# Amplification of feature selectivity by spatial convolution in primary visual cortex

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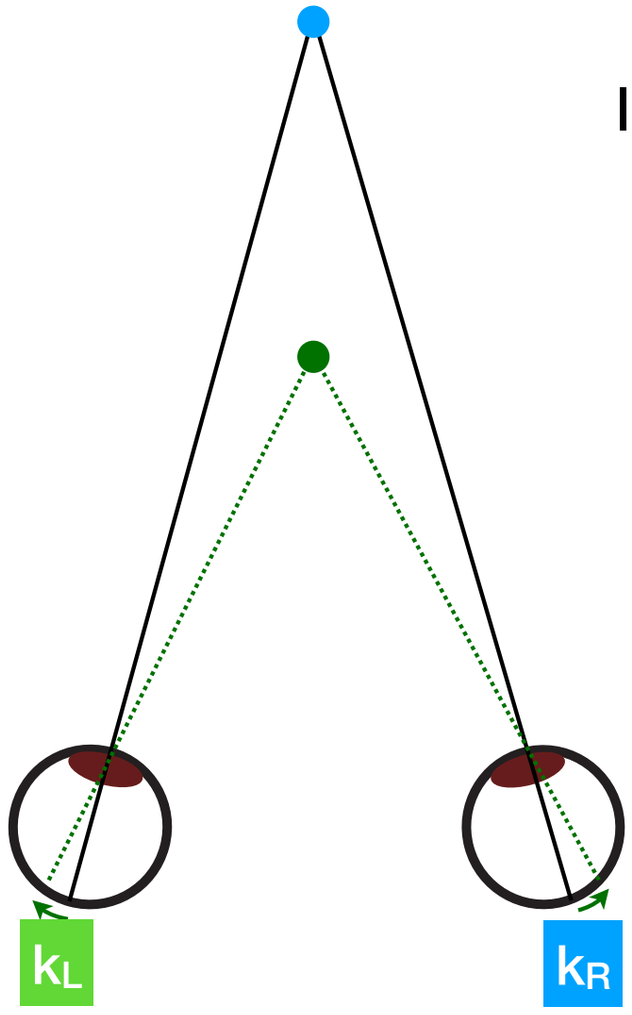
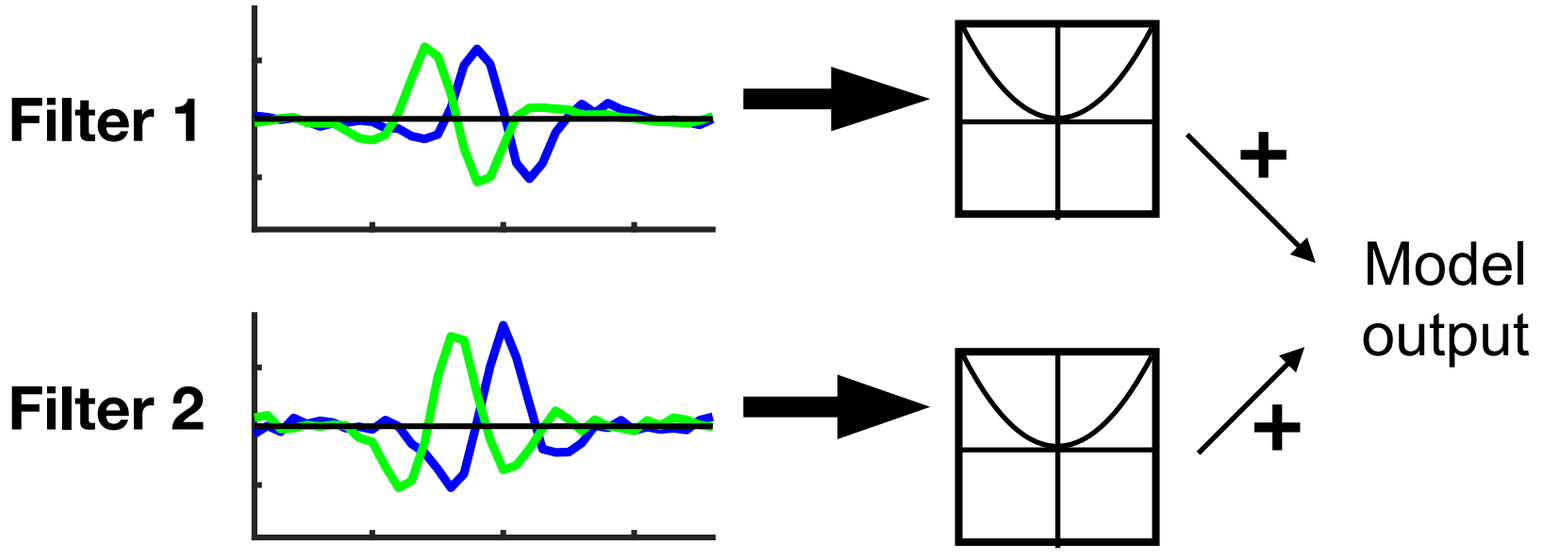
# The Binocular Energy Model




Integrates two simple disparity detectors from orthogonal phases




$$R = (\mathbf{k}_L \cdot \mathbf{s}_L + \mathbf{k}_R \cdot \mathbf{s}_R)^2 + (\mathbf{k}_L^* \cdot \mathbf{s}_L + \mathbf{k}_R^* \cdot \mathbf{s}_R)^2$$

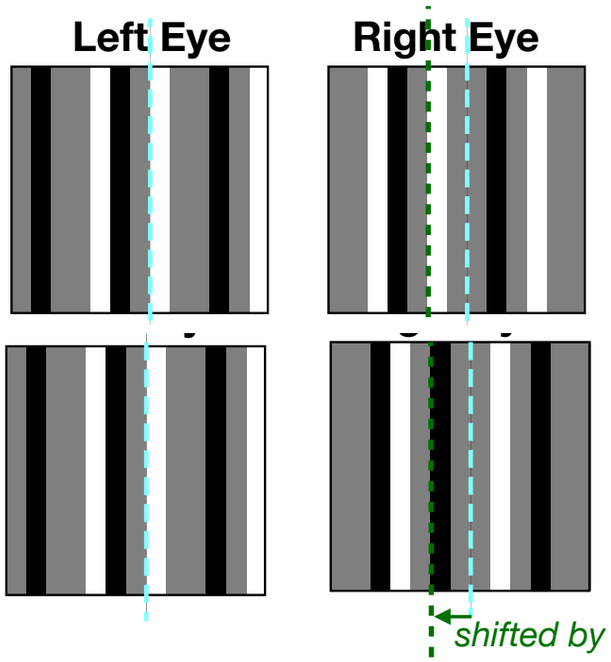
**Does V1 combine inputs from each eye using the same computation as the BEM?**

**Does this computation generalize to other stimuli despite being designed for gratings?**

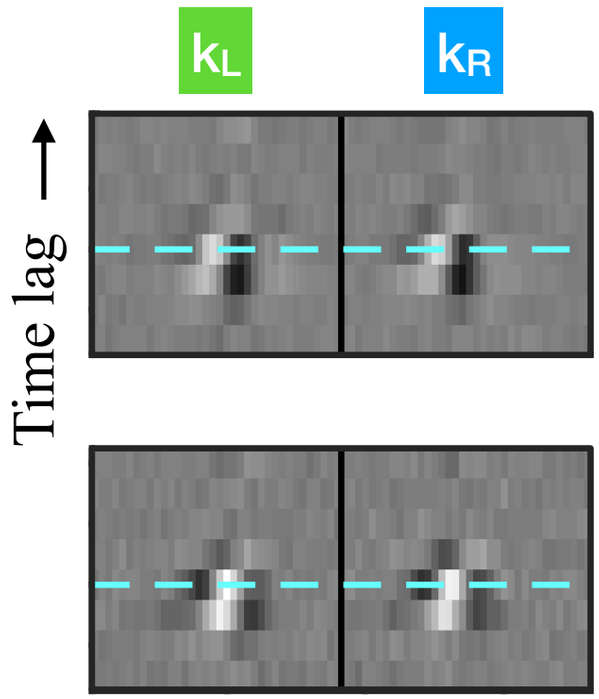
Ohzawa, DeAngelis & Freeman, 1996

# Directly fitting a BEM

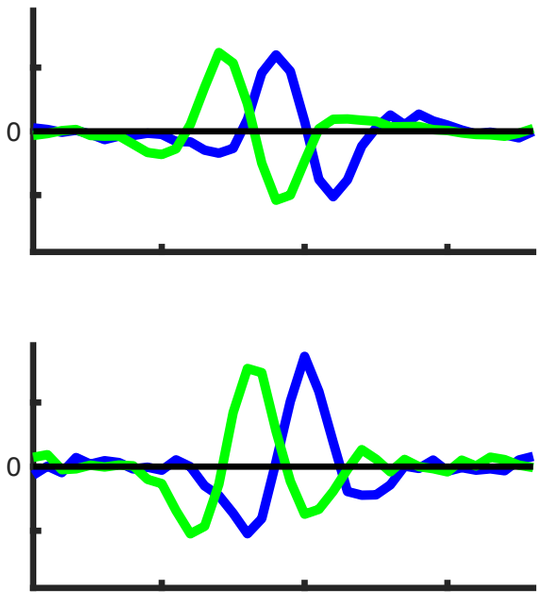
## Stimuli



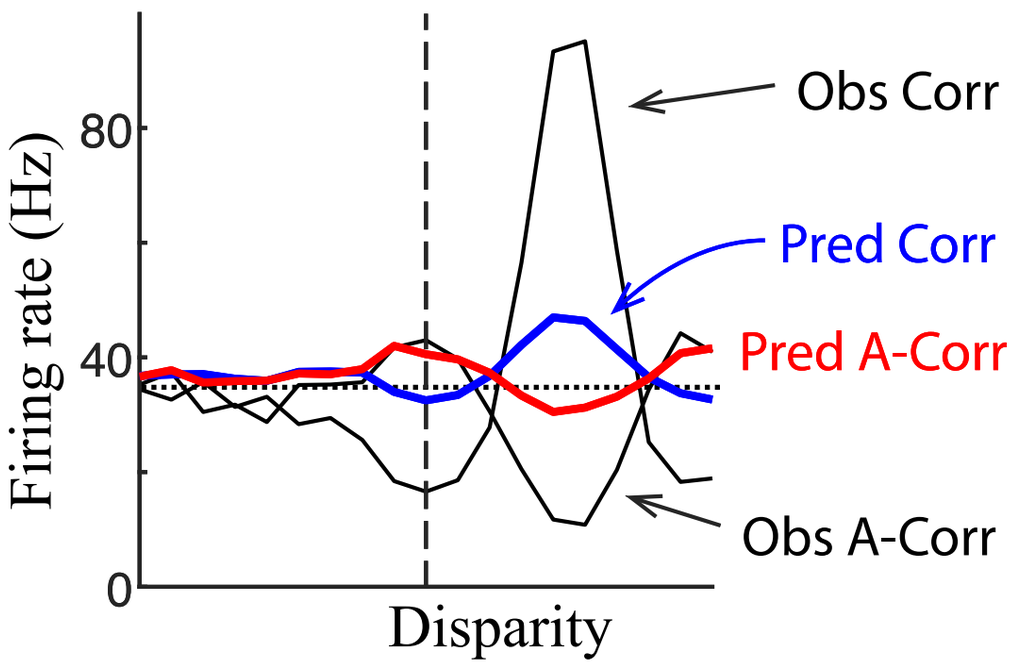

## Spatiotemporal filters

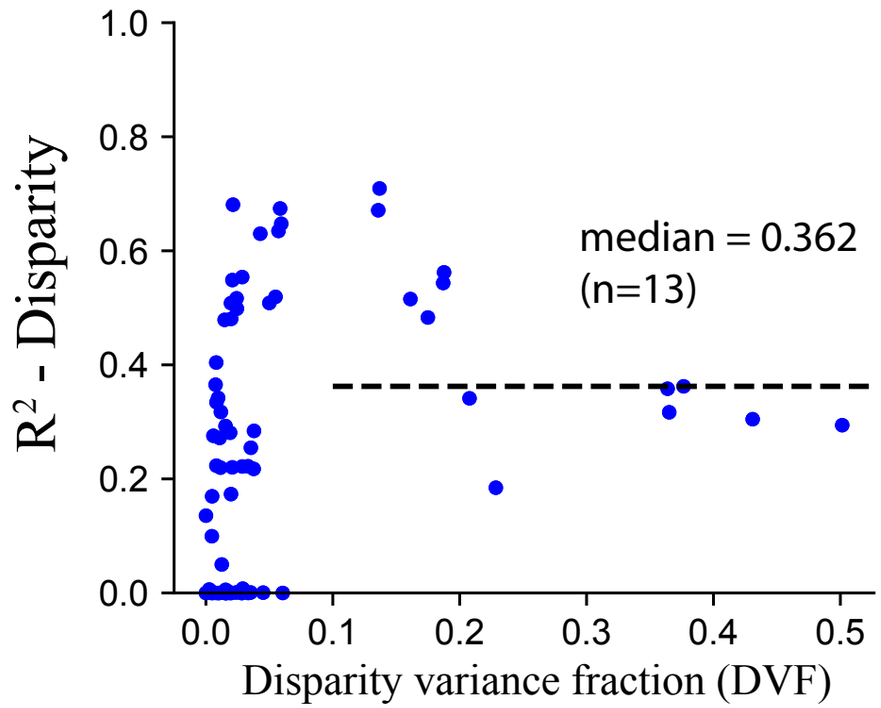



Spatial profiles at the best lag




BEM generates a symmetric response to correlated and anticorrelated stimuli



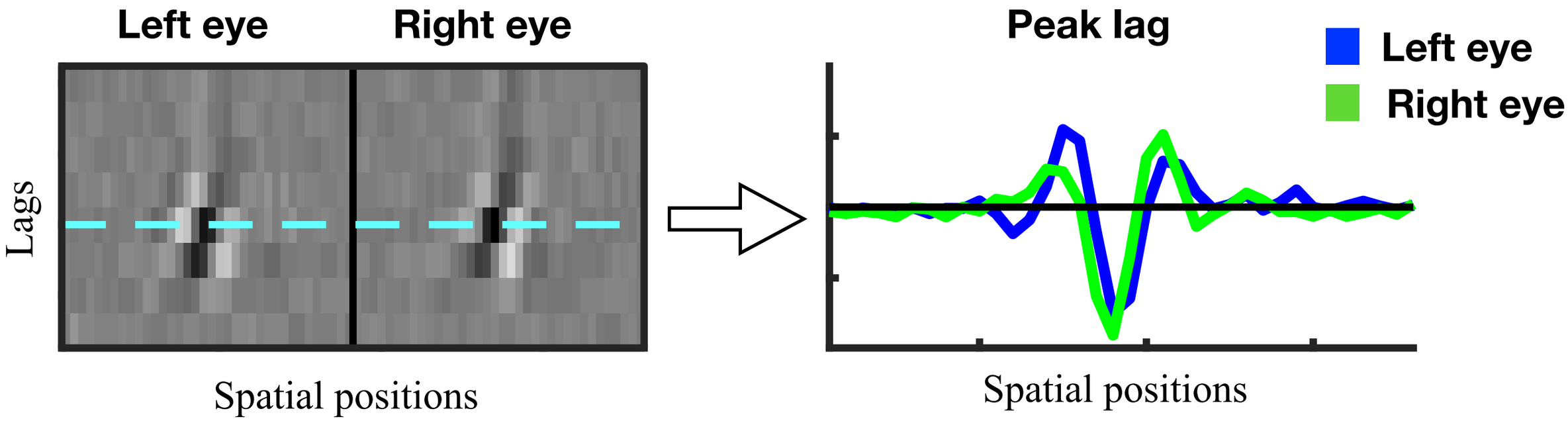
# Generating disparity variance in a single BEM filter

$$\mathrm{Var}[r(\mathbf{p},d)] = \langle \mathrm{Var}_{\mathbf{p}}[r(\mathbf{p},d)] \rangle_d + \mathrm{Var}_d\left[\langle r(\mathbf{p},d) \rangle_{\mathbf{p}}\right]$$

calculated using 2 repeats

Average variance driven by patterns at fixed disparity

The variance due to disparity alone (averaging over all patterns)




Disparity variance (DV) = 0.0055
Pattern variance (PV) = 0.1348
Total variance (TV) = 0.1402

**Disparity variance fraction (DVF) = DV/TV = 0.039**

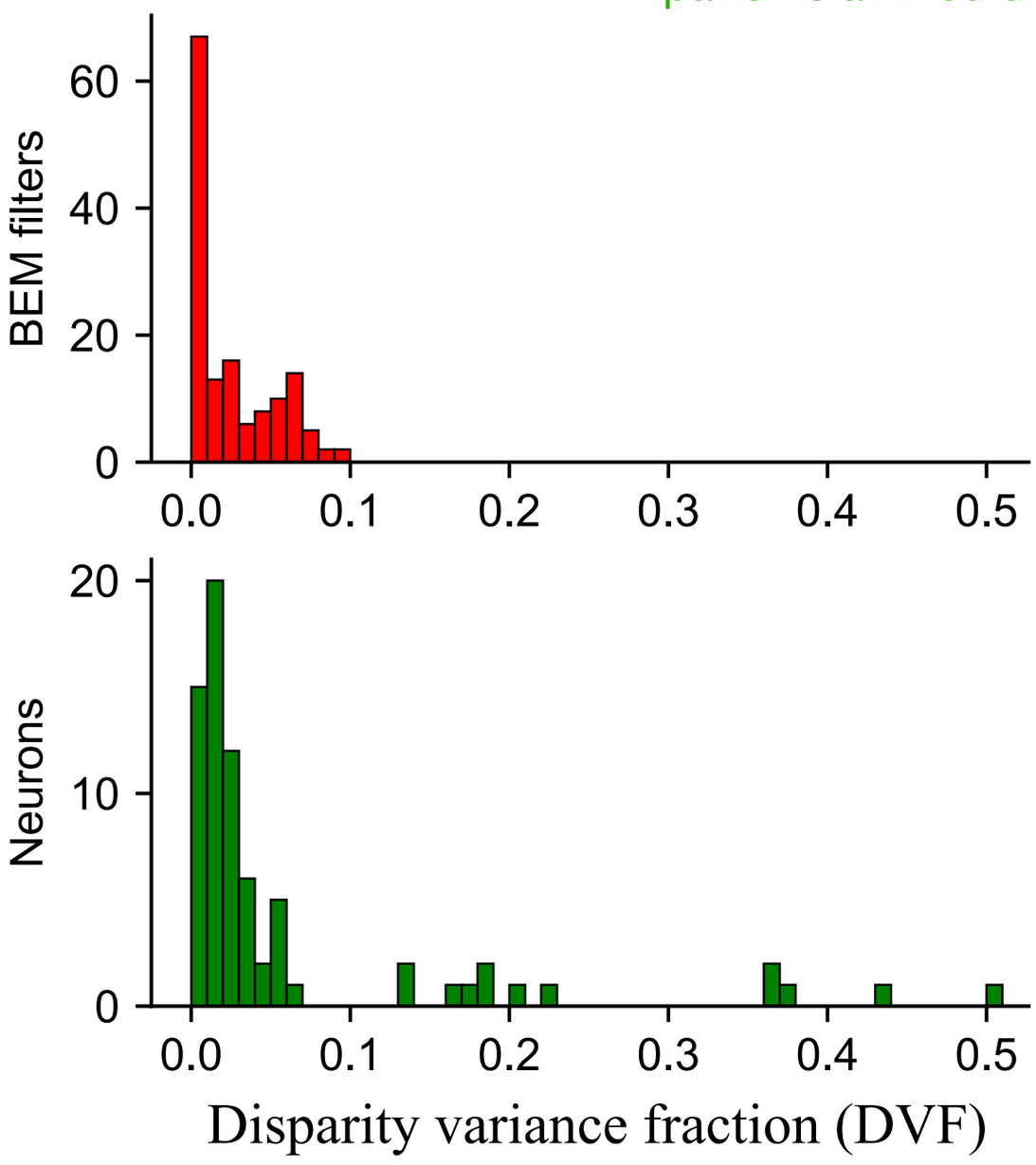
# Disparity variance across recorded cells

$$\mathrm{Var}[r(\mathbf{p},d)] = \langle \mathrm{Var}_{\mathbf{p}}[r(\mathbf{p},d)] \rangle_d + \mathrm{Var}_d\left[\langle r(\mathbf{p},d) \rangle_{\mathbf{p}}\right]$$

calculated using 2 repeats

Average variance driven by patterns at fixed disparity

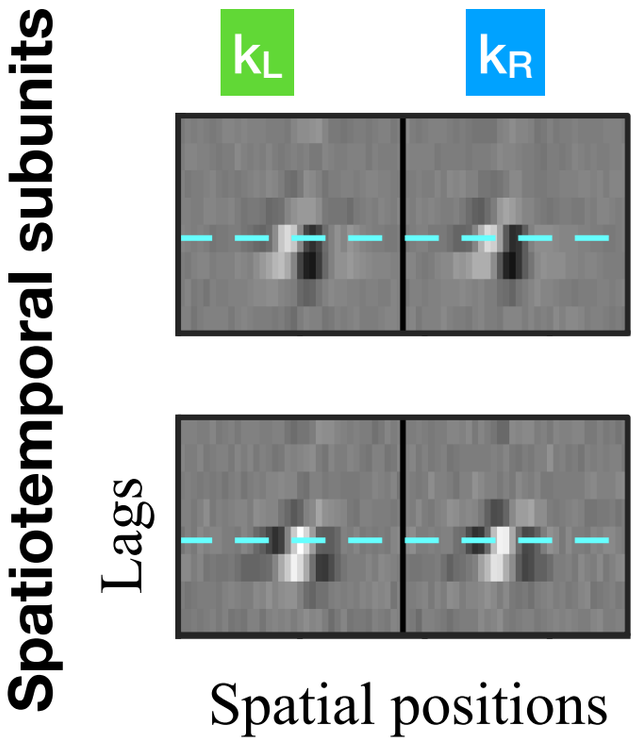
The variance due to disparity alone (averaging over all patterns)

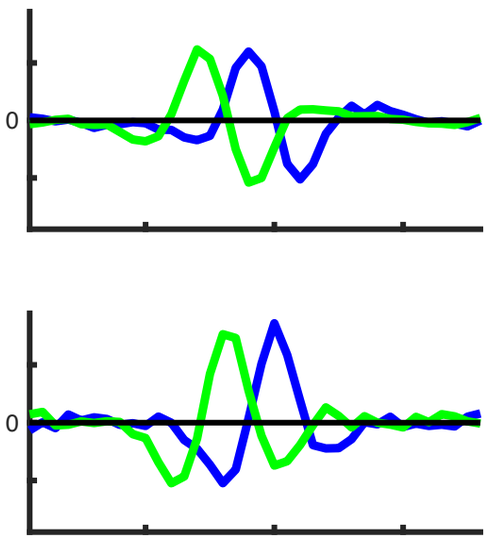



- Even our clearly disparity-detecting example filter had a DVF of 0.039, an order of magnitude lower than the DVFs observed in cells

- **Disparity-tuned cells have significantly amplified DVFs**
- Many binocular cells are not disparity tuned

# BEM: filter combination amplifies disparity variance




DV1 = 0.0055
PV1 = 0.1348
TotVar1 = 0.1402

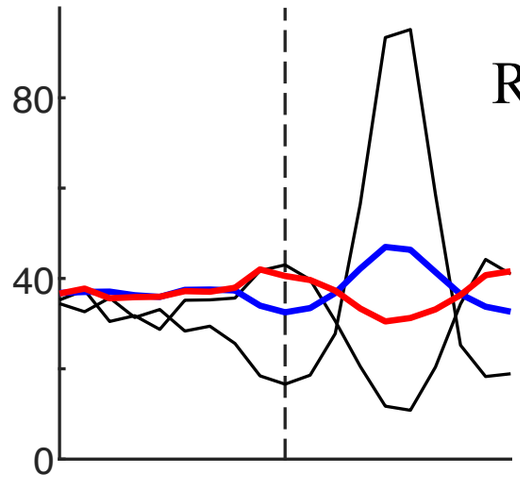
DV1 frac = 0.039

DV2 = 0.0046
PV2 = 0.1211
TotVar2 = 0.1258

DV2 frac = 0.037

BEM total:
DV = 0.0199
PV = 0.2565
TotVar = 0.2765

**DV frac = 0.077**
**2x amplification**

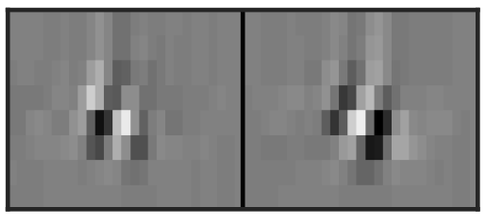



$R^2$=0.333

**Pattern variance is uncorrelated between subunits, and sums linearly**
**Disparity variance is correlated between subunits, and combines super-linearly**

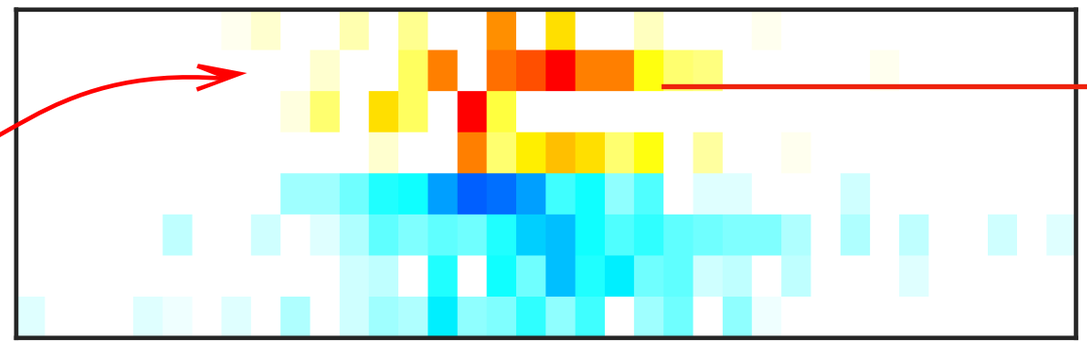
# Convolutions amplify disparity selectivity in the model

**Exc #2**



**DVF of individual subunit: 0.009**

**Subunit weights**

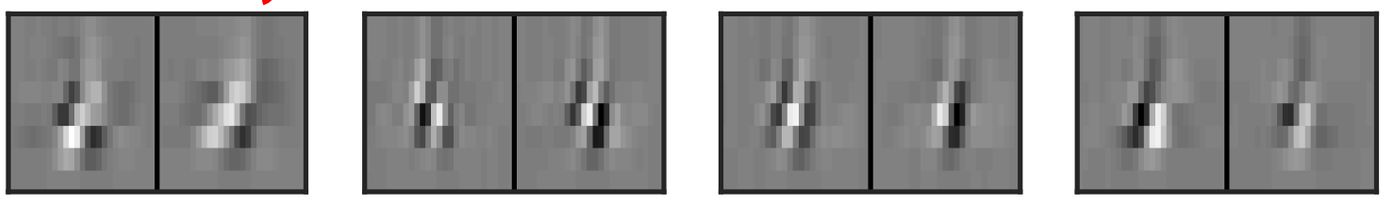


Spatial position

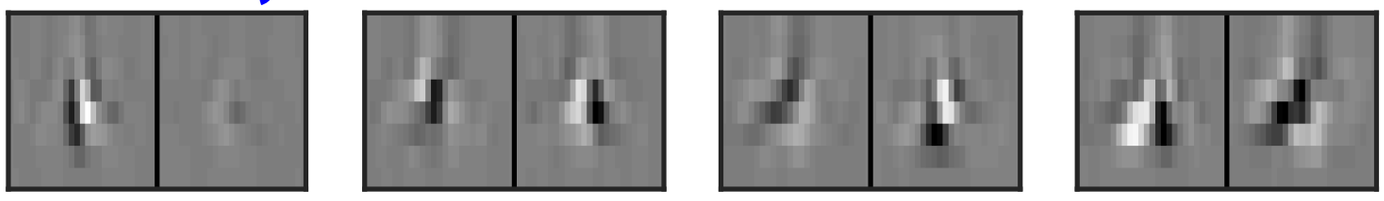
DVF of Exc #2, summed across spatial convolutions: 0.084
**9x amplification**

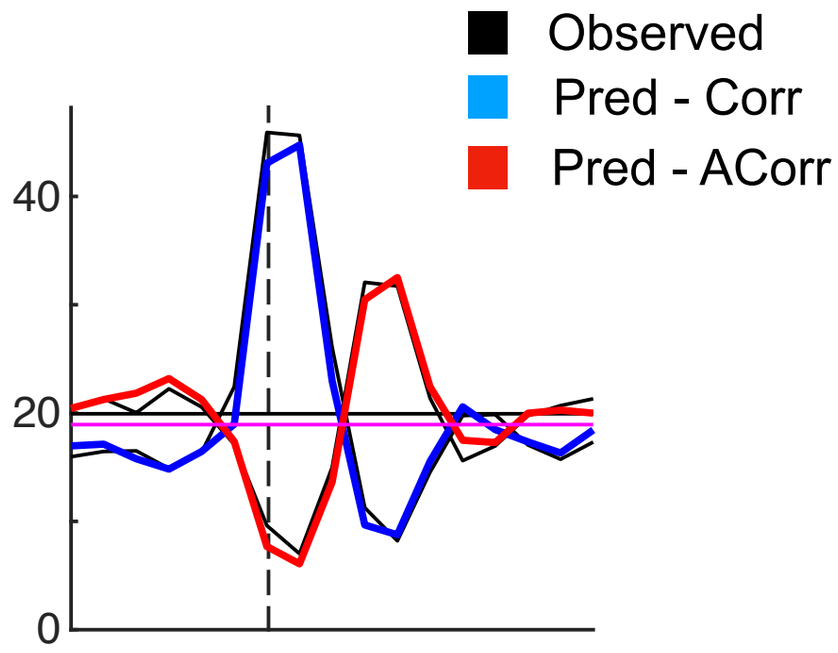
**Binocular Convolution (BC) model**

Excitatory



Inhibitory

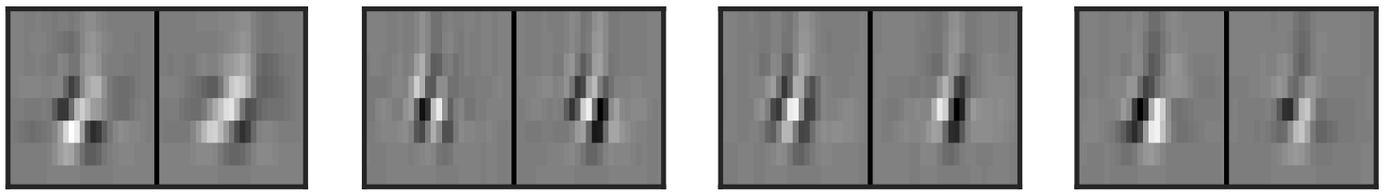




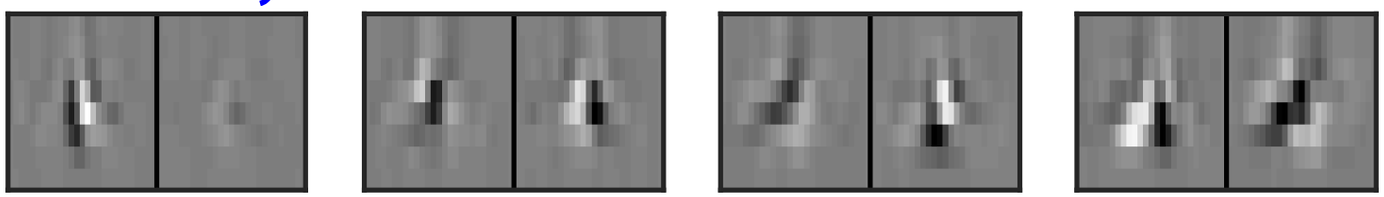

McFarland et al., 2013
Vintch et al., 2016
Butts, ARVS, 2019

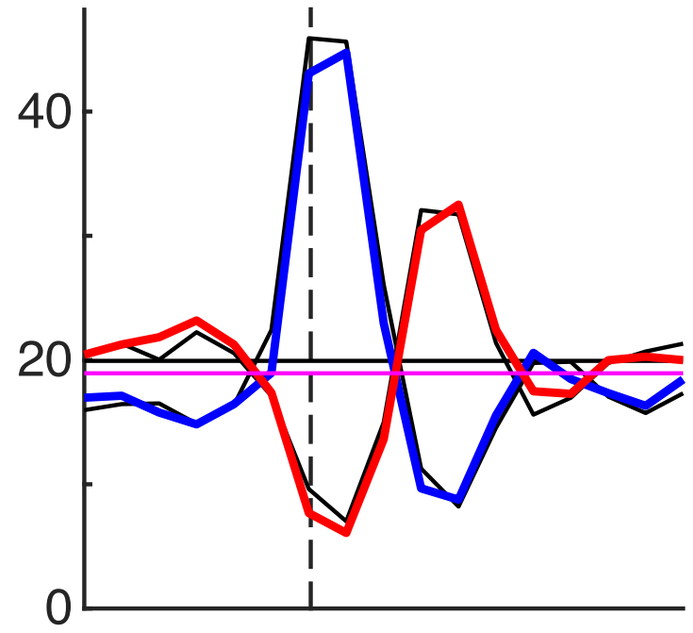
# Inhibition further amplifies disparity variance

Excitatory

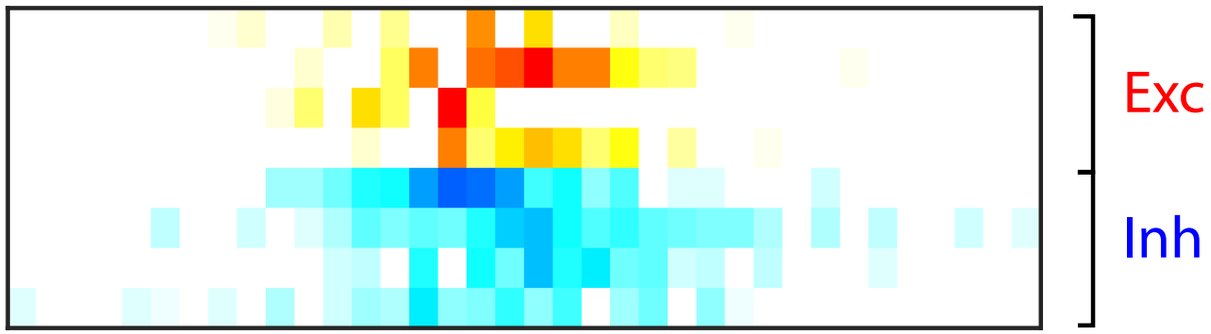


Inhibitory






**Subunit weights**




Sum Exc total:
DV = 0.0909
PV = 0.6768
DVF = 0.1185

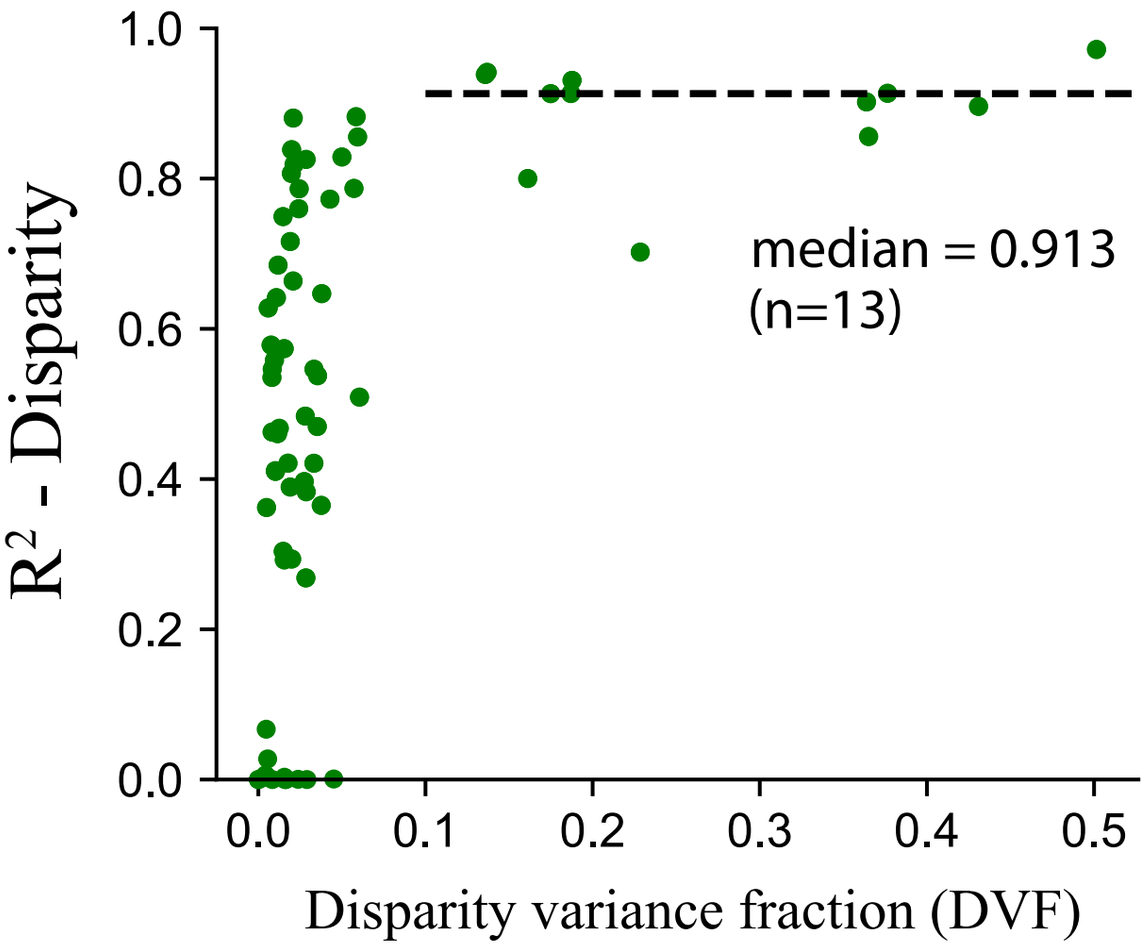
Sum Inh total:
DV = 0.0430
PV = 0.5813
DVF = 0.0689

Dvar total
Sum=0.134
Actual=0.239
**1.78x amp**

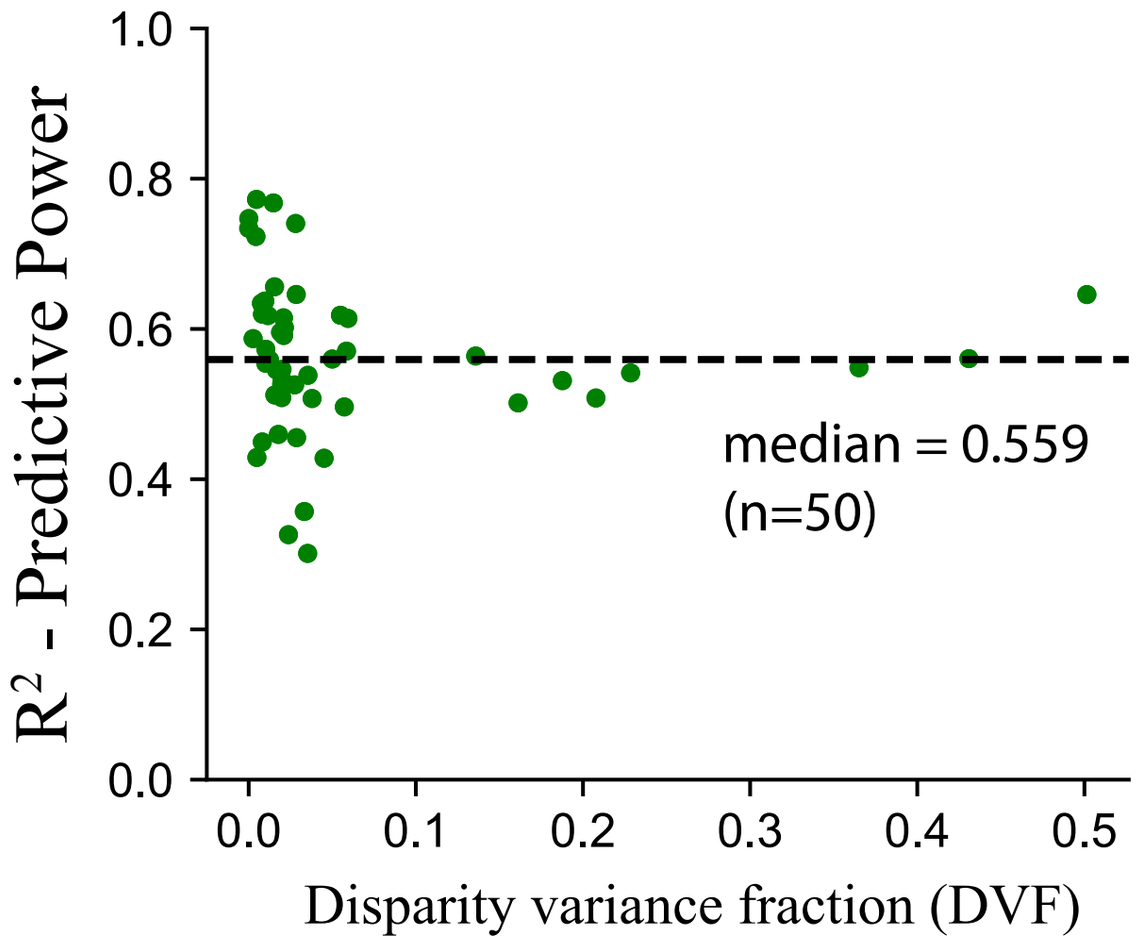
Pvar total
Sum=1.258
Actual=0.731
**0.58x amp**

# Population results

We can explain almost all disparity variance in strongly disparity-tuned cells




The model also captures large fractions of variance across all cells



# Summary

- The Binocular Convolution model is a data-driven model than can capture binocular integration of V1 neurons almost completely
- Its core computation is spatial convolutions of binocular filters, which amplifies disparity tuning
  - The BC model can capture disparity tuning of cells where previous models fail, explaining a median of over 90% of disparity variance in disparity-tuned V1 neurons
  - Measures of pattern and disparity variance provide insight into the function of the model structure
    - They also reveal a subset of V1 neurons specialized for disparity information
- The BC model generalizes to non-disparity-tuned cells, explaining on average over 50% of the explainable variance across all neurons

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