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DOI:
10.1007/BF00336939

Document status and date:
Published: 01/01/1980

Document Version:
Publisher's PDF, also known as Version of Record (includes final page, issue and volume numbers)

Biol. Cybern. 39, 11–14 (1980)

Biological Cybernetics

Instabilities in a Continuous Medium Model for the Retina

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Abstract. The shape of the spatial response of the retina on a small light stimulus as found by Rodieck (1965) for the cat, and proposed for the human retina among others by Korn and von Seelen (1972), resembles a Mexican hat known as a sombrero. A model presented by Röhler (1976), using a continuous medium as a description of the retina, can lead to such a "Mexican hat" response function for a specific choice of parameters. The spatial Fourier transform of this response function has a general appearance that corresponds to that calculated for stationary signals. However, such an analysis of the model for stationary signals is incomplete. Inspection of the time-dependent equations shows that it is unstable precisely for those parameter values that give the stationary response function its desired shape. Such stationary situations cannot be physically realized since the model is unstable.

Introduction

Electrophysiological signals in the peripheral vertebrate retina are known to vary continuously with receptor illumination if the photon rate has an appreciable value. The action potentials in the optic nerve (spikes) are generated in the ganglion cell layer. These signals transmit information by pulse-interval modulation[1], the intervals varying continuously with receptor illumination. In psychophysics an approach in terms of continuous signals in time or space domain has been shown to be useful for predicting the detectability of stimuli (e.g. Roufs, 1974; Wilson and Bergen, 1979).

1 For reviews of retinal signal processing see for instance Davson (1976), Fuortes (1972), Kuffler (1977) or Rodieck (1973)

Various models have been proposed to describe the response of the retina to a stimulus varying both in space and time. Usually one is particularly interested in responses to basic stimuli which are suitable for the prediction of the response of arbitrary stimuli. For example, in the case of linear models this may be the response to a pulsed point source. The state of the art is still a venture in exploring the possibilities of various models with respect to time-dependent and position-dependent input signals. From those available we mention a model given by Korn and von Seelen (1972). Inspired by physiological findings in the cat retina reported by Rodieck (1965), they postulate for the response to a point source a function of the shape shown in Fig. 1.

Following Rodieck (1965) they argue that the "Mexican hat" is the sum of two antagonistic mechanisms, the "bowl" of the sombrero being a curve of gaussian shape due to excitative processes, and the "rim" a broader gaussian curve originating from in-

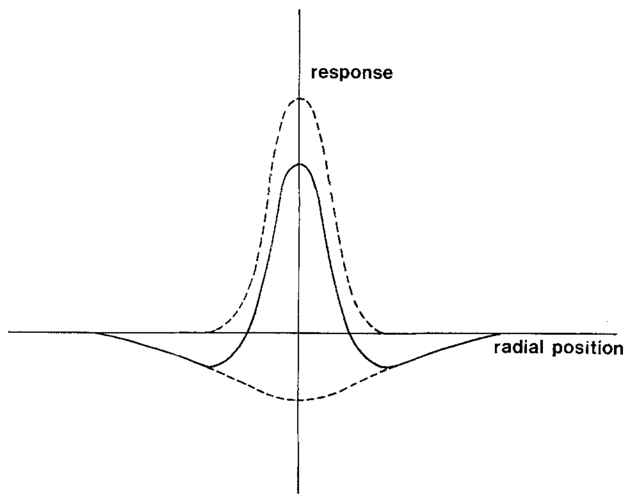

Fig. 1. Response to a point source as postulated by Korn and von Seelen (1972)

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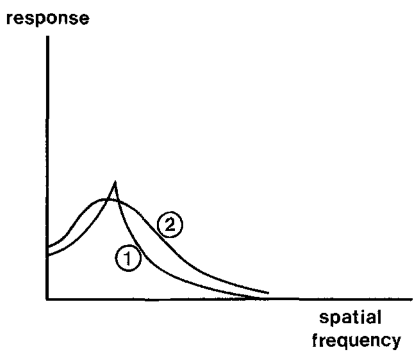

Fig. 2. Oualitative comparison of spatial Fourier transforms of responses to a line source 1. according to Röhler (1978), 2. corresponding to the "Mexican hat" response Korn and von Seelen (1972) used

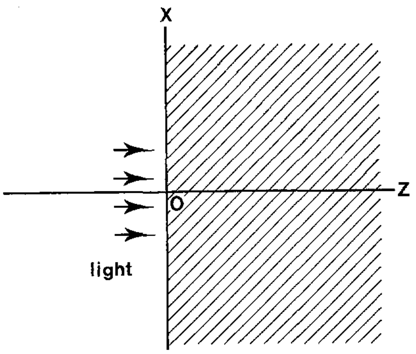

Fig. 3. The shaded area represents the continuous medium in the half-space $z \geqq 0$ as a model for the retina

hibitive processes with different relaxation times. They needed two superimposed systems of this kind to obtain the right type of temporal response. Röhler (1978) proposes a continuous model for the propagation of electrochemical signals in the retina, which has the interesting feature that the spatial Fourier transform of the response to a line source is similar to that of the "Mexican hat" used by Korn and von Seelen and others. The spatial Fourier transforms are compared qualitatively in Fig. 2.

In view of the attractive property that it leads to a "Mexican hat"-like response in a natural way, we analyzed Röhler's model in more detail in the time-space domain.

Analysis

Röhler simulates the retina by a continuous medium covering the half-space as drawn in Fig. 3. His model description results in a differential equation for signal transmission in the retina in terms of $u(x, z, t)$, the local value of the membrane potential. When S_τ is the time-shift operator with the property $S_\tau u(x, z, t) = u(x, z, t-\tau)$, a shift over a time interval τ, the equation is:

$$\frac{1}{k}\frac{\partial u}{\partial t} = \Delta u - \alpha_1 u - \alpha_2 S_\tau u .$$

Here Δ is the Laplacian differential operator, k an effective signal diffusivity. The terms $\alpha_1 u + \alpha_2 S_\tau u$ are interpreted as losses, instantaneous and with a delay time τ respectively, when α_1 and α_2 are positive. Negative values of the α's are not excluded. These two terms represent a simplification proposed by Röhler of an originally more general term:

$$\int_0^t u(x, z, t')\,\alpha(t-t')\,dt' .$$

For a stationary periodic signal input (grating pattern)

$$u = f(x) = \sum_{v=0}^{\infty} a_v \cos vx \quad \text{at the plane } z=0$$

the solution obtained is

$$u = \sum_v a_v e^{-\gamma z} \cos vx$$

with $\gamma = \sqrt{v^2 + \alpha_1 + \alpha_2}$, if $v^2 + \alpha_1 + \alpha_2 > 0$.

The condition $u \to 0$ as $z \to \infty$ is used as boundary condition. When $\alpha_1 + \alpha_2 < 0$, for small values of v such that $v^2 + \alpha_1 + \alpha_2 < 0$, the solution is

$$u = \sum_{v=0}^{\infty} (B_v^* \cos \gamma z + C_v^* \sin \gamma z) \cos vx$$

with $\gamma = \sqrt{-(v^2 + \alpha_1 + \alpha_2)}$.

The constants C_v^* are undetermined and Röhler (1976) (arbitrarily) leaves out the sine part of the solution. With that choice, for a particular value $z = z_0$ representing the lower boundary of the retina, a transfer function

$$P(v) = \begin{cases} e^{-\gamma z_0}, & \gamma = \sqrt{v^2 + \alpha_1 + \alpha_2} \quad v^2 + \alpha_1 + \alpha_2 > 0 \\ \cos \gamma z_0, & \gamma = \sqrt{-(v^2 + \alpha_1 + \alpha_2)} \quad v^2 + \alpha_1 + \alpha_2 < 0 \end{cases}$$

is obtained which may have the form of Fig. 2 for a suitably chosen z_0.

$P(v)$ has a maximum of 1 at $v = \sqrt{-(\alpha_1 + \alpha_1)}$.

This form, compared with the Fourier transform of the response function obtained by Rodieck (1965), is taken as a confirmation of the possible usefulness of the model. Note that a negative value of $\alpha_1 + \alpha_2$ has to be chosen!

Now consider the full time-dependent equation to determine the evolution for $t > 0$ of a sudden deviation u_1 at $t = 0$ from the stationary situation u (hence $u_1 = 0$ for $t < 0$). This deviation represents a disturbance of the system. The equation for the deviation $u_1(x, z, t)$ is

$$\frac{1}{k}\frac{\partial u_1}{\partial t}=\frac{\partial^2 u_1}{\partial x^2}+\frac{\partial^2 u_1}{\partial z^2}-\alpha_1 u_1-\alpha_2 S_\tau u_1 .$$

We suppose that this equation has to be solved for the boundary conditions $u_1=0$ at $z=0$ and $u_1 \to 0$ as $z \to \infty$. This implies that we assume that the value of the total potential $u+u_1$ in the plane $z=0$ can be exactly prescribed. [An exactly prescribed flux $\frac{\partial}{\partial z}(u+u_1)$ would have led to the condition $\frac{\partial u_1}{\partial z}=0$ at $z=0$. The same conclusions would be obtained. Even functions then replace odd functions in the following.]

An arbitrary initial condition for u_1 may be continued as an odd function into the half-space $z<0$ and written as

$$u_1(x, z, 0)=\int_{-\infty}^{+\infty}\int_{-\infty}^{+\infty} w(v, \lambda, 0) \exp i(\lambda z+v x) d\lambda dv$$

in terms of its Fourier transform $w(v, \lambda, 0)$, which is odd in λ. Similarly we write the solution as

$$u_1(x, z, t)=\int_{-\infty}^{+\infty}\int_{-\infty}^{+\infty} w(v, \lambda, t) \exp i(\lambda z+v x) d\lambda dv .$$

w must then satisfy the equation

$$\frac{1}{k}\frac{dw}{dt}=-(v^2+\lambda^2+\alpha_1) w-\alpha_2 S_\tau w .$$

Note that w does not change its odd parity with respect to λ as time proceeds. Hence u_1 will be odd in z and the boundary condition $u_1(x, 0, t)=0$ is satisfied at all times.

For $0<t<\tau$ the solution is $w(v, \lambda, t)=w(v, \lambda, 0) e^{-\mu_1 t}$ with $\mu_1/k=v^2+\lambda^2+\alpha_1$.

The Fourier components vary exponentially with time, but also those which decay remain present in the spectrum if τ is finite. For $t>\tau$ the solution is

$$w(v, \lambda, t)=w(v, \lambda, \tau) e^{-\mu_2(t-\tau)}$$

with

$$\mu_2/k=v^2+\lambda^2+\alpha_1+\alpha_2 e^{+\mu_2 \tau} .$$

For small values of $v^2+\lambda^2$ negative values of μ_2 may occur when $\alpha_1+\alpha_2<0$, which implies that the corresponding Fourier components will grow with time. The components with $\mu_2=0$, for which $v^2+\lambda^2=-(\alpha_1+\alpha_2)$, lie between the decaying ones with $\mu_2>0$, and those with $\mu_2<0$ which grow without limit.

For initial conditions having Fourier components with $v^2+\lambda^2<-(\alpha_1+\alpha_2)$ the solution of Röhler's model "explodes". As a system is considered stable only if it is stable for arbitrary initial conditions representing disturbances, Röhler's model should be classified as unstable when $\alpha_1+\alpha_2<0$. A more exact analysis using the Laplace transformation provides complete information about the solution and its stability. The regions of instability are shown in Fig. 4.

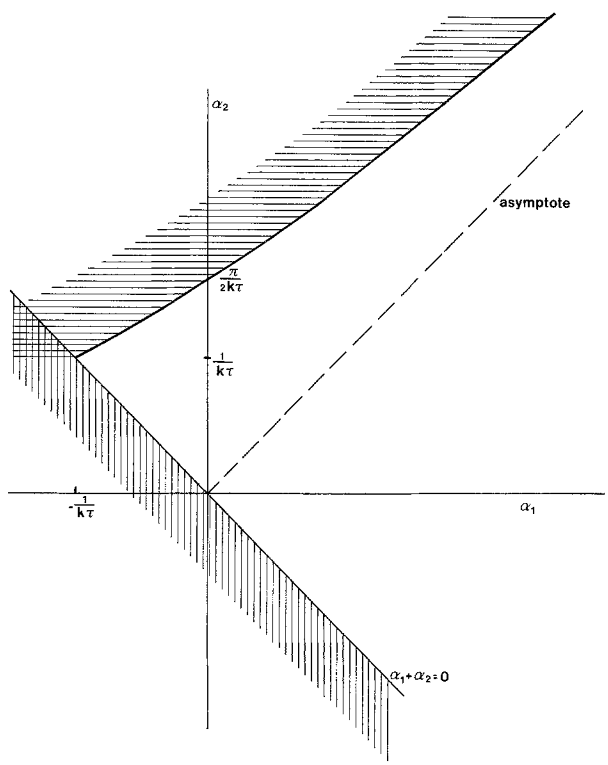

Fig. 4. The shaded area is the region of instability of Röhler's (1976) model in the α_1, α_2 plane

We have found no other way than by spatial superposition of two stable Röhler-type models to arrive at a response function of the shape described by Korn and von Seelen. Such a model is intellectually not very attractive.

Conclusion

The simple correspondence between Rodieck's response function (1965) and Röhler's model (1976) rests on the similarity of their response function for stationary signals when the parameters in Röhler's model are chosen such that $\alpha_1+\alpha_2<0$. Since Röhler's model is unstable in that case, the calculated response for stationary signals is not physically realistic.

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Received: April 10, 1980

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