Optimal connectivity profiles for the transmission of population coded signals.

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Across many systems in the brain, information appears to be encoded by a population of neurons. In a population coded signal, activity is distributed over a population of neurons with broad, overlapping tuning curves. The distribution of the activity over many neurons renders the population code fail-safe, fast, and accurate (hyper-acuity). Population codes have been described in the primary and higher visual cortices, motor cortex and hippocampus.

Given the noisy discharges of cortical neurons (Softky and Koch 1993), there has been a large effort to estimate the effect of such noise on the maximal accuracy attainable by a population code (Seung and Sompolinsky 1993). This can be measured, for instance, using the so called Fisher information. Important questions have involved: how does the shape of the tuning functions, the noise, and possible correlations in the noise affect the Fisher information (Abbott and Dayan 1999, Sompolinsky et al 2002).

Another approach has been to investigate possible de-coding schemes (Zhang et al 1999). The Cramer-Rao bound says that an unbiased estimator's variance is larger or equal to the inverse Fisher-information. The optimal decoders are able to reach the Cramer-Rao bound and thus estimate the population coded quantity with the smallest error possible. It has been shown that virtually optimally read-out can be implemented by a (noise-free) recurrent network (Deneve 1999).

Here we take a different approach: We consider the transmission of a population coded quantity through a feed-forward network with many layers. The neurons in the network are modelled with integrate-and-fire neurons and are injected with a noisy bias current so that the firing statistics mimic those found in vivo (van Rossum, Nelson and Turrigiano, 2002).

We posed the question: how well are population quantities preserved during the propagation through a multi layer network? Note that noise is injected to each neuron at each layer, which makes it a different problem than read-out with noiseless networks. We think that this question is relevant in many situations: For instance, consider a monkey that has to make an arm movement to the location of a spot on the screen after the spot turns off. In that case the (population coded) location information has to be preserved from visual system to motor system, presumably passing through many processing stages.

We measure the quality of the population code at different layers in the network using the variance in the estimates as a quality measure. In contrast to earlier work we consider both the information in the 'angle' and in the amplitude of the signal. We vary the connectivity profile between the layers (assuming identical connectivity for all neurons within a layer, and also identical connectivity for all layers). We find that using a centre-surround connectivity profile the deterioration of the population code is minimal. The standard deviation in the estimate only deteriorates weakly when then number of layers is increased (constant + sqrt{ #layers })

The centre-surround connectivity followed by the rectification of the neurons, implements effectively a matched filter. We show that the matched filter performs close to optimal performance. The matched filter analogy connects this work to object recognition models based on matched filters. Furthermore, matched filter are well understood and easily extended to different noise properties.

The connectivity profile induces correlation in the neural activities. Correlation in general deteriorates population coded signals (Sompolinsky et al 2002). Substantial noise correlation has been observed in cortex (Zohary et al 1984), leading to the question whether the correlation is a nuisance for the nervous system. Our results shine a different light on this issue and indicate that although correlations arise as a necessary consequence from the connectivity, the network still performs better than it would otherwise.

Our results suggest a functional basis for the ubiquitous presence of centre-surround arrangements in the nervous system, namely centre-surround connectivity optimally preserves population coded information.