

# Exact solution of the nonlinear dynamics of recurrent neural mechanisms for direction selectivity

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**Abstract** Different theoretical models have tried to investigate the feasibility of recurrent neural mechanisms for achieving direction selectivity in the visual cortex. The mathematical analysis of such models has been restricted so far to the case of purely linear networks. We present an exact analytical solution of the nonlinear dynamics of a class of direction selective recurrent neural models with threshold nonlinearity. Our mathematical analysis shows that such networks have form-stable stimulus-locked traveling pulse solutions that are appropriate for modeling the responses of direction selective cortical neurons. Our analysis shows also that the stability of such solutions can break down giving raise to a different class of solutions ("lurching activity waves") that are characterized by a specific spatio-temporal periodicity. These solutions can not arise in models for direction selectivity with purely linear spatio-temporal filtering.

# 1 Introduction

Direction selectivity in the primary visual cortex has been accounted for by feed-forward (e.g. [1, 2, 3, 4]) as well as by recurrent neural mechanisms [5, 6, 7]. The mathematical analysis of recurrent mechanisms for direction selectivity has so far been based on methods from linear systems theory by neglecting the nonlinear properties of the neurons. The nonlinear dynamic phenomena resulting from the interplay between the recurrent connectivity and the nonlinear threshold characteristics of the neurons have not been tractable in this theoretical framework.

In this paper we present a mathematical analysis that takes the nonlinear behavior of the individual neurons into account. We present the result of an analysis of networks with two different types of threshold nonlinearities for which closed-form analytical solutions of the network dynamics can be derived. Our result extends previous mathematical work on the the dynamics of nonlinear cortical networks with strong recurrent feedback [8, 9, 10] to the case of stimulus-driven moving solutions in networks with asymmetric lateral connections.

We show that nonlinear recurrent networks with asymmetric lateral connections have a class of form-stable solutions, in the following signified as *stimulus-locked traveling pulses*, that are suitable for modeling the activity of direction selective neurons. The stability of the traveling pulse solutions of the nonlinear network can break down giving raise to another class of solutions (*lurching activity waves*) that is characterized by spatio-temporal periodicity. Our analysis showed that networks with a biologically realistic degrees of direction selectivity typically also show transitions between traveling pulse and lurching solutions.

## 2 Basic model

Ensembles of direction selective neurons with the same receptive field center and preferred speed are modeled as points of a continuous neural media, or neural field. Spatially continuous models have been proposed before to analyze the dynamic behavior of a large ensembles of neurons in the visual cortex [11, 8, 12, 9]. The scalar quantity  $u(x, t)$  represents the activity of neurons with receptive field center  $x$  at time  $t$ . Its dynamics is given by the integro-differential equation:

$$\tau \dot{u}(x, t) + u(x, t) = \int w(x - x') f(u(x', t)) dx' + b(x, t) \quad (1)$$

The function  $f$  is nonlinear and characterizes the relationship between the input current and the firing rate of the individual neuron ensembles. Two different forms of this nonlinearity are discussed below.  $\tau$  is a time constant of the dynamics. The function  $w(x)$  characterizes the strength of the excitatory and inhibitory lateral connections, dependent on the positions of the neurons in the neural field. Direction selectivity arises when this function is asymmetric. In the following we always assume that the

stimulus has a constant shape that is translating with the constant stimulus velocity  $v$ , leading to an input signal distribution  $b(x, t) = B(x - vt)$  in the neural dynamics.

To analyze the dynamics Eq. (1) we introduce a new coordinate system that moves together with the stimulus by defining the new spatial coordinate  $y = x - vt$  and the activity distribution  $U(y, t) = u(x, t)$  (Cf. [9]). This results in the dynamics:

$$\tau \frac{\partial}{\partial t} U(y, t) - \tau v \cdot \frac{\partial U(y, t)}{\partial y} + U(y, t) = \int w(y - y') f(U(y', t)) dy' + B(y) \quad (2)$$

A stationary solution in the moving frame corresponds to a traveling pulse solution with velocity  $v$  in the original stationary coordinate system. We will analyze below the existence and stability of form-stable solutions of the nonlinear integro-differential equation Eq. (2) for two cases, in which closed-form solutions can be derived.

### 3 Analysis for step function threshold

The nonlinear activation function is taken to be the Heaviside step function  $f(z) = \Theta(z)$ , where  $\Theta(z) = 1$  for  $z > 0$ , and zero otherwise. The dynamics with a constant input was analyzed by Amari [8], whose approach does not apply directly to Eq. (1) because of the presence of the spatial gradient. We assume in the following the existence of a single activation peak, and we signify by the interval  $I = [y_1(t), y_2(t)]$  the set of neurons with non-negative activation ( $U(y, t) \geq 0$ ). Using the fact that, by continuity,  $U(y_1, t) \equiv U(y_2, t) \equiv 0$  we can derive the following self-consistent equations for the boundaries of the interval  $I$  in the stationary state

$$\tilde{W}(y_1^* - y_2^*) - \tilde{W}(0) = \tilde{B}(y_1^*) \quad (3)$$

$$\tilde{W}(0) - \tilde{W}(y_2^* - y_1^*) = \tilde{B}(y_2^*) \quad (4)$$

with  $W(z) = \int_0^z w(y) dy$  and the functions  $\tilde{W}(y) = O[W(y); \tau v]$  and  $\tilde{B}(y) = O[B(y); \tau v]$ , where  $O$  is the integral operator defined by

$$O[g(z); \alpha] = \begin{cases} \frac{1}{\alpha} \int_x^\infty g(z') \exp(\frac{z-z'}{\alpha}) dz' & \text{for } \alpha > 0 \\ g(z) & \text{for } \alpha = 0 \\ \frac{-1}{\alpha} \int_{-\infty}^z g(z') \exp(\frac{z-z'}{\alpha}) dz' & \text{for } \alpha < 0. \end{cases} \quad (5)$$

The stationary solution is completely defined by the two boundary points  $y_1^*$  and  $y_2^*$  through  $U^*(y) = \tilde{W}(y - y_1^*) - \tilde{W}(y - y_2^*) + \tilde{B}(y)$ . The stability of this solution is analyzed by perturbing  $U^*(y)$ . The dynamics of the perturbation  $\delta U(y, t)$  is given by the linearized dynamics

$$\tau \frac{\partial \delta U}{\partial t} - \tau v \frac{\partial \delta U}{\partial y} + \delta U(y, t) = \frac{w(y - y_1^*)}{c_1^*} \delta U(y_1^*, t) - \frac{w(y - y_2^*)}{c_2^*} \delta U(y_2^*, t) \quad (6)$$

where  $c_i^* = \partial U^*(y_i)/\partial y$  for  $i = 1, 2$  are gradients of  $U^*(y)$  at boundaries.

By solving the perturbation dynamics using Laplace transformation it can be shown that the stationary solution is asymptotically stable if the following equation

$$(G(0, s) - c_1^*)(G(0, s) + c_2^*) = G(y_1^* - y_2^*, s)G(y_2^* - y_1^*, s) \quad (7)$$

with  $G(z, s) = O[w(z); \tau v/(1 - \tau s)]$  has no solutions in the open right half of the complex plane (i.e. for  $\text{Re}\{s\} > 0$ ).

## 4 Analysis for half-wave rectifying threshold

The general proceeding used in section 3 can in principle be extended for networks with half-wave rectifying threshold. In the general case, however, no closed form solutions can be derived (See [13]). A closed form solution can be obtained by extending methods from [10]. Assume that the network is defined over the periodic spatial domain  $[-\pi/2, \pi/2]$ . When the stimulus distribution and the interaction kernel have only a small number of Fourier components, a closed form solution can be derived. We analyzed the case for  $B(x) = b_0 + b_2 \cos(2(x - x_b))$  and  $w(x) = w_0 + w_2 \cos(2(x - x_w))$  with  $b_i$ ,  $w_i$ , and  $x_b$  and  $x_w$  being constants. In this case the dynamics is fully determined by the behavior of the order parameters

$$r_0(t) = \int_{-\pi/2}^{\pi/2} \frac{dx'}{\pi} u(x', t) \quad (8)$$

$$r_2(t) = \int_{-\pi/2}^{\pi/2} \frac{dx'}{\pi} u(x', t) e^{2i(x' - \Psi(t))} \quad (9)$$

where  $\Psi(t)$  is chosen as to keep  $r_2$  real.  $r_0(t)$  measures the mean neural activities across the network and  $r_2(t)$  signifies the spatial modulation in the activity profile of  $u(x, t)$ . Different from Hansel's and Sompolinsky's model [10], the network we analyzed is stimulus driven and uses an asymmetric interaction kernel. The details of the mathematical analysis are given in [13].

Figure 1 shows the comparison between the results from the mathematical analysis and simulations. (The network with step threshold leads to very similar simulation results). Panel A shows the speed tuning curve plotted as values of the order parameters  $r_0$  and  $r_2$  with respect to different stimulus velocities  $v$ . The solid lines indicate the numerical simulation results, and the dotted lines the results from the analytical solution. For both, the analytical and the simulated solution the velocity tuning curve depends critically on the asymmetrical part of the interaction kernel. The asymmetry determines in particular the optimal velocity of the direction selective neurons [13]. Panel B shows the largest real part of the eigenvalues of a stability matrix that can be obtained by linearizing the order parameter dynamics around the stationary solution. For small and very large stimulus velocities the largest real parts of the eigenvalues

become positive indicating a loss of stability of the form-stable solution. To verify this result we calculated the variances of the order parameters  $r_0$  and  $r_2$  over time from the simulations. Panel C shows the average variations as function of the stimulus velocity. At the velocities for which the eigenvalues indicate a loss of stability the variability of the amplitudes suddenly increases, consistent with our interpretation.

An interesting observation is illustrated in panels D and E that show a color-coded plot of the space-time evolution of the activity. Panel E shows the propagation of the form-stable peak over time. Panel D shows the solution that arises when stability is lost. This solution is characterized by a spatio-temporal periodicity that is defined in the moving coordinate system by  $U(y, t + nT_0) = U(y, t)$ ,  $T_0$  being a constant that depends of the network dynamics. Solutions of this type have been described before in spiking thalamic networks [14]. We found that this solution type arises very robustly for both types of threshold functions when the network achieved substantial direction selective behavior.

## 5 Conclusion

We have presented different methods for an analysis of the nonlinear dynamics of simple recurrent neural models for the direction selectivity of cortical neurons. Compared to earlier work, we have taken into account the essentially nonlinear effects that are introduced by the nonlinear threshold characteristics of the cortical neurons. The key result of our work is that such networks have a class of form-stable traveling pulse solutions that behave similar as the solutions of linear spatio-temporal filtering models within a certain regime of stimulus speeds. By the essential nonlinearity of the network, however, bifurcations can arise for which the traveling pulse solutions become unstable. We observed that in this case a new class of spatio-temporally periodic solutions ("lurching activity waves") arises. Since we found this solution type very frequently for networks with substantial direction selectivity our analysis suggests that such "lurching behavior" might be observable in the primary visual cortex, providing strong evidence for the hypothesis that direction selectivity is essentially based on lateral connectivity. An experimental demonstration of this effect might, however, be complicated by the mutual inhibition of neuron ensembles that are selective for different stimulus speeds.

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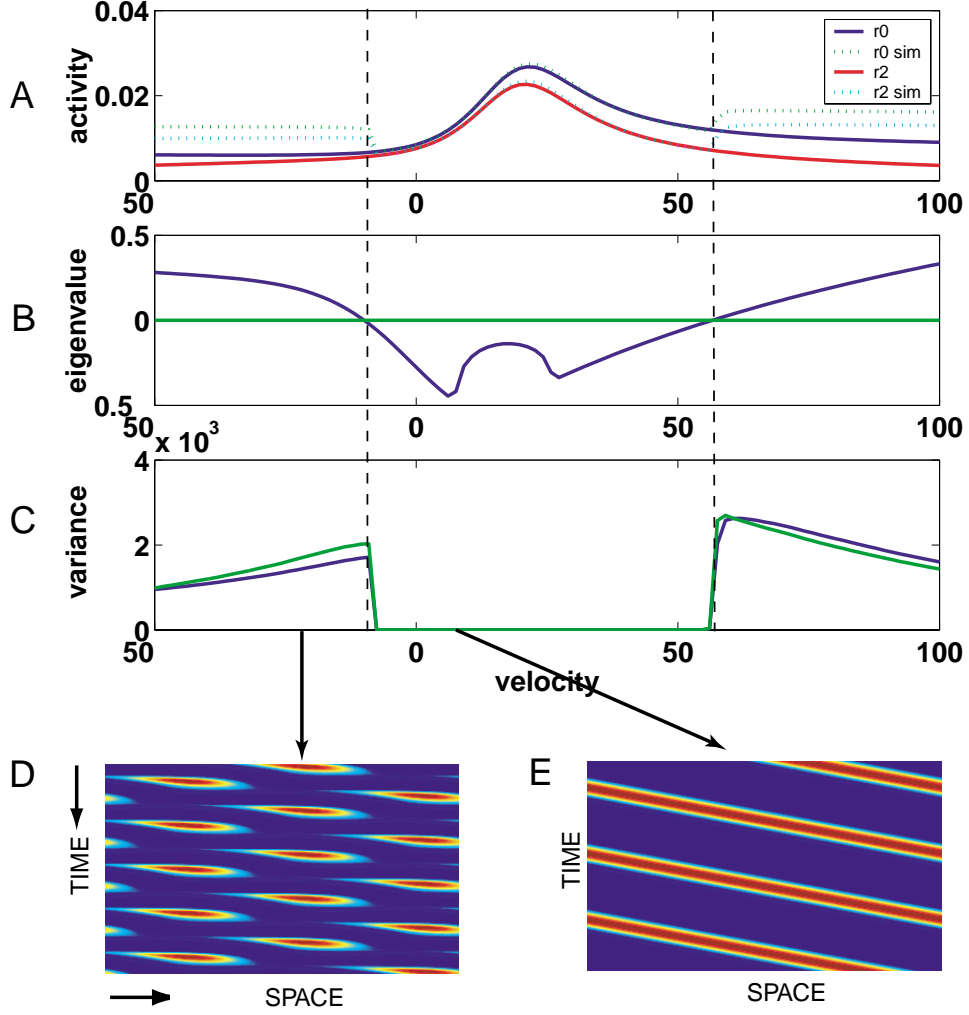


Figure 1: Traveling pulse solution and its stability for the half-wave rectifying threshold model. Panel A shows the velocity tuning curves of the order parameters  $r_0$  and  $r_2$ . The solid lines indicate the results from the numerical simulation, while dotted lines represent the results from the analytical solution. Panel B shows the maximum real part of the eigenvalues of a stability matrix that can be obtained from perturbed linear dynamics around the stationary solution. For small and very large stimulus velocities the largest real part of the eigenvalues becomes positive indicating a loss of stability of the form-stable solution. Panel C shows the average variances over time of the order parameters  $r_0$  (blue curve) and  $r_2$  (green curve) obtained from the simulation. A nonzero variance signifies a loss of stability of the traveling pulse solution. This result is consistent with eigenvalue analysis in Panel B. A color coded plot of spatial-temporal evolution of the activity  $u(x,t)$  is shown in panels D and E. Panel E shows the propagation of the form-stable peak over time. Panel D shows the lurching activity wave that arises when stability is lost.

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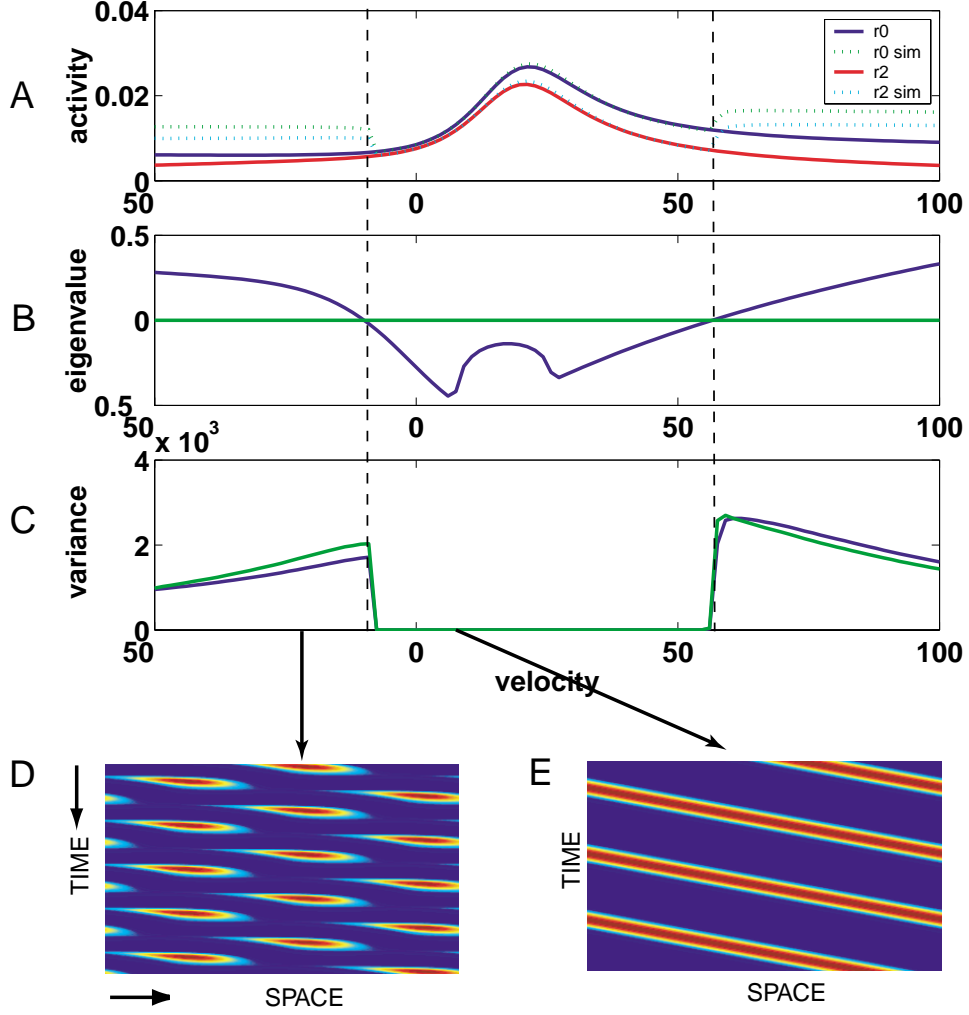


Figure 1: Traveling pulse solution and its stability for the half-wave rectifying threshold model. Panel A shows the velocity tuning curves of the order parameters  $r_0$  and  $r_2$ . The solid lines indicate the results from the numerical simulation, while dotted lines represent the results from the analytical solution. Panel B shows the maximum real part of the eigenvalues of a stability matrix that can be obtained from perturbed linear dynamics around the stationary solution. For small and very large stimulus velocities the largest real part of the eigenvalues becomes positive indicating a loss of stability of the form-stable solution. Panel C shows the average variances over time of the order parameters  $r_0$  (blue curve) and  $r_2$  (green curve) obtained from the simulation. A nonzero variance signifies a loss of stability of the traveling pulse solution. This result is consistent with eigenvalue analysis in Panel B. A color coded plot of spatial-temporal evolution of the activity  $u(x,t)$  is shown in panels D and E. Panel E shows the propagation of the form-stable peak over time. Panel D shows the lurching activity wave that arises when stability is lost.