

Wilson-Cowan Model

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Definition

The Wilson-Cowan model describes the evolution of excitatory and inhibitory activity in a synaptically coupled neuronal network. As opposed to being a detailed biophysical model, the system is a coarse-grained description of the overall activity of a large-scale neuronal network, employing just two differential equations. Key parameters in the model are the strength of connectivity between each subtype of population (excitatory and inhibitory) and the strength of input to each subpopulation. Varying these generates a diversity of dynamical behaviors that are representative of observed activity in the brain, like multistability, oscillations, traveling waves, and spatial patterns.

Detailed Description

Many regions of the brain process large-scale spatiotemporally structured inputs (Wang 2010). Understanding the resulting neural activity requires macroscopic models that can track the average firing rate across many areas of a neuronal network (Ermentrout 1998). This was the approach in the seminal work of Wilson and Cowan (1972, 1973), who derived effective equations for the macroscopic behavior of a large network of neurons. The approach is analogous to using statistical thermodynamics to relate the Brownian motion of particles to a mean ensemble motion of a whole fluid or gas (Reichl and Prigogine 1980). Thus, Wilson and Cowan (1972, 1973) derive an effective system for the mean field of an underlying statistical process.

Space-Clamped Model

Starting with a large population of densely coupled neurons, Wilson and Cowan (1972) derived effective equations for the proportion of cells in a population that are active per unit time. Crucially, the effective behavior of the population relies on interactions between excitatory and inhibitory cells, where $a_e(t)$ and $a_i(t)$ are the proportion of excitatory and inhibitory cells firing per unit time at instant t . Thus, $a_{e,i}(t) = 0$ corresponds to a low-activity resting state. Excitatory (inhibitory) neurons make their neighbors more (less) likely to become active, and activation is a nonlinear function F_e (F_i) of the presently active proportion of cells. These assumptions yield the system

$$\tau_e \frac{da_e}{dt} = -a_e(t) + [1 - r_e a_e(t)] F_e(w_{ee} a_e(t) - w_{ei} a_i(t) + I_e(t)), \quad (1a)$$

$$\tau_i \frac{da_i}{dt} = -a_i(t) + [1 - r_i a_i(t)] F_i(w_{ie} a_e(t) - w_{ii} a_i(t) + I_i(t)). \quad (1b)$$

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Thus, the activity variables $a_{e,i}(t)$ obey first-order kinetics with timescales $\tau_{e,i}$, tracking the response of each subpopulation. The nonlinearities are typically chosen to be sigmoidal

$$F_j(x) = \frac{1}{1 + e^{-\gamma_j(x-\theta_j)}}, \quad j = e, i, \quad (2)$$

where the gain γ_j and threshold θ_j can depend on the population type $j = e, i$. The argument x is a weighted sum of the proportion of active excitatory and inhibitory cells, where $w_{jk} \geq 0$ describes the strength of connection from cell type k to j . The system Eq. (1) also captures the refractory dynamics of both populations, defined by the pre-factors $[1 - r_j a_j(t)]$, tracking the period of time during which cells are incapable of stimulation following an activation. This term has often been neglected in subsequent considerations of the model, and Pinto et al. (1996) showed that it effectively rescales the parameters of the nonlinearities $F_{e,i}$. The inputs $I_j(t)$ represent the sum of currents arriving to population j from external sources (e.g., other brain areas or an implanted electrode). The derivation of Eq. (1) also presumes important characteristics of time-dependent rates $a_{e,i}$ for large-scale computation that are captured by temporally coarse-grained traces (Wilson and Cowan 1972).

By performing a phase plane analysis on Eq. (1), to find the stability of fixed points $(a_e(t), a_i(t)) = (\bar{a}_e, \bar{a}_i)$, Wilson and Cowan (1972) observed two typical modes of behavior. First, when the strength of synapses between excitatory cells is sufficiently strong, multiple stable fixed points can exist: a high excitation and a low excitation state. Alternatively, when the strength of connections between inhibitory subpopulation is sufficiently weak, the system Eq. (1) supports limit cycle solutions. In these limit cycles, a small proportion of active excitatory cells kindle other cells' activation, eventually recruiting inhibitory cells that turn all cells off, starting the cycle over. Thus, Wilson and Cowan (1972) presented a simple mechanism for oscillations in firing rate activity, an ubiquitous neural phenomenon (Wang 2010). Notably, mutually inhibitory models were adapted from Eq. (1) by considering an arbitrary number N of neural populations coupled together solely by inhibition. Each population is then conceived of as representing a separate stimulus or percept, making such models ideal for studying the neural mechanisms of decision making (Usher and McClelland 2001; Bogacz et al. 2006) and perceptual rivalry (Laing and Chow 2002; Wilson 2003).

Spatially Structured Model

The model Eq. (1) ignores potential spatial structure in the network of synaptic connections or the external inputs to the network. Upon considering a spatially organized network of neurons, Wilson and Cowan (1973) described the connectivity between different regions of the network using functions that depend on the position of the origin y and target x of a synaptic connection. In doing so, this yields a set of partial integral equations

$$\tau_e \frac{\partial a_e(x, t)}{\partial t} = -a_e(x, t) + [1 - r_e a_e(x, t)] F_e(w_{ee}^* a_e - w_{ie}^* a_i + I_e(x, t)) \quad (3a)$$

$$\tau_i \frac{\partial a_i(x, t)}{\partial t} = -a_i(x, t) + [1 - r_i a_i(x, t)] F_i(w_{ei}^* a_e - w_{ii}^* a_i + I_i(x, t)) \quad (3b)$$

where $w_{jk} * a_k$ is a convolution operator

$$w_{jk} * a_k = \int_{\Omega} w_{jk}(x - y) a_k(y, t) dy \quad (4)$$

representing the effective drive to population j at location x received from population k . Writing the network of synaptic interactions as a spatial convolution gives a more general definition of the geometry of the network than discrete neural network models that use matrices to describe connectivity (McCulloch and Pitts 1943; Hopfield 1984). Typical weight functions are the Gaussians

$$w_{jk}(x - y) = k_{jk} e^{-(x-y)^2 / \sigma_k^2} \quad (5)$$

which represent a distance-dependent decay in cortical connectivity. The spatial domain Ω can be of arbitrary dimension and size, but it is usually taken to be one or two dimensional as we describe below. The nonlinearities $F_{e,i}$ are often sigmoids Eq. (2), and refractoriness is modeled by the term $[1 - r_j a_j]$ as before. We note that in Eq. (3), it is possible to track the spatiotemporal evolution of inputs, not just the temporal evolution. A key assumption in deriving Eq. (3) is that the intricacies in firing rate variation that occur on very fine spatiotemporal scales can be coarse-grained (Wilson and Cowan 1973). This results in a system of partial integrodifferential equations that are amenable to mathematical analysis (Bressloff 2012).

Applications and Extensions

Originally, Wilson and Cowan (1973) developed the spatial model Eq. (3) to analyze neural hysteresis phenomena related to binocular vision. Since then, the system Eq. (3) has been used as a canonical model of visual cortical activity, since higher mammals' visual systems possess spatially organized feature maps (Hubel and Wiesel 1977). For instance, a mathematical theory of geometric visual hallucination patterns was developed by using symmetric bifurcation theory to analyze the emergence of Turing patterns when Eq. (3) evolved in $\Omega = \mathbb{R}^2$ (Ermentrout and Cowan 1979; Bressloff et al. 2001). Aside from spontaneous visual experience, the model Eq. (3) was also modified with an additional equation for Hebbian plasticity in the weights w_{jk} to understand the spontaneous organization of the cortical feature maps that underlie the processing of spatiotemporally structured inputs (Kohonen 1982). All the periodically ordered maps for certain features like ocular dominance and orientation selectivity can be incorporated into Eq. (3) by employing the appropriate spatial domain Ω (Ben-Yishai et al. 1995; Bressloff and Cowan 2003).

Since its inception, the system Eq. (3) has also been used to model a variety of other sensory, memory, and motor processes. Early on, work in a related model to Eq. (3) showed the combination of short-range excitation and long-range inhibition ($\sigma_e < \sigma_i$ in Eq. (5)) could stabilize persistent activity into the shape of a bump (Amari 1977). Thus, even in the absence of inputs $I_j(x, t)$, the system Eq. (3) can support a nontrivial profile of spatiotemporal activity due to the activity sustained by recurrent excitation w_{ee} . This mechanism has now been used extensively as a model of visuospatial working memory (Camperi and Wang 1998), since the spatial position of a transient stimulus is known to be stored in cortex as persistent activity that can last for up to several seconds (Durstewitz et al. 2000). Related to this, lateral inhibitory networks have also been employed as idealized models of spatial navigation (Samsonovich and McNaughton 1997) and movement preparation (Erlhagen and Schoner 2002), whose neural correlates are also known to be spatially localized, tuned, persistent activity.

The Wilson-Cowan model Eq. (3) has been extended in many ways to account for the rich diversity of currents, synaptic processes, and fluctuations present in the brain. Spike rate adaptation was considered by Hansel and Sompolinsky (1998), who showed that this resulted in traveling waves of neural activity. Similar phenomena arise upon considering the effects of short-term plasticity (Kilpatrick and Bressloff 2010), which dynamically modulates the strength of the synaptic weight functions w_{jk} . Finally, there has been a lot of interest recently in capturing the effects of fluctuations on spatially extended rate models like Eq. (3). Early efforts have simply considered additive spatiotemporal noise processes (Hutt et al. 2008), but a great deal of progress has been made in deriving effective Langevin equations from stochastic neural networks using path integral methods (Buice and Cowan 2007) or a system size expansion (Bressloff 2012).

Cross-References

- ▶ [Amari Model](#)
- ▶ [Bifurcations, Neural Population Models and](#)
- ▶ [Cognition and Control, Neural Population Models for](#)
- ▶ [Neural Field Model, Continuum](#)
- ▶ [Neural Population Model](#)
- ▶ [Pattern Formation in Neural Population Models](#)
- ▶ [Stochastic Neural Field Theory](#)

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