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(SUMMARIES)



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PHYSICAL PRINCIPLES OF NON-LINEAR NEURONAL INFORMATION PROCESSING

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This paper attempts to abstract physical "first principles" from physiological concepts and data and to convert them into mathematical formula - notwithstanding the fact that the necessary oversimplification of highly subtle biological complexities may be quickly dismissed as naive by biologists.

To begin with, we set up a mathematical equation of a single neuron by starting from a few experimental electrophysiological facts which can be considered basic for an overall description of neuronal activities at an "above-biochemical" level, thereby considering a neuron as an object of electro-dynamics. There are three experimental results sufficient to derive a neuron's differential equation between the input current $I(x,t)$ (related to the postsynaptic potential) and the membrane potential $u(x,t)$, x being the axial space co-ordinate and t the time, viz., (i) the reaction current in the membrane to a voltage jump in the potential u in a voltage-clamp experiment; (ii) the form of the non-linear characteristics $N(u)$ and K of the sodium and potassium currents (and the delay of the K with respect to the Na current in time); (iii) the frequency responses of the transversal and longitudinal impedances of a nerve fibre.

These principles lead to the following differential equation for a neuron:

$$\frac{\partial^2 u}{\partial x^2} - LKCr \frac{\partial^2 u}{\partial t^2} - \left[rC + KLr \frac{\partial N(u)}{\partial u} \right] \frac{\partial u}{\partial t} + LK \frac{\partial^3 u}{\partial x^2 \partial t} - Kru - rN(u) = - LKr \frac{\partial I}{\partial t} - rI - Kru_0, \quad (1)$$

where $u(x,t)$ is the membrane potential, $I(x,t)$ the input current, x the axial space co-ordinate, t the time, r the longitudinal resistance, C a capacitive delay, K the K -conductance, L an inductive storage element due to a biochemical transport delay and $N(u)$ the non-linear membrane characteristic of the sodium current which is responsible for the fundamental dynamical properties of a neuron. Passing to $r = 0$, Eq.(1) reduces to the

non-linear oscillator equation for an infinitesimal element of the neuron, viz.

$$LKC\ddot{u} + [C + LK \partial N(u)/\partial u]\dot{u} + N(u) + Ku = LK\dot{I} + I + Ku_0 \quad (2)$$

or $\ddot{u} + g(u)\dot{u} + f(u) = F(t)$ which, as does Eq.(1), carries all the characteristics of van der Pol and Duffing's equations for relaxation oscillations and jump phenomena, etc. (In Eqs.(1) and (2), u_0 is a fixed constant.)

We make a stability analysis of Eq.(1) and find the relation $K \gg \sqrt{C/L}$ to be necessary for the neuron to be capable of developing oscillatory instability (pulse production). Solving Eq.(1) by perturbation theory, we derive an analytic relation for the dependence of the output impulse frequency ω on the average amplitude of the input excitatory post-synaptic potential, an expression which is in excellent agreement with experimental results obtained for *Limulus* and *Carcinus*. Finally we analyse what happens if a neuron is excited periodically with a frequency $\omega_{\text{psp}} \approx \omega_{\text{pulse}}$. We derive a relation between the energy stored in a neuron E and the excitation frequency ω . The diagram $E(\omega)$ consists of a set of resonance curves from which one infers how the neuron's non-linear structure causes discontinuities in its response, known as jump effects, bursts or rhythmic discharges, in virtue of infinitesimal frequency changes due to internal noise. This is a typical example of the Thom-Zeeman "Catastrophe Theory".

We then discuss two aspects of neural networks, namely inhibition fields and non-linear neural nets under the action of stochastic inputs. First, considering an array of receptor cells along the x-axis, inhibition of the cell at point x by those at points $x-\xi$ and $x+\xi$ means that, given an input $i(x)$, the output $o(x)$ is $o(x) = i(x) - \lambda i(x-\xi) - \lambda' i(x+\xi)$. Expanding into a Taylor series, dropping all terms of order ξ^3 and higher gives the result $o(x) = i(x) - \alpha i'(x) - \beta i''(x)$, where $\alpha \equiv 0$ for symmetric inhibition ($\lambda = \lambda'$). Approximating $i(x)$ by a (smeared-out) step function $\theta(x)$ we obtain the output $o(x) = \theta(x) - \beta \delta'(x)$ in case of symmetric inhibition, where $\delta'(x)$ is a (smeared-out) delta-function. This formula ($o(x)$ plotted against x) shows the familiar contrast accentuation (Mach bands) if $i(x)$ and $o(x)$ are interpreted, e.g., as light intensities. We then analyse the case of unsymmetric inhibition ($\alpha \neq 0$) which gives rise to a shift in the extrema, the case of a bimodal inhibition function, giving rise to fluctuations in intensity around the conventional extrema and, finally, study

non-linear phenomena in the auditory system, such as the frequency shift of tones when their intensity is increased.

In the last part of the paper the following problem is discussed: Given a neural net, made up of non-linear neurons, into which stochastic signals are fed. We ask under which circumstances will the output's range of fluctuation be increased or decreased by the net. That is, under which conditions does the coupling mechanism make the output more indeterminate or more deterministic. We indicate how to extend these considerations to the case of spatial information processing in non-linear neural nets.

REFERENCES

H. Hahn and W. Güttinger, Internat. J. Neuroscience 3, 67 (1972) and
W. Güttinger, Internat. J. Neuroscience 3, 61 (1972). A detailed bibliography
may be found in these papers; cf. also the papers of J. Taylor and E. Zeeman
(this report).