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The Stabilized Supralinear Network Model of Cortical Circuitry: The Importance of Being Loosely Balanced

Cortical neurons have expansive, supralinear input/output functions over their entire dynamic range. We start with this simple fact; the assumption that feedback inhibition is strong enough to keep the network stable despite the destabilizijng nature of expansive input/output functions; and simple assumptions on connectivity, i.e. that connectivity strength and/or probability decrease with cortical distance and with decrease in signal correlations. These ingredients suffice to explain a wide variety of nonlinear cortical behaviors. These include sublinear summation of responses to multiple stimuli, which becomes more linear for weak stimuli; summation field sizes (optimal stimulus sizes) that shrink with contrast, in real space and, as we predicted, in feature space, as well as the related fact that a high-contrast surround can facilitate response to a weak center stimulus but suppress response to stronger center stimuli; the suppression of correlated neuronal variability by a stimulus; and multiple ways in which attention modulates neural responses. These outcomes result from the fact that, given supralinear input/output functions and stabilization by feedback inhibition, the dynamics leads recurrent input to cancel or "balance" external input, so that most of the external input a cell receives is cancelled and the net input after cancellation grows sublinearly as a function of the external input. This occurs robustly, without need for fine tuning of parameters. The balance is "loose", meaning that the net input after cancellation is comparable in size to the factors that cancel. A classic "balanced network" model considered tight balancing, meaning that the factors that cancel were very large compared to the net input. At least in its simplest implementation, tight balance allows only linear response. We argue that cortex operates in a loosely balanced regime, which naturally explains the wide variety of nonlinear behaviors described above.