## Characterizing receptive field selectivity in area V2

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The computations performed by neurons in area V1 are reasonably well understood, but computation in subsequent areas such as V2 have been more difficult to characterize. When stimulated with visual stimuli traditionally used to investigate V1, such as sinusoidal gratings, V2 neurons exhibit similar selectivity (but with larger receptive fields, and weaker responses) relative to V1 neurons. However, we find that V2 responses to synthetic stimuli designed to produce naturalistic patterns of joint activity in a model V1 population are more vigorous than responses to control stimuli that lacked this naturalistic structure (Freeman, et. al. 2013). Armed with this signature of V2 computation, we have been investigating how it might arise from canonical computational elements commonly used to explain V1 responses. The invariance of V1 complex cell responses to spatial phase has been previously captured by summing over multiple "subunits" (rectified responses of simple cell-like filters with the same orientation and spatial frequency selectivity, but differing in their receptive field locations). We modeled V2 responses using a similar architecture: V2 subunits were formed from the rectified responses of filters computing the derivatives of the V1 response map over frequencies, orientations, and spatial positions. A "V2 complex cell" sums the output of such subunits across frequency, orientation, and position. This model can qualitatively account for much of the behavior of our sample of recorded V2 neurons, including their V1-like spectral tuning in response to sinusoidal gratings as well as the pattern of increased sensitivity to naturalistic images.



Figure 1 (*a*) An input image is convolved with a model V1 front-end with units tuned to different orientations and spatial frequencies. The first V2 stage computes derivatives over the activation map of V1 across space, as well as orientation and spatial frequency. We modelled "V2 simple cells" as the rectified output of these filters. The final V2 stage pools and rectifies the output of these "V2 simple cells". (*b,c*) Single unit modulation indices for V1 and V2 cells adapted from Freeman et al. (2013). The modulation index represents the normalized difference in firing rate between naturalistic and control stimuli. The V1 neurons show an average modulation close to zero, whereas the V2 population was consistently positive. (*d,e*) Modulation indices for a simulated population of V2 "simple" and "complex" cells. Units were simulated to have random parameters for derivative and pooling weights. While "V2 simple" cells had a slightly positive modulation index on average, "V2 complex" cells approached the magnitude of the recorded V2 population. (*f*) The average modulation of "V2 simple" cells failed to account for the strength of V2 modulation across different categories of naturalistic images, (*g*) while The average modulation of "V2 complex" cells across categories was correlated with recorded V2 population.