

## The Wilson–Cowan model, 36 years later

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**Abstract** The Wilson–Cowan model of interacting neurons (1973) is one of the most influential papers published in *Biological Cybernetics* (*Kybernetik*). This paper and a companion paper published in 1972 have been cited over 1000 times. Rather than focus on the microscopic properties of neurons, Wilson and Cowan analyzed the collective properties of large numbers of neurons using methods from statistical mechanics, based on the *mean-field* approach. New experimental techniques to measure neuronal activity at the level of large populations are now available to test these models, including optical recording of brain activity with intrinsic signals and voltage sensitive dyes, and new methods for analyzing EEG and MEG. These measurement techniques have revealed patterns of coherent activity that span centimetres of tissue in the cerebral cortex. Here the underlying ideas are reviewed in a historic context.

The Wilson–Cowan (1972; 1973) model is a set of differential equations that describe the time evolution of the mean level of activity of populations of neurons, using the now familiar nonlinear sigmoidal function to represent the interactions between the populations. This mean-field approach has been used to address many problems in computational

neuroscience (Sejnowski 1976a; Amit and Brunel 1997; Brunel 2000; Latham et al. 2000; Hertz et al. 2004; Renart et al. 2007). The Wilson–Cowan model has also been the starting point for many extensions. The special case with symmetric connectivity allowed an energy function to be defined and was analyzed by Hopfield (1982) and Hopfield and Tank (1986). They showed that the point attractors in this model could be used to store content-addressable memories and that constraint satisfaction problems could also be solved with these equations. Continuum extensions have also been proposed (van Hemmen 2004), where the differences with excitable media are analyzed.

Another important special case is the “balanced” network, in which the excitatory and inhibitory inputs on average cancel (Shadlen and Newsome 1998; Haider et al. 2006; Renart et al. 2007). In the balanced condition, fluctuations can drive the neuron to fire, thereby producing an irregular firing patterns. Equations governing the second-order correlations and covariances have been proposed and used to study balanced networks (Sejnowski 1976b; van Vreeswijk and Sompolinsky 1996, 1998; Moreno-Bote and Parga 2006; Soula and Chow 2007; El Boustani and Destexhe 2009). Similar approaches were also proposed for networks of binary neuron models (Hinton and Sejnowski 1983; Ackley et al. 1985; Ohira and Cowan 1993; Ginzburg and Sompolinsky 1994). A field-theoretic approach that generalizes the mean-field equations is also under way (Buice et al. 2009).

Other extensions include more complex intrinsic properties of neurons such as spike-frequency adaptation and bursting. In the simplest case, it is possible to obtain a second-order mean-field model by using a discretized time frame (Soula and Chow 2007), or in continuous-time (El Boustani and Destexhe 2009). The core of this approach is the “transfer function”, which relates the output of the neuron (firing rate and its variance) to its inputs (mean rate and variance of

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excitatory and inhibitory inputs). Transfer functions can be estimated analytically using the Fokker–Planck approach (Tuckwell 1988; Abbott and van Vreeswijk 1993; Brunel and Sergi 1998; Brunel 2000; Fourcaud and Brunel 2002). However, such results apply only to continuous-time descriptions, and exact solutions are possible only for current-based models, which are not realistic and cannot take into account properties of neurons obtained from conductance measurements in vivo. More realistic transfer functions can be obtained from approximations (Kuhn et al. 2004) or numerical estimates (Kumar et al. 2008; Soula and Chow 2007). It should also be possible to estimate the transfer function directly from real cortical neurons in vitro using a dynamic-clamp with injection of different combinations of conductance-based excitatory and inhibitory synaptic inputs (Bal and Destexhe, work in progress).

The derivation of the Wilson–Cowan model depended on taking the “thermodynamic limit” (in which the number of neurons approaches infinity), but finite-size effects in systems with a finite number of neurons can be important. This results in intermediate “mesoscopic” models that may be appropriate for modelling intermediate spatial scales, such as the number of neurons covered by a camera pixel in optical imaging, which ranges from hundreds to thousand of neurons (Brunel 2000; Renart et al. 2007; Soula and Chow 2007; El Boustani and Destexhe 2009). The extension of this approach to the spatial domain is a challenge for future studies.

To conclude, we have listed here just a few of the many theoretical developments that the Wilson–Cowan model has inspired. As experimental advances in recording from large populations of neurons are refined it will be possible to test the predictions of these models. Multi-scale models are now being developed that will integrate macroscopic models at large spatial scales with models at the microscopic scale, such as the Hodgkin–Huxley biophysical models of single neurons.

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