Thus, the activity variables a

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

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

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

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

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).

The Wilson-Cowan model Eq. (3) has been extended in many ways to account for the rich diversity of currents, synaptic processes, and ßuctuations 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}