

A spherical model for orientation and spatial frequency tuning in a cortical hypercolumn

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Summary

We introduce a population model to represent neurons with specific orientation and spatial frequency preferences in a single hypercolumn of V1. Each neuron receives both feedforward input from the lateral geniculate nucleus (LGN) and recurrent intracortical input. The strengths of the recurrent connections depend on the preferences of the pre- and post-synaptic neurons. Their topology is taken to be a sphere with orientation and spatial frequency preferences represented by the two angular spherical coordinates. Such a topology naturally accommodates the two orientation preference pinwheels within a single ocular dominance column by placing them at the poles of the sphere (see Fig. 1).

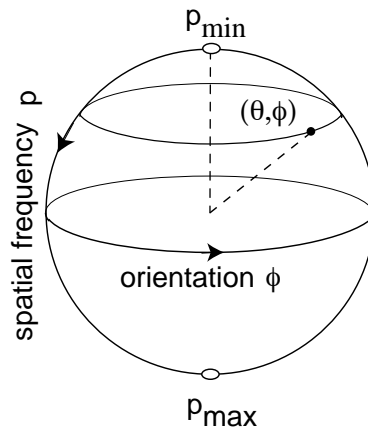


Fig. 1 Network topology of a sphere. Orientation preference ϕ and spatial frequency preference p are taken to be the angular coordinates (θ, ϕ) on the sphere such that $\theta = Q(p) = b(\log p - \log p_{\min})$, where $b = \pi / \log(p_{\max}/p_{\min})$ and $p_{\min} \leq p \leq p_{\max}$.

Given such a topology, we formulate a population model of orientation and spatial frequency tuning. The population response evolves according to a generalization of the Wilson-Cowan equations¹. The distribution of connections is chosen so that away from the pinwheels, neurons with similar orientation preferences excite each other, whereas those with differing preferences inhibit each other². On the other hand, around the pinwheels all neurons uniformly excite, which is consistent with the observation that local interactions depend on cortical separation³.

It has previously been established in network models of orientation tuning alone that strong recurrent interactions can provide an amplification mechanism for certain Fourier components of network activity, leading to sharp orientation tuning curves even for weakly biased LGN inputs. Such an amplification mechanism provides one explanation for the approximate contrast invariance of the tuned response. We find a similar result for the spherical model, except that now particular *spherical harmonic* components of network activity are amplified. This generates a localized activity surface on the sphere that simultaneously produces sharp orientation and spatial frequency tuning.

We assume that the population response occurs in a regime of strong cortical modulation. The shape of the tuning surface is then determined by the recurrent interactions, whereas the location of the optimal response is determined by the LGN input. There is a non-trivial relationship between the optimal spatial frequency and the spatial frequency of a visual stimulus, reflecting the non-separability of the feature preferences. However, we expect approximate separability, at intermediate spatial frequencies (away from pinwheels). Recent data by Mazer *et.al.*⁴ is consistent with this.

A basic feature of the model is that recurrent cortical interactions amplify certain spherical harmonic components of network activity. However, this presupposes that the corresponding harmonic components of the feedforward input from the LGN faithfully

encode the orientation and spatial frequency of a visual stimulus. Consider a stimulus consisting of a sinusoidal grating with fixed spatial frequency and orientation. If the low order spherical harmonic components of the resulting feedforward input to a hypercolumn are amplified, the spatial frequency at which the response is optimal is shifted relative to the stimulus frequency— there is no corresponding shift in orientation. Such a shift is not an artifact of the spherical topology. A similar conclusion obtains for any recurrent mechanism that amplifies both orientation and spatial frequency components of a stimulus. From linear filter theory it can be shown that if the feedback from a cortical neuron is taken to be the reciprocal of the corresponding feedforward receptive field (in the two-dimensional Fourier domain), then the mismatch between the feedforward and cortical frequency representations can be eliminated, at least at the linear level. We speculate that the patterned feedback from V1 back to LGN recently found by Murphy *et.al.*⁵ modulates LGN activity to produce a more faithful encoding of spatial frequency. The patterned feedback found in the model seems to be consistent with that observed by Murphy *et.al.* in that it depends on the orientation preference of its V1 origin.

Recent observations by Sharon & Grinvald⁶ also appear to be consistent with the model. They found that orientation tuning does not sharpen during a cortical evoked response: instead there is an amplification of cortical modulation. They also found that the time course of this amplification is not smooth but slows down about 50 msec. after onset and then accelerates again. This is consistent with the postulated feedback process coming online after some 50 msec. Such a feedback could also be responsible for the predicted change in direction of shifts in spatial frequency preferences⁷. That is, downward shifts are consistent with the properties of the geniculo-cortical pathways before the effects of the cortico-geniculate feedback have time to act. We predict that the earliest responses of cortical neurons should all exhibit downward shifts in spatial frequency tuning, but for

high spatial frequencies such shifts should eventually disappear or even reverse, when measured at later times. Some observations appear to be consistent with this prediction⁸.

There are three major conclusions of this work. First, orientation and spatial frequency preferences can be represented as the surface coordinates of a sphere in each region of V1 that corresponds to a Hubel-Wiesel hypercolumn. Second, amplification by recurrent cortical interactions leads to a tuned population response that is non-separable with respect to orientation and spatial frequency preferences, and produces a mismatch between the feedforward and cortical representations of spatial frequency. Third, a possible mechanism for counteracting such a mismatch is through patterned cortico-geniculate feedback. We believe that similar considerations will apply to other examples of multiple feature selectivity and tuning in V1 and elsewhere, whenever one or more features are not angular variables.

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