the first entry as the only nonzero entry representing the electrical potential φ_i. Let us transform Eq. (4.8) in the laboratory frame under the Lorentz transformation λ_i. Under this similarity transformation the four-vectors and matrices take the form

$$(4.9a) \qquad \phi_i \longrightarrow A_i = \lambda_i\,\phi_i$$

$$(4.9b) \qquad \mathcal{D}_i(\tau) \longrightarrow \Delta_i(\tau) = \lambda_i\,\mathcal{D}_i(\tau)\,\tilde{\lambda}_i$$

$$(4.9c) \qquad \mathcal{N}_i(\tau) \longrightarrow \eta_i(\tau) = \lambda_i\,\mathcal{N}_i(\tau)\,\tilde{\lambda}_i$$

$$(4.9d) \qquad \mathcal{K}_i^j(\tau) \longrightarrow \mathscr{K}_i^j(\tau) = \lambda_i\,\mathcal{K}_i^j(\tau)\,\tilde{\lambda}_i$$

Eq. (3.8), therefore, becomes

$$(4.10) \qquad \ddot{A}_i + \Delta_i(\tau)\,\dot{A}_i + \eta_i^2(\tau)\,A_i = \sum_j \mathscr{K}_i^j((\tau)\,A_j$$

The state transition matrix was constructed by defining new variables $\Omega_k = f(A_i, \dot{A}_i)$, $k = 1, 2, \ldots, m$ where $m = 2n$ analogous to the variables $z_k = f(\varphi_i, \dot{\varphi}_i)$ in the linear model of Wright and Kydd (1984). In terms of Ω_k, Eq. (4.10) can be written as

$$(4.11) \qquad d\mathcal{Z}/d\tau = \mathbb{A}\,\mathcal{Z}$$

where $\mathbb{Z} = [\Omega_k]$ is a $4m \times 1$ column vector (each Ω_k is a 4×1 column vector) and $\mathbb{A}$ is the state transition matrix of order $4m \times 4m$. The form of $\mathbb{A}$ is similar to $\mathcal{A}$ given in Eq. (4.4) with each D_i replaced by Δ_i, N_i by η_i and K_i^j by $\mathcal{K}_i^j$. The numbers 0 and 1 are replaced by 4 x 4 null and unit matrices respectively.

Under the similarity transformations defined by Eq. (4.9) the eigenvalues remain invariant i.e.

(4.12a) $$D_{lab} = D_{comoving}$$

(4.12b) $$N_{lab} = N_{comoving}$$

(4.12c) $$K_{lab} = K_{comoving}$$

4.3 GENERALIZATION OF THE COVARIANT MODEL

In the covariant model described above we have written 4 x 4 matrices in place of simple parameters representing damping coefficients, coupling constants and natural frequencies. However, in all the matrix representations in the comoving frame of the signal only one of the eigenvalues is nonzero. In the spirit of complete symmetry among all the space-time coordinates we are introducing 4 eigenvalues for each parameter i.e. the diagonal entries of the matrices $\mathcal{D}_i(\tau)$, $\mathcal{N}_i(\tau)$ and $\mathcal{K}_i^j(\tau)$ are $D_i^\mu(\tau)$, $N_i^\mu(\tau)$ and $K_i^{j\mu}(\tau)$; μ = 0,1,2,3 respectively (Kamal, Siddiqui, Husain 1989b). All the nondiagonal entries are zero. The eigenvalues corresponding to $\mu = 0$ are the ones present even in the absence of magnetic fields. These will show up in the model of Wright and Kydd

(1984). The other eigenvalues would not be observed because their projections on the four-vector ϕ_i will vanish. These eigenvalues will show up when we transform Eq. (4.8) to the laboratory frame as (4.10). In Chapter 5 we shall consider the effects of weak magnetic fields on these eigenvalues.