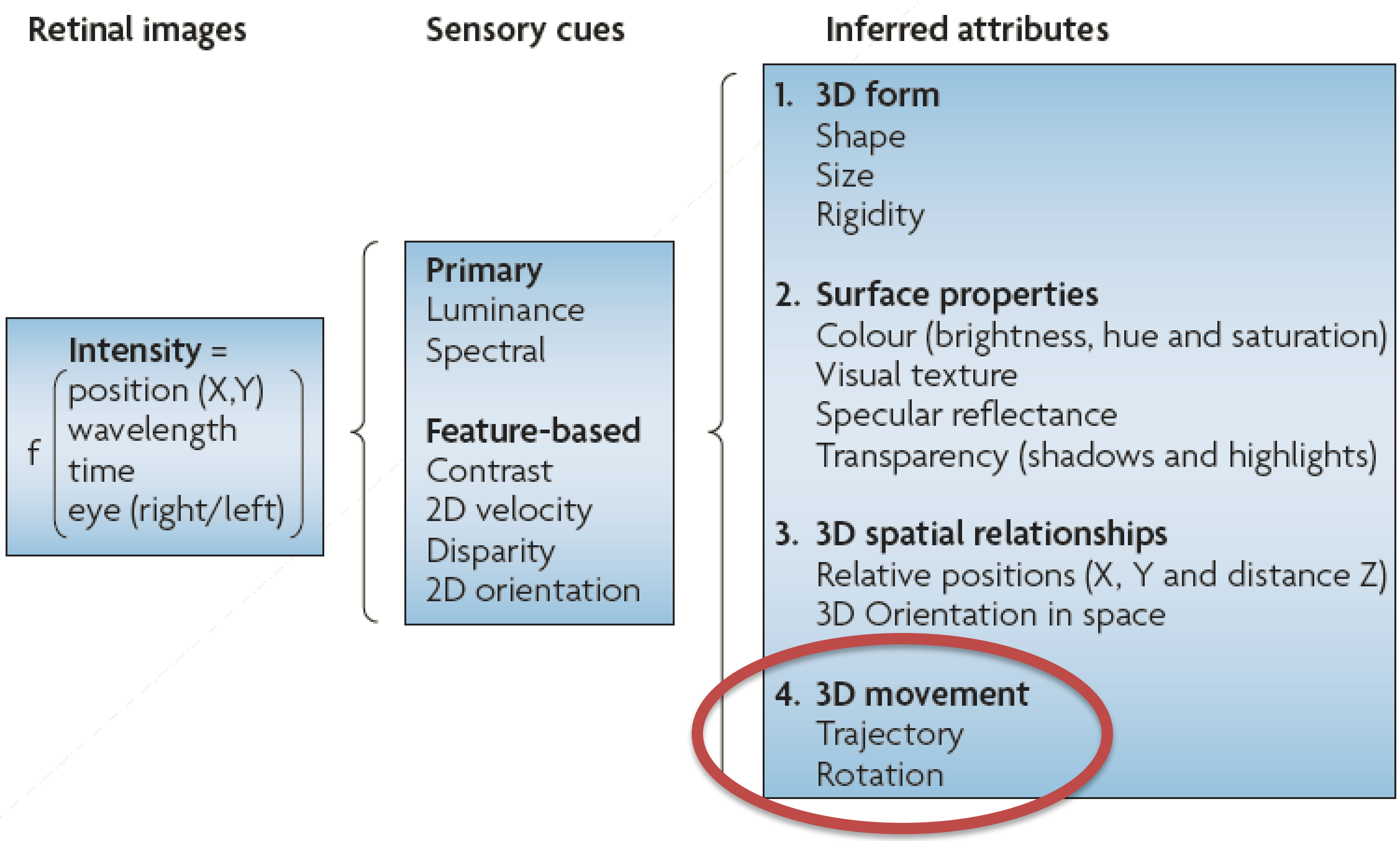
The Cortical Basis of Motion Perception

PSYCH-508: Core Concepts in Perception

Michael Beyeler

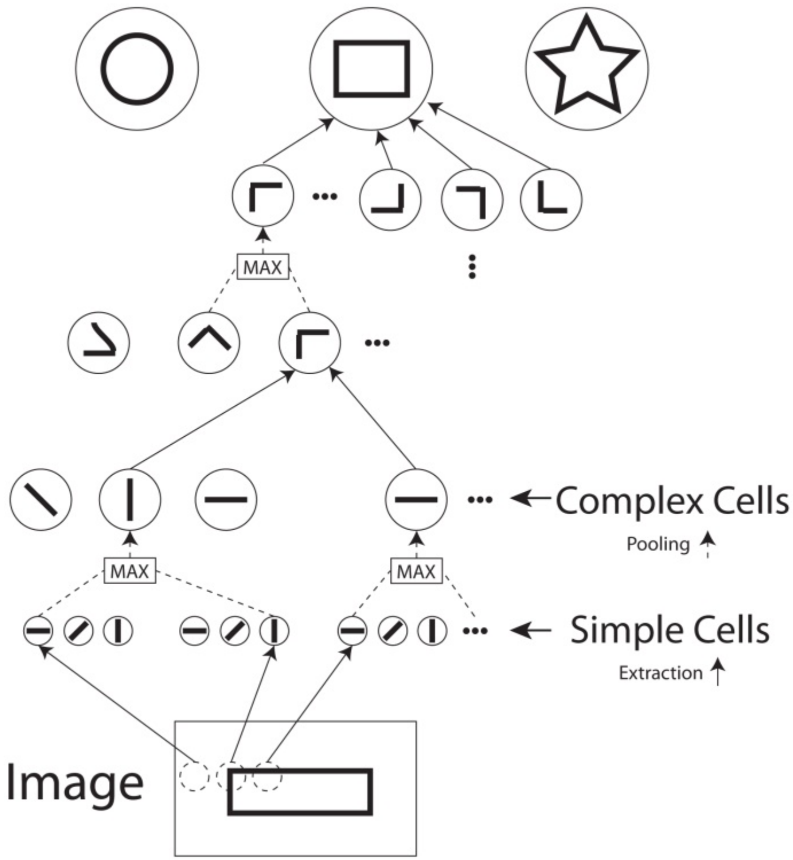
11/1/18

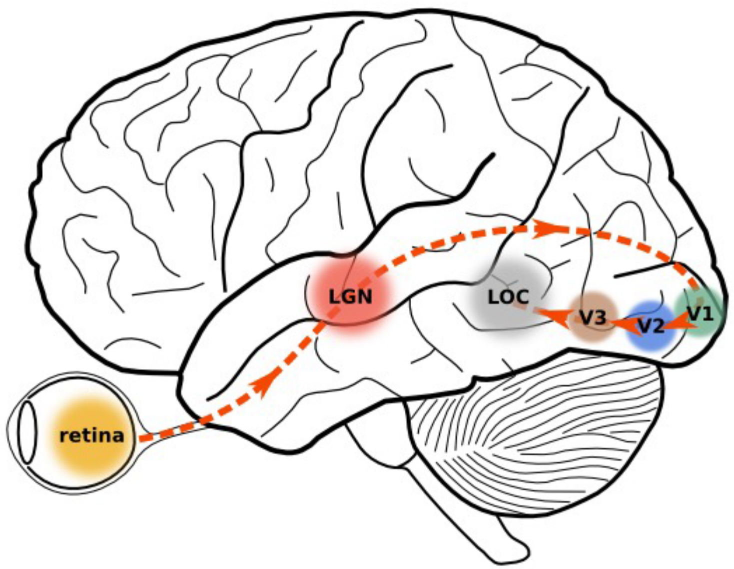
From Retinal Input to Perception



(Nassi & Callaway, 2009)

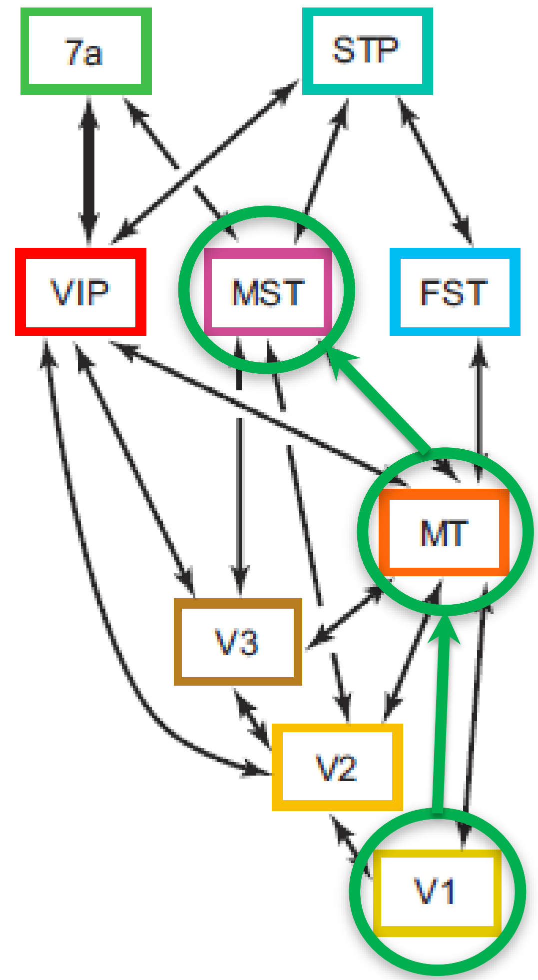
Hierarchical Processing of Vision





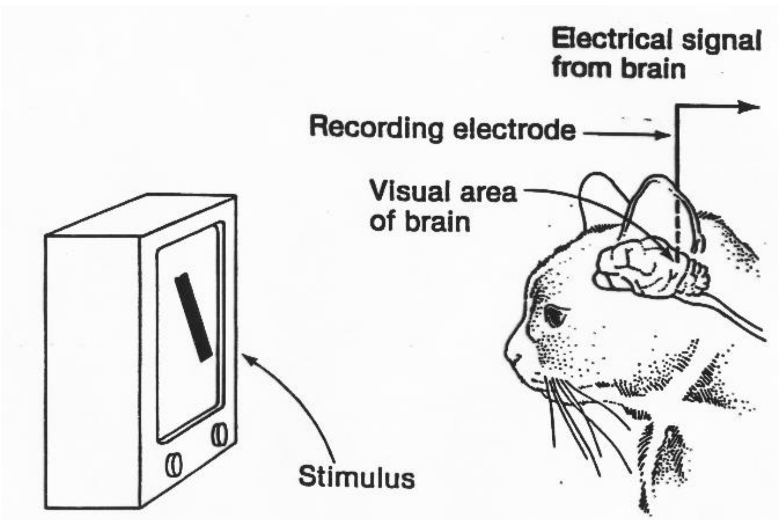
Visual Motion Pathway

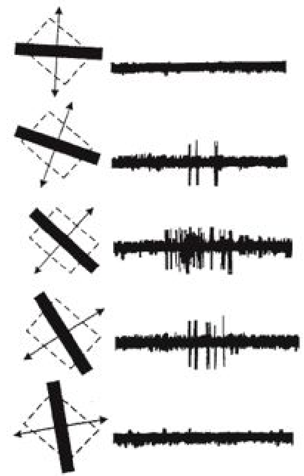
- Primary visual cortex (V1)
  - tuned to simple attributes of shape, motion, color, texture, depth
- Middle temporal (MT) area
  - tuned to coherent local motion (retinal flow)
- Medial superior temporal (MST) area
  - tuned to global, complex motion
  - self-motion (MSTd), object motion (MSTv)
  - tuned to visual, vestibular cues
- Posterior parietal cortex (PPC)
  - polysensory: visual, vestibular, somatosensory, auditory cues
  - self-motion vs. object motion
  - spatial planning, path integration(?)
  - eye, arm, head movements

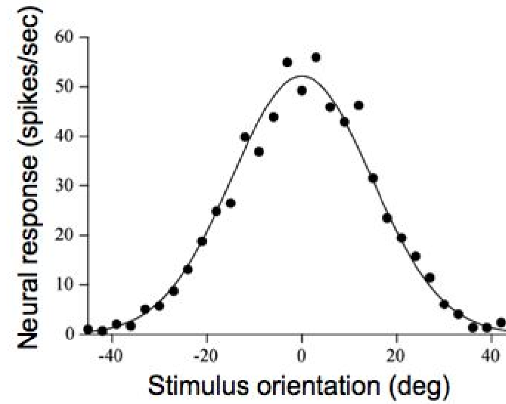


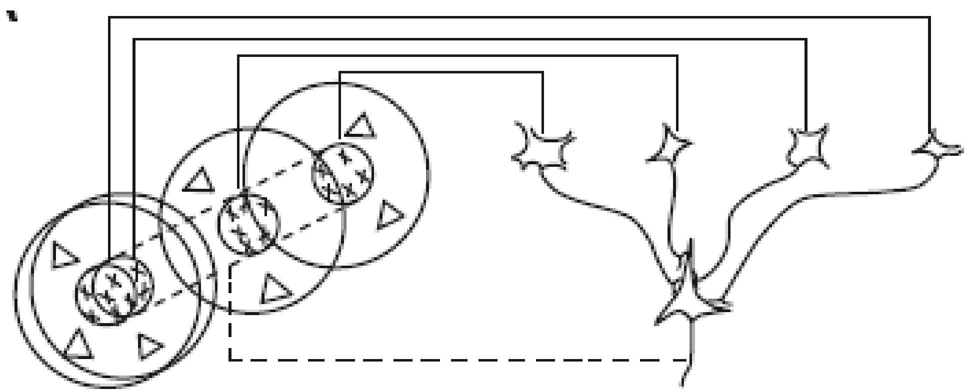
(Britten, *Annu Rev Neurosci*, 2008)

V1 simple cells



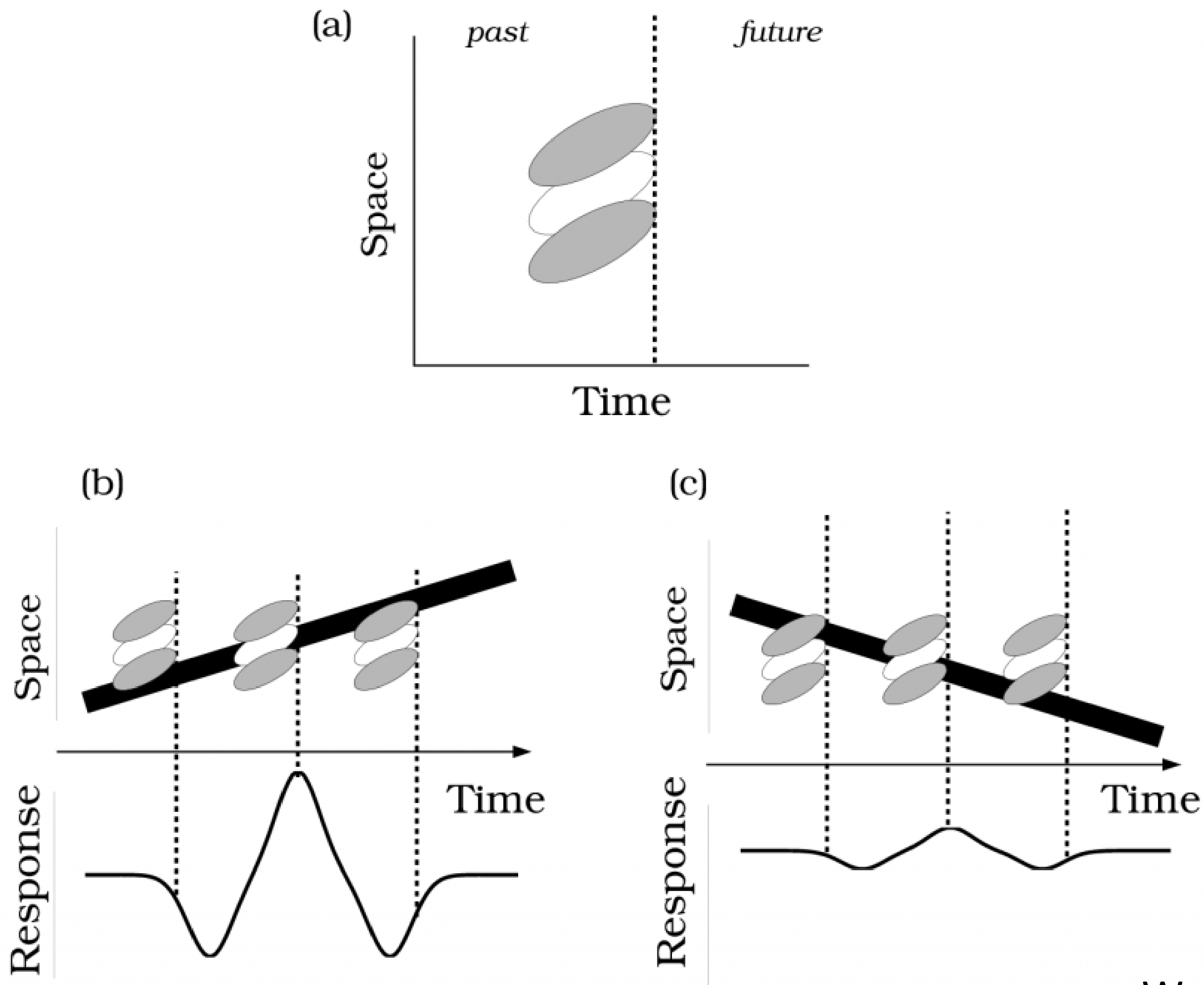






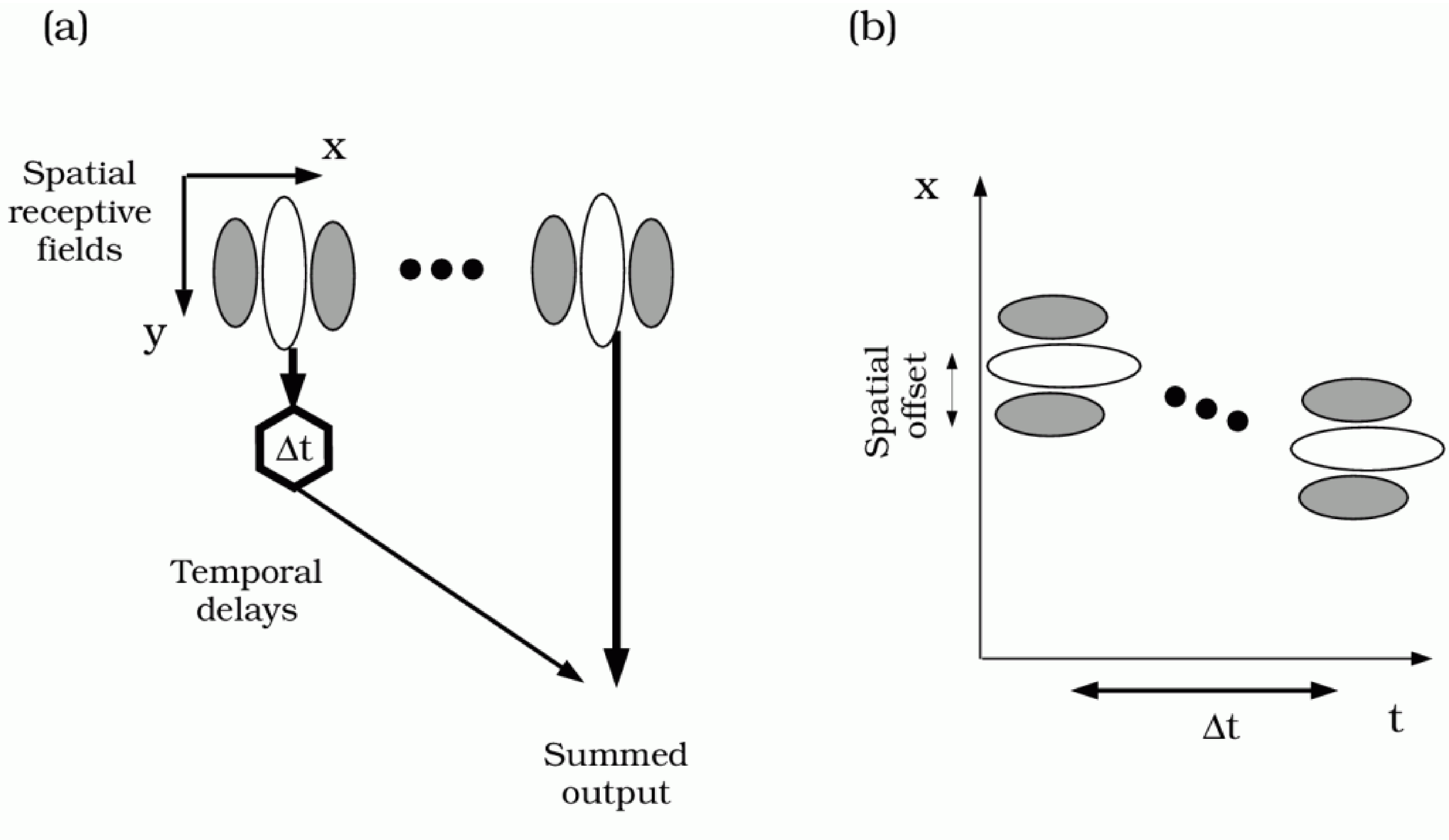
Hubel & Wiesel, 1968

Space-time oriented receptive fields



Wandell Ch.10

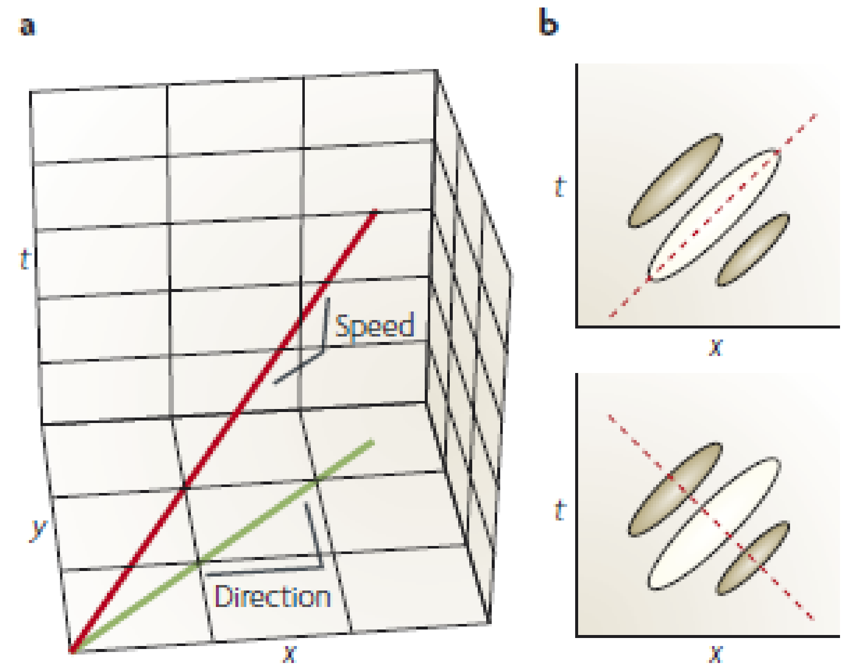
Space–time oriented receptive fields



Spatiotemporal-energy models

- Three steps:
  - 1. Linear filtering
  - 2. Motion energy
  - 3. Opponent energy

- 1. Linear filtering:
  - motion is an orientation in space-time
  - V1 simple cells: space-time oriented receptive fields



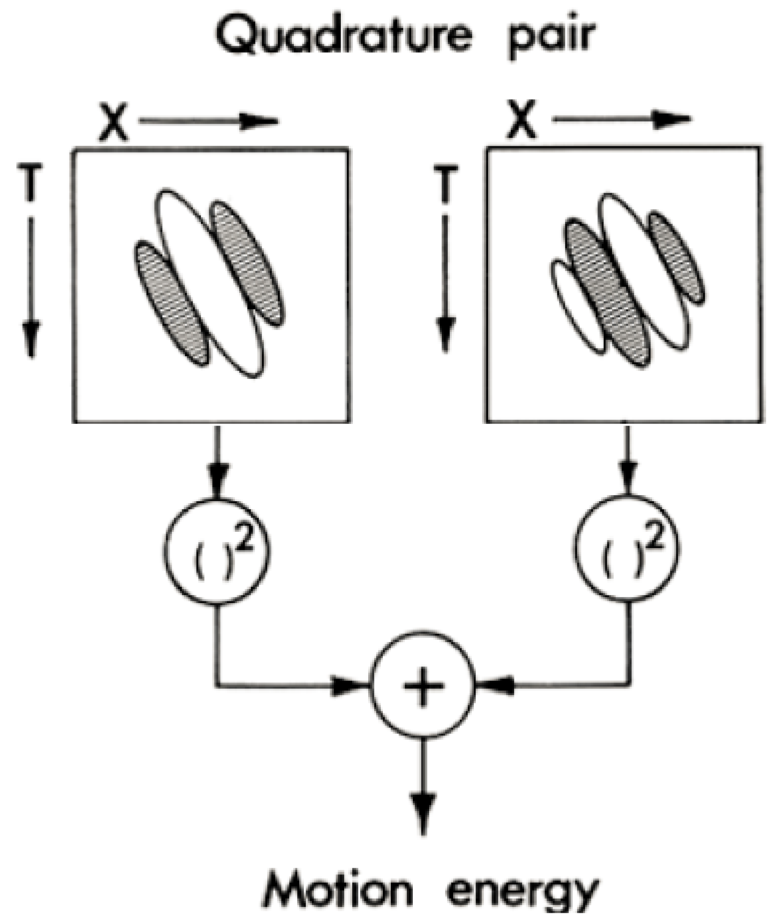
(Bradley & Goyal 2009)

Spatiotemporal-energy models

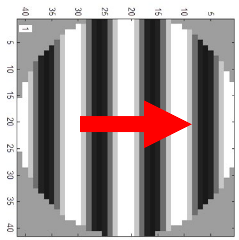
- 2. Motion energy
  - Constant grating motion gives oscillating output → not a useful indicator of motion
  - Measure the energy of the signal instead:

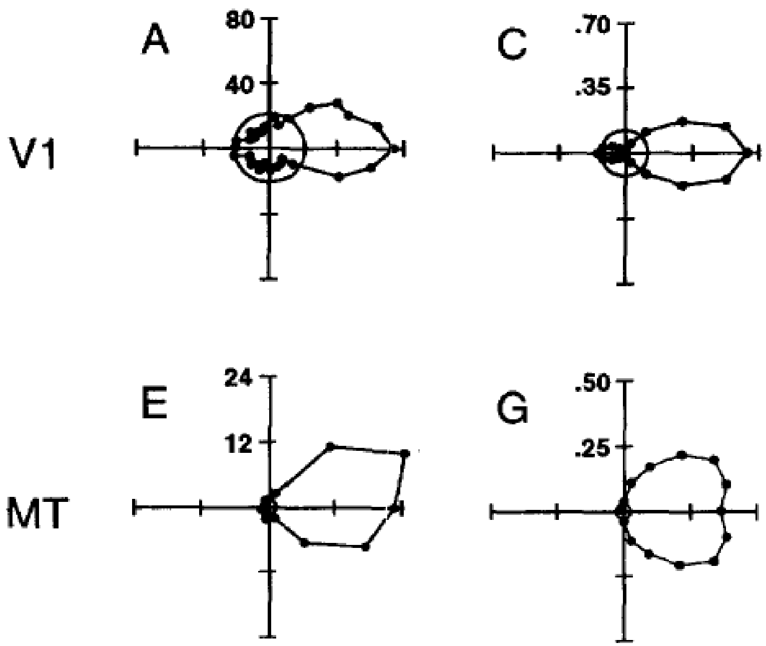
$$E_s = \int_{-\infty}^{\infty} |x(t)|^2 dt$$

  - Shortcut: Square and sum quadrature pair to remove phase dependence from the output



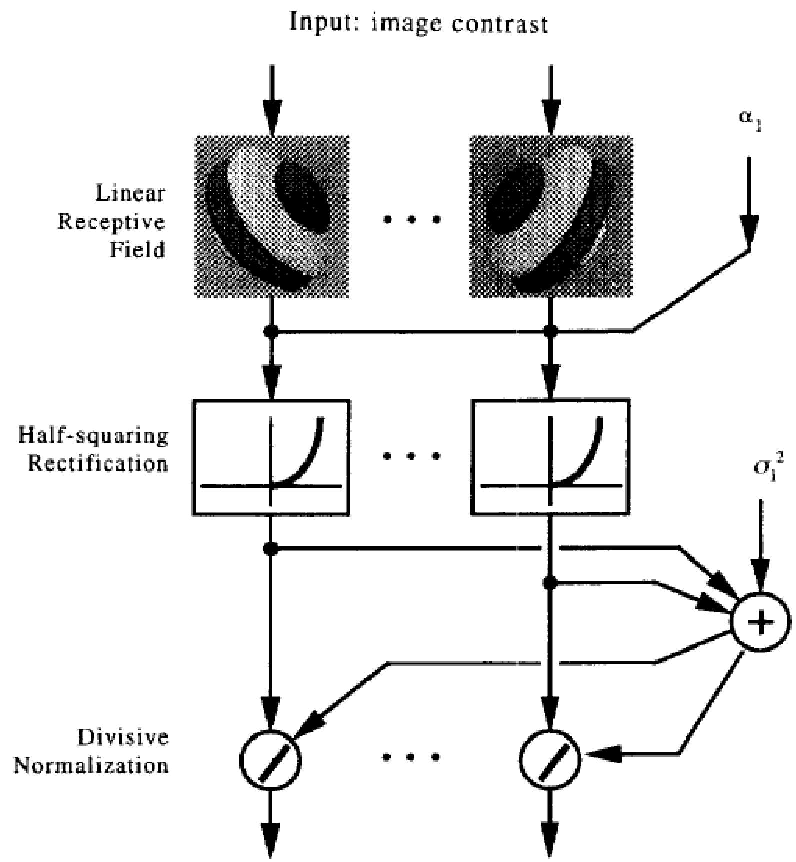
Simoncelli & Heeger model





monkey
(Movshon et al. 1983)

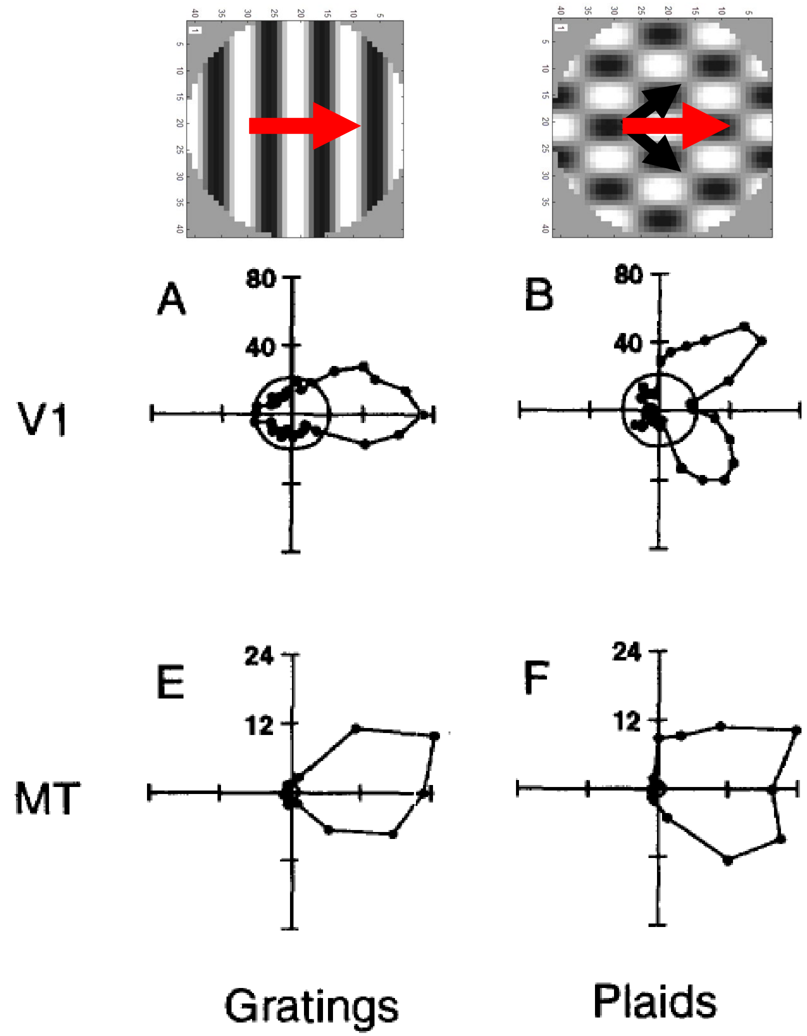
model



(Simoncelli & Heeger 1998)

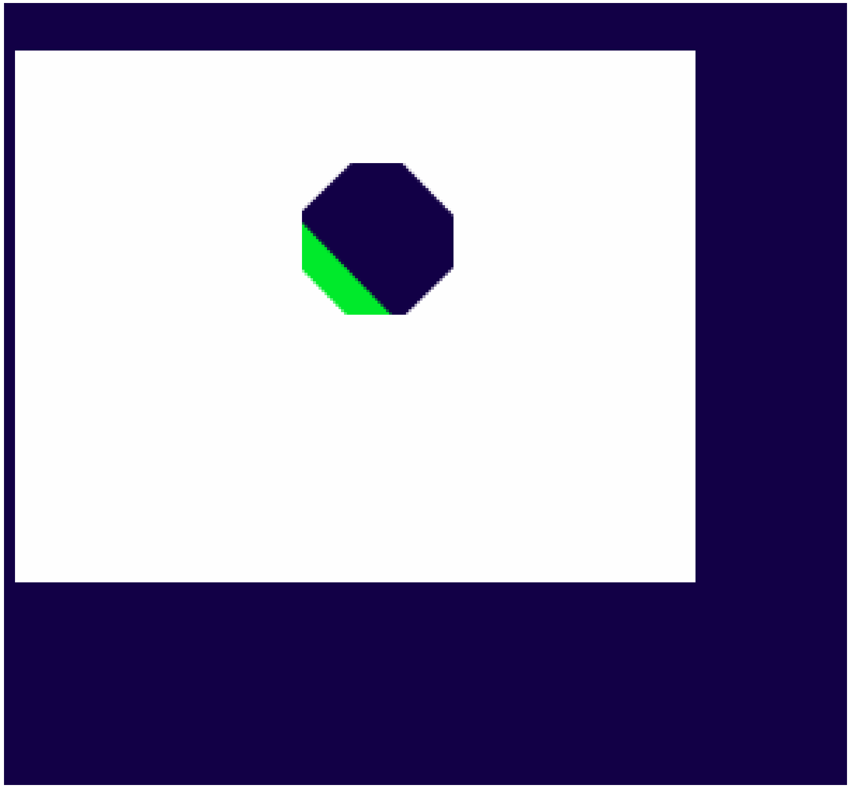
Simoncelli & Heeger model

- What if multiple motion components are present in the stimulus?
- Component-direction-selective (CDS):
  - responds to both components in the plaid
- Pattern-direction-selective (PDS) cell:
  - responds to global/pattern/perceived direction of motion



Aperture problem

- Problem: Local-velocity sample is different from the object velocity
- Goal: Disambiguate local-velocity samples and integrate them into an accurate estimate of the global (object) velocity



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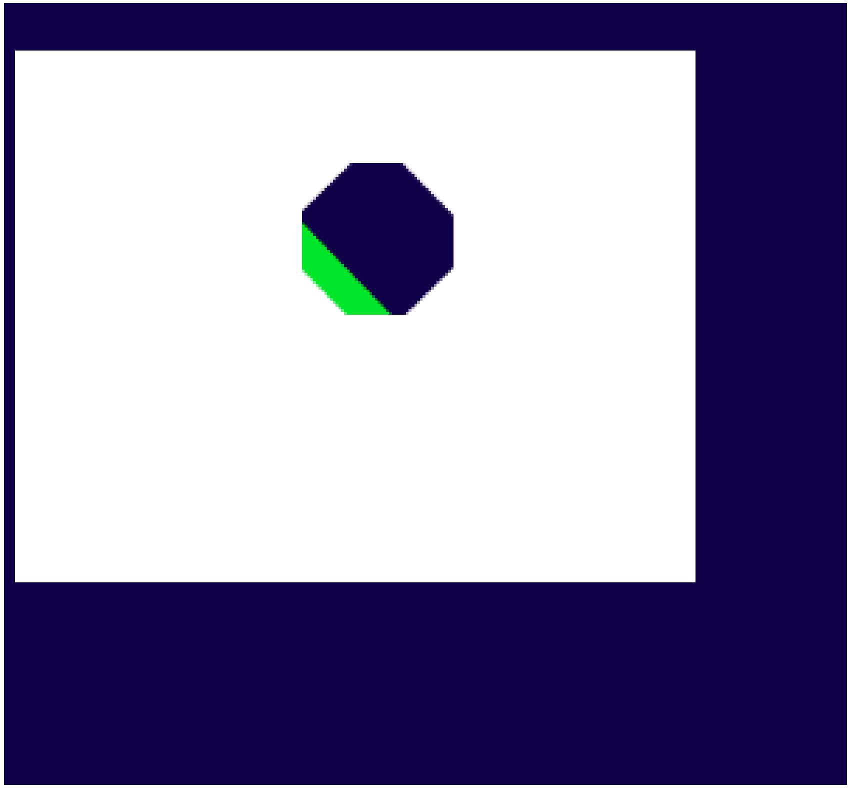
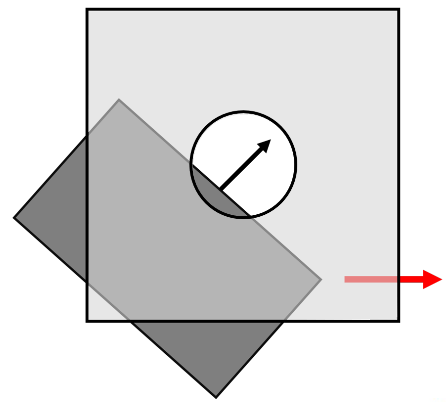
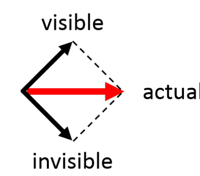


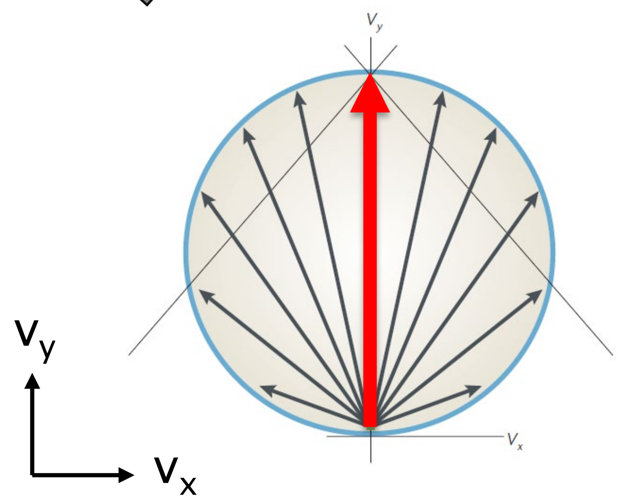
Aperture Problem

- Problem: Local-velocity samples are intrinsically ambiguous
- Solution: Infer global (object) velocity from many local-motion samples





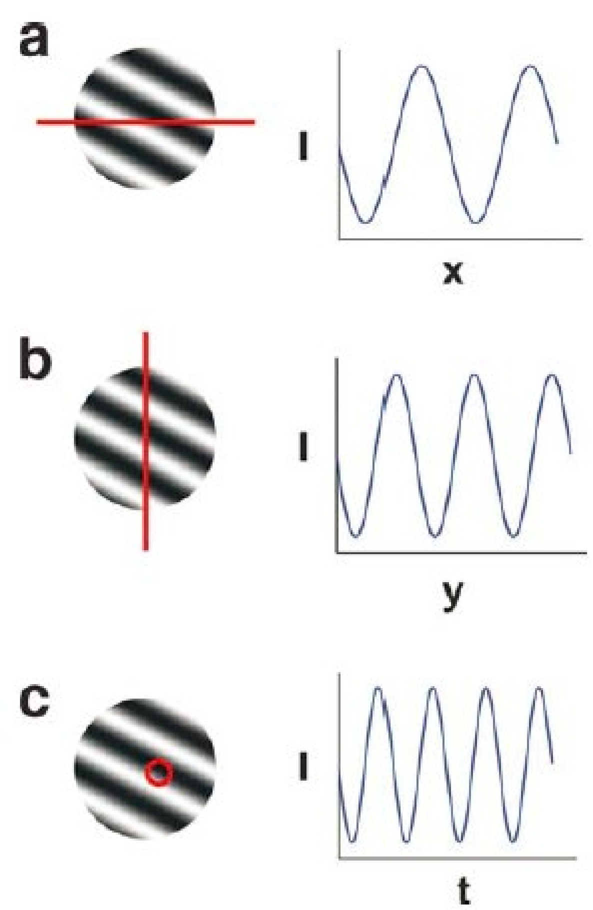
- Vector average
- Feature tracking
- Intersection-of-constraints (IOC):
  - Each local velocity sample *constrains* the global object velocity
  - Find object velocity by integrating local samples
  - MT firing rates may represent the velocity of moving objects using IOC



(Bradley & Goyal, *Annu Rev Neurosci*, 2008)

Spatiotemporal energy models

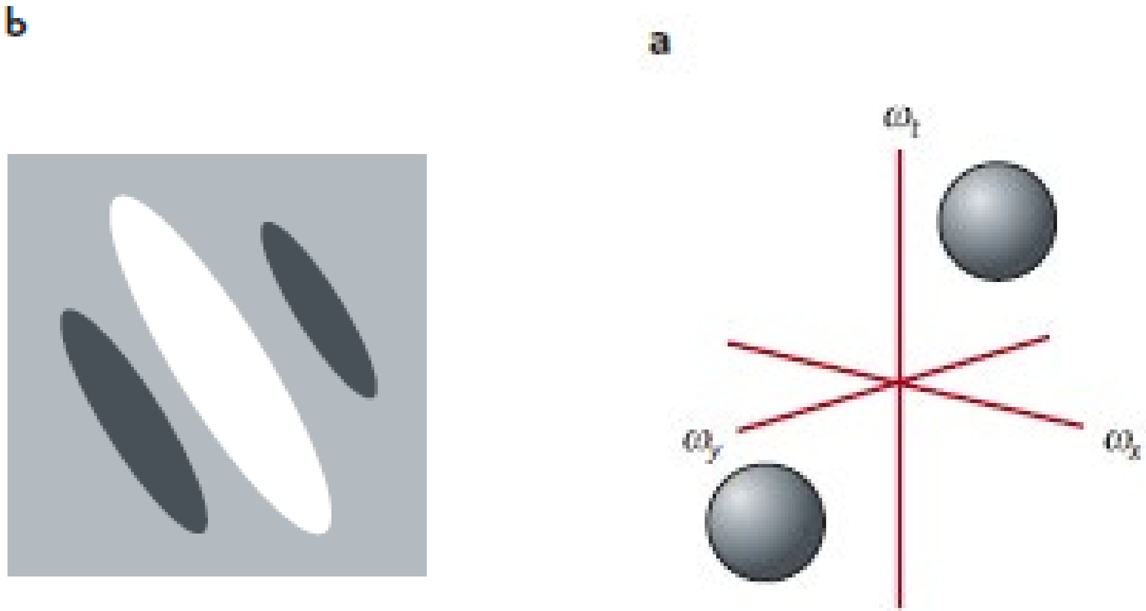
- Toward Fourier transform:
  - a) horizontal slice reveals a sinusoidal modulation of intensity vs. x (ω_x)
  - b) same for y (ω_y)
  - c) looking at a fixed location as the grating moves (ω_t)
- The velocity (direction and speed) of the grating is completely characterized by a single 3-D frequency: $(\omega_x, \omega_y, \omega_t)$



Born & Bradley, 2005

Spatiotemporal energy models

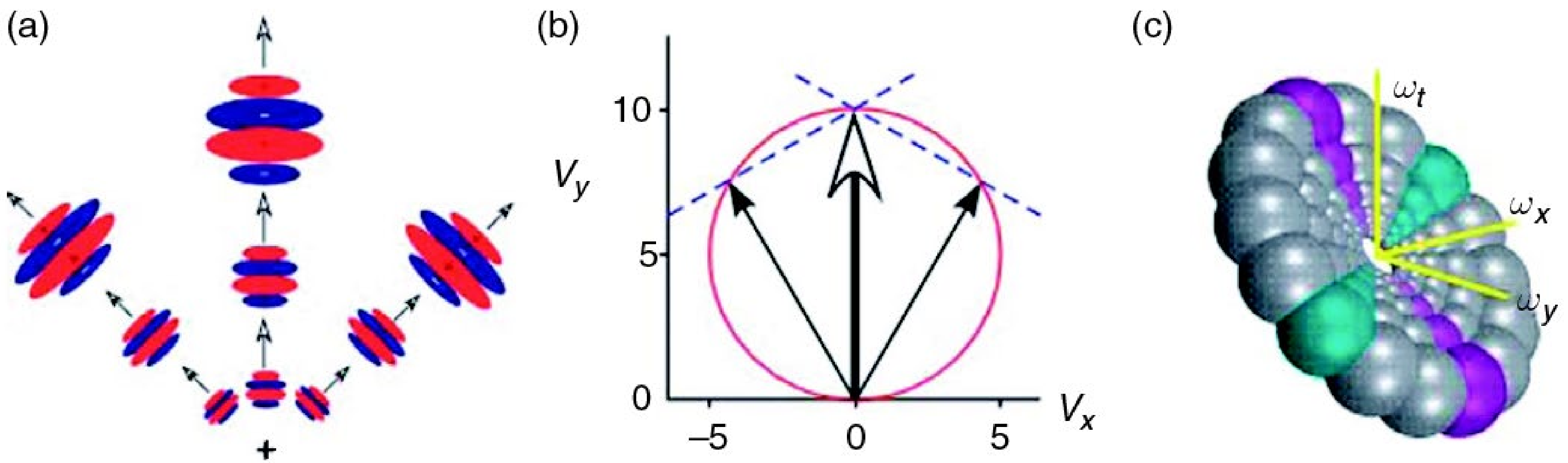
- Space–time oriented filters:
  – Space–time domain: Gabor function
  – Fourier domain: “fuzzy blob”, the density of which decreases with distance from the center frequency



(Bradley & Goyal 2009)

Aperture problem in the Simoncelli & Heeger model

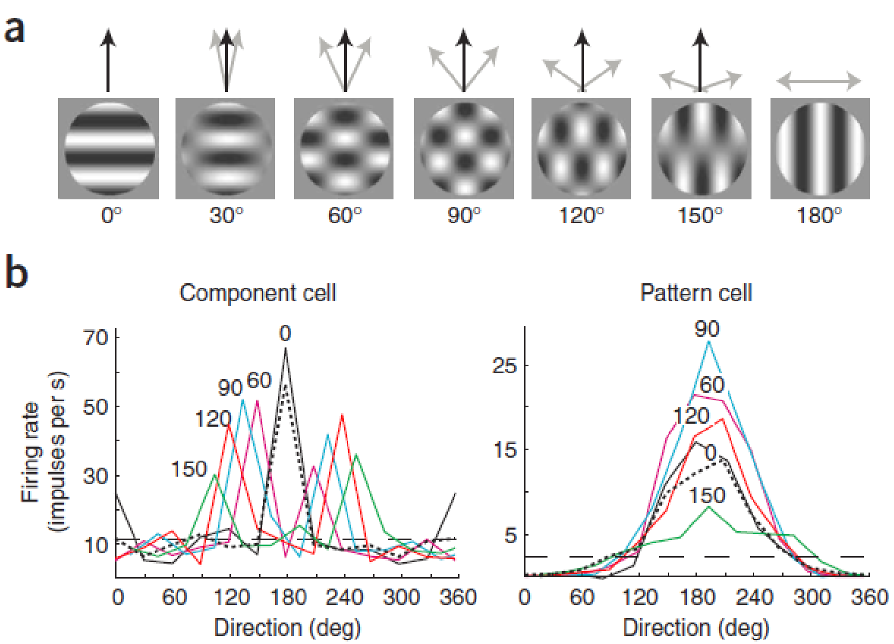
- The Simoncelli & Heeger (1998) model provides an IOC solution to the aperture problem
- Each 1D local-motion measurement (by a CDS cell) is consistent with a number of possible 2D velocities, all of which must fall on a line in velocity space
- A PDS cell in MT is created by summing the outputs of CDS cells with spectra centered on a common plane



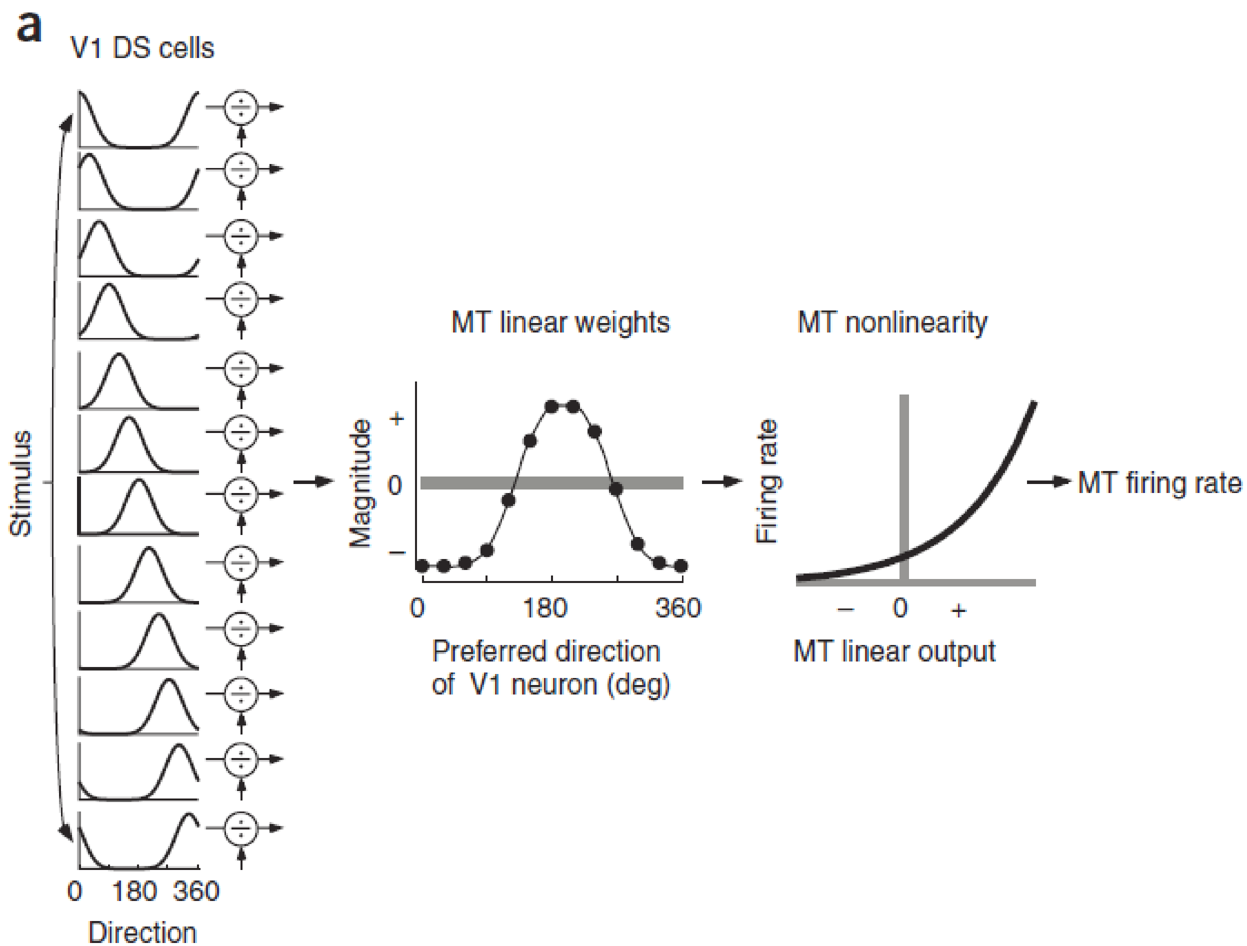
(Pack & Born, *Senses*, 2008)

Middle temporal (MT) area

- Rust et al. (2006):
  - Presented sequence of random pattern stimuli
  - Made from 12 gratings drifting in different directions
  - Fit to L-N cascade model
  - Explained full range of pattern motion selectivity found in MT

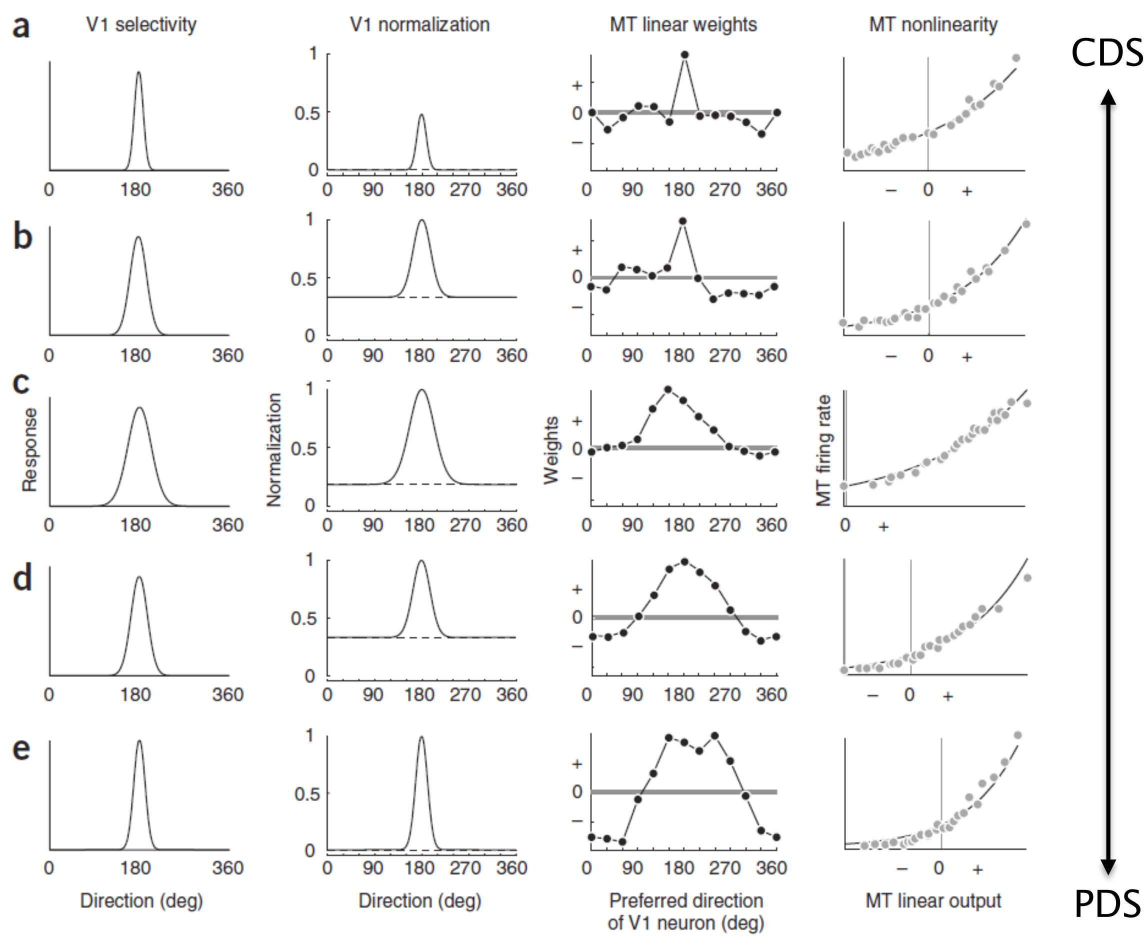


L-N cascade model



(Rust et al 2006)

L-N cascade model



(Rust et al 2006)

3D visual response properties of MSTd emerge from an efficient, sparse population code

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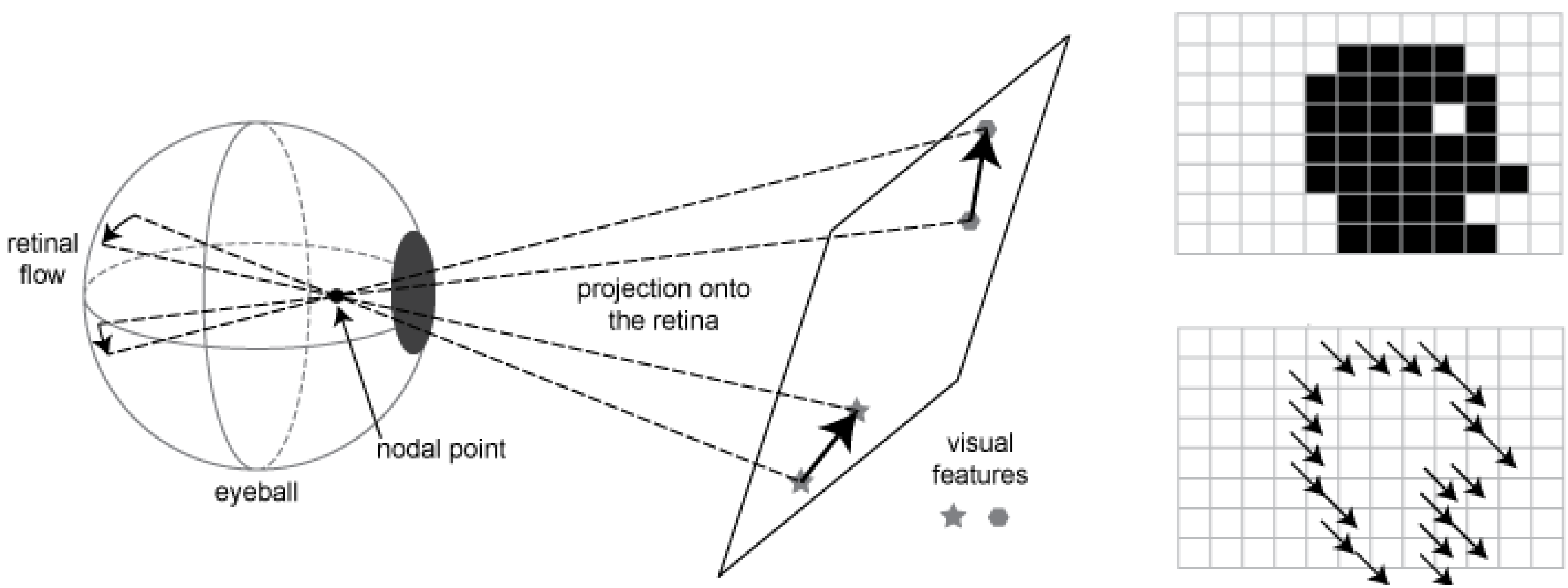
[1]University of California, Irvine

[2]University of Washington

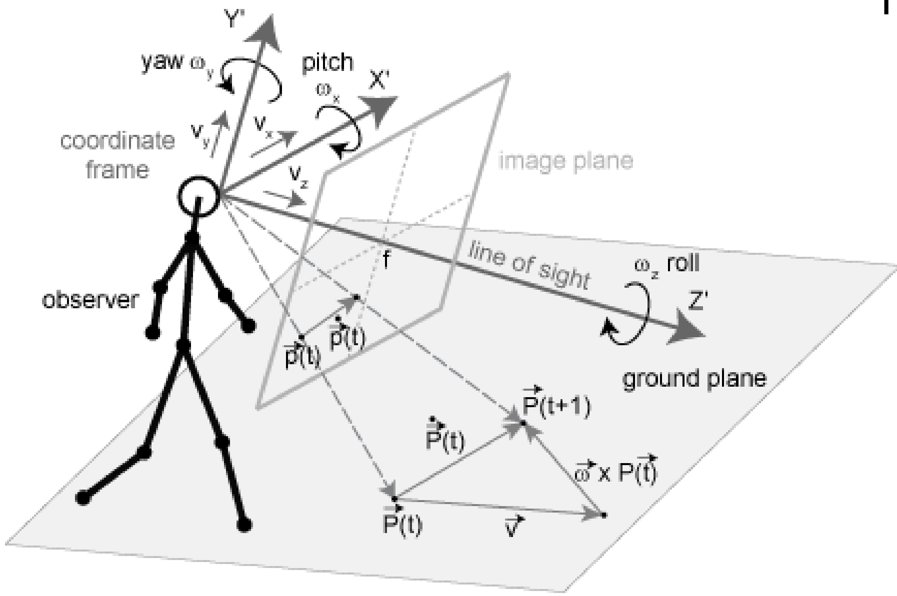
Retinal optic flow

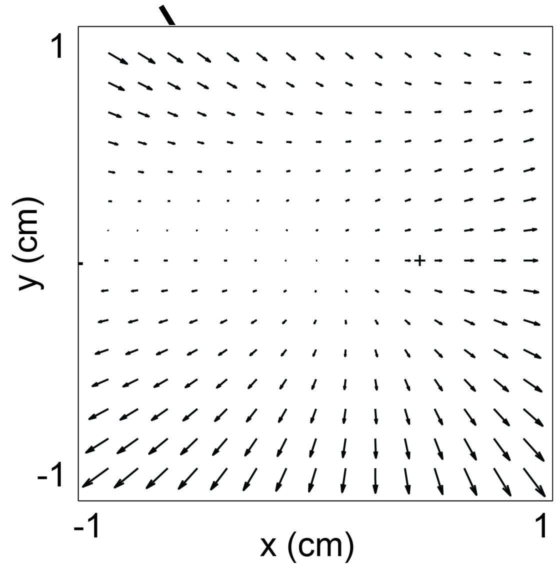
- Apparent motion on the retina caused by relative movement between observer and environment



(Raudies & Neumann, *CVIU*, 2012)

Motion field model



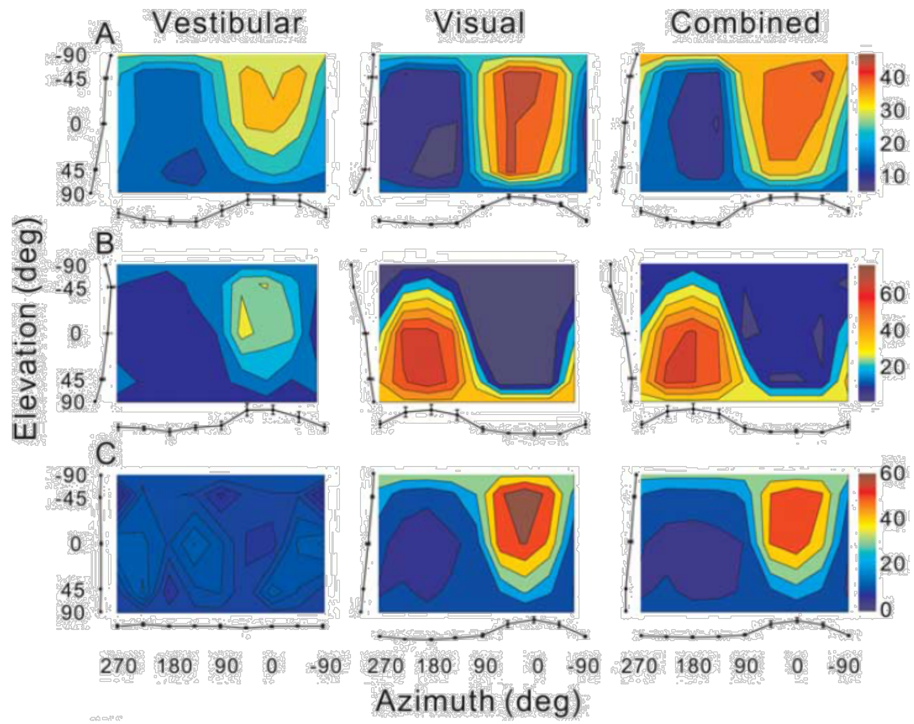


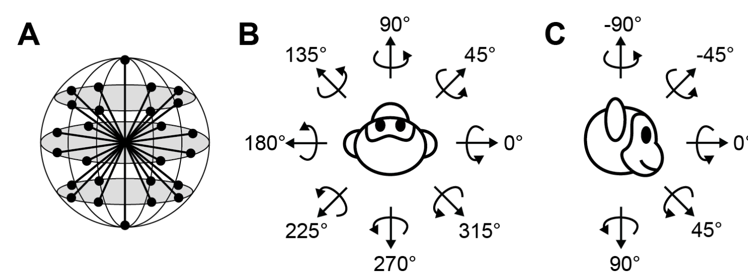
- Project 3D world points $\vec{P} = (X, Y, Z)^T$ onto 2D image points $\vec{p} = (x, y)^T$
- $$\begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix} = \underbrace{\frac{1}{Z}\begin{bmatrix} -f & 0 & x \\ 0 & -f & y \end{bmatrix}\begin{bmatrix} v_X \\ v_Y \\ v_Z \end{bmatrix}}_{\text{translation}} + \underbrace{\frac{1}{f}\begin{bmatrix} xy & -(f^2 + x^2) & fy \\ f^2 + y^2 & -xy & -fx \end{bmatrix}\begin{bmatrix} \omega_X \\ \omega_Y \\ \omega_Z \end{bmatrix}}_{\text{rotation}}$$

(Longuet-Higgins & Prazdny, *Proc Royal Soc London*, 1980)

MSTd response properties

- Main visual input from MT
- Large receptive fields (up to $40° \times 40°$)
- encodes visual and vestibular signals
- responds to optic flow
  - responds to 3D observer translations (heading)
  - responds to 3D observer rotation
  - act like template matches
- encodes eye position / eye velocity

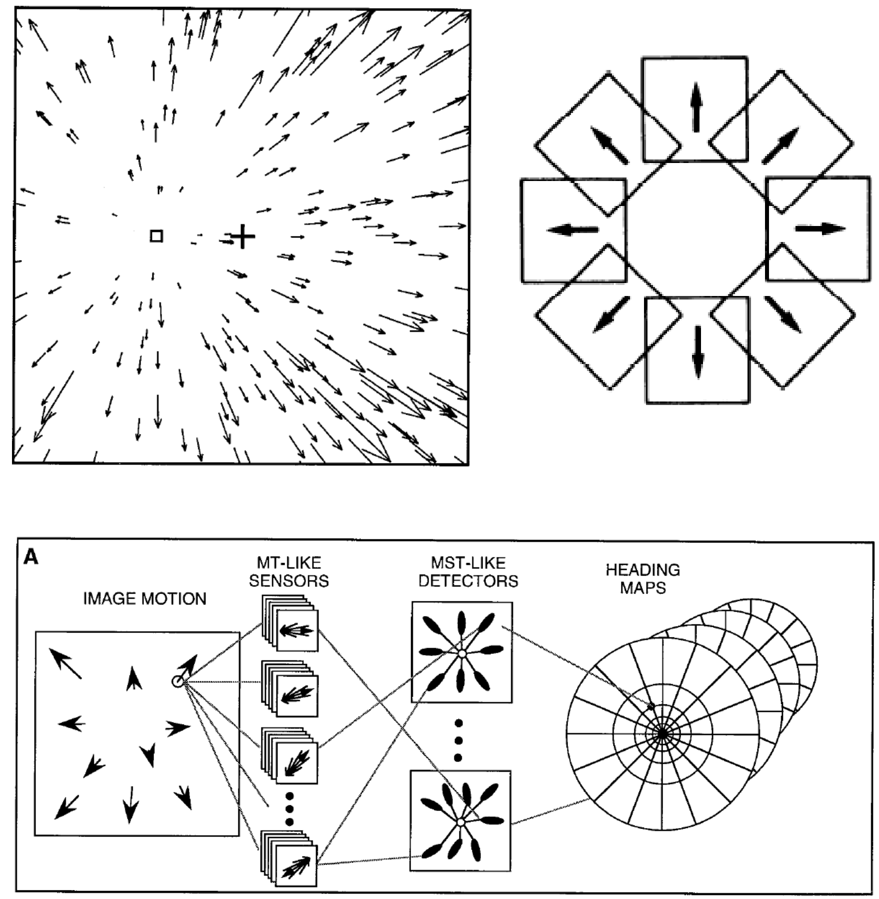




(Gu et al., *J Neurosci*, 2006)

Heading template model of MSTd

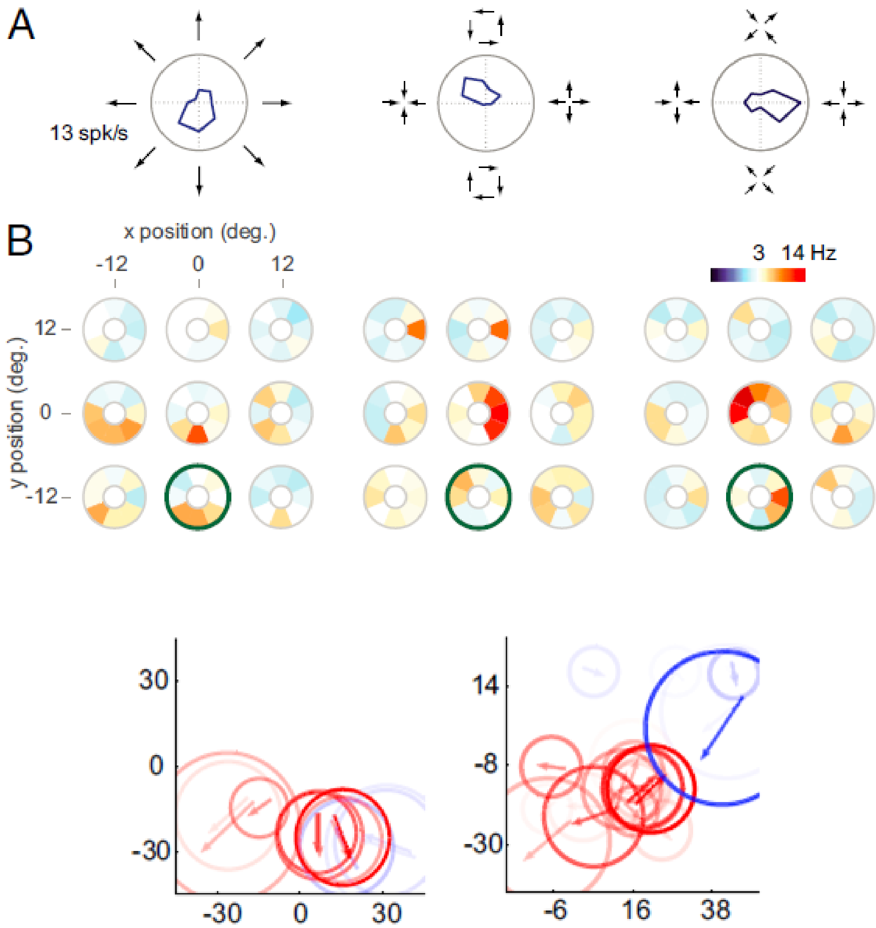
- MSTd units receive input from a mosaic of MT local-motion detectors
- Detected heading corresponds to the position of the most active MSTd unit
- Many models have followed this idea
  - Perrone & Stone (1994,1998)
  - Lappe et al. (1996)
  - Beintema & van den Berg (2000)
  - Browning et al. (2009)
- Limitations:
  - Combinatorial explosion of required heading templates
  - Heading in MSTd is a population code
  - Cannot explain some of the less intuitive response properties



(Perrone & Stone, *J Opt Soc Am* A,1992)

Complex motion selectivity in MSTd

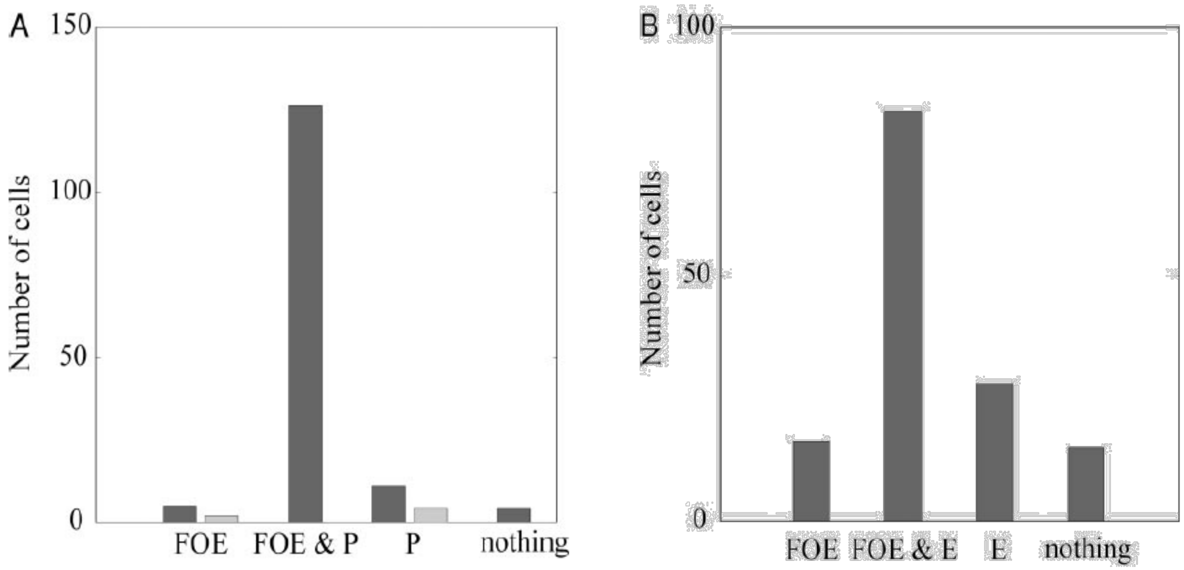
- MSTd responds to complex motion
  - No perfect heading templates
  - Neurons prefer an intricate mixture of flow components
  - Tuning varies in different subfields of the receptive field
- MSTd encodes vestibular signals
- MSTd codes in both retinal and head-centered coordinates



(Mineault et al., *PNAS*, 2012)

Complex motion selectivity in MSTd

- MSTd simultaneously encodes multiple perceptual variables
  - Distributed representation of heading, eye position, eye velocity
  - Most neurons participate in encoding multiple variables (“basis functions”)
  - Nonlinear interactions



FOE: 3D heading
P: eye position
E: eye velocity

- How can these nonintuitive response properties be explained?

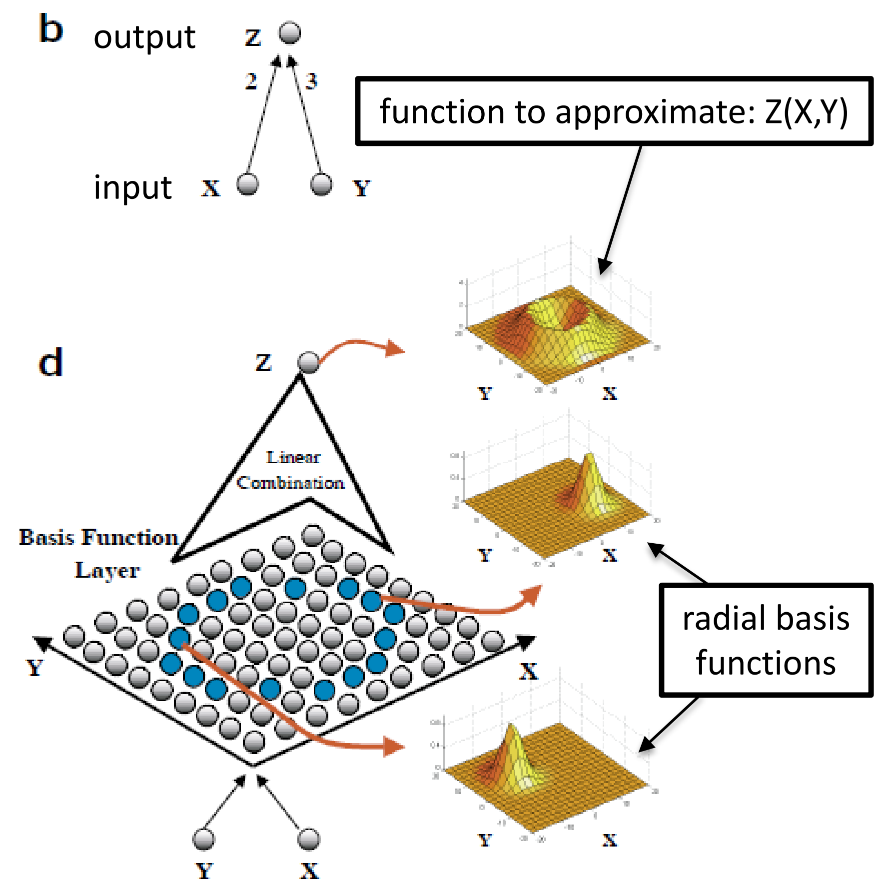
(Ben Hamed et al., *J Neurophys*, 2003; Mineault et al., *PNAS*, 2012)

Efficient coding of optic flow

- What if MSTd is trying to find an efficient encoding of visual input from MT?
  - such that any optic flow pattern / relevant perceptual variable can be decoded from a small number of MSTd neurons (accuracy)
  - such that any given stimulus activated only a small number of MSTd neurons (population sparsity)
  - such that any MSTd neuron responded to only a small number of stimuli (lifetime sparsity)

Basis function representations

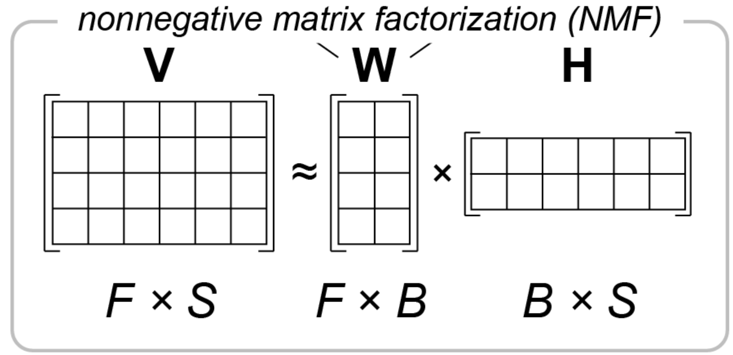
- Form of population code
- Allows for flexible intermediate representations
- Most functions of interest can be computed using a linear combination of basis functions
- Examples of a basis set:
  - Coordinate axes in 3D space
  - Fourier transform: Any function = linear sum of a series of sin / cos
  - Radial basis functions (Gaussians)
- Many different basis sets possible…
  - Cartesian (x,y,z)? Spherical (r,θ,ϕ)?
  - Which one to choose?
  - What are the constraints?



(Pouget & Snyder, *Nat Neurosci*, 2000)

Nonnegative matrix factorization (NMF)

- Dimensionality reduction technique
  - Similar to PCA, ICA
  - Unsupervised statistical learning
  - Reconstruct input data matrix from product of two much smaller matrices
- Use NMF to find basis set



- **V**: Observed data
- **W**: Basis vectors
- **H**: Hidden coefficients

F: features
S: stimuli (observations)
B: basis vectors

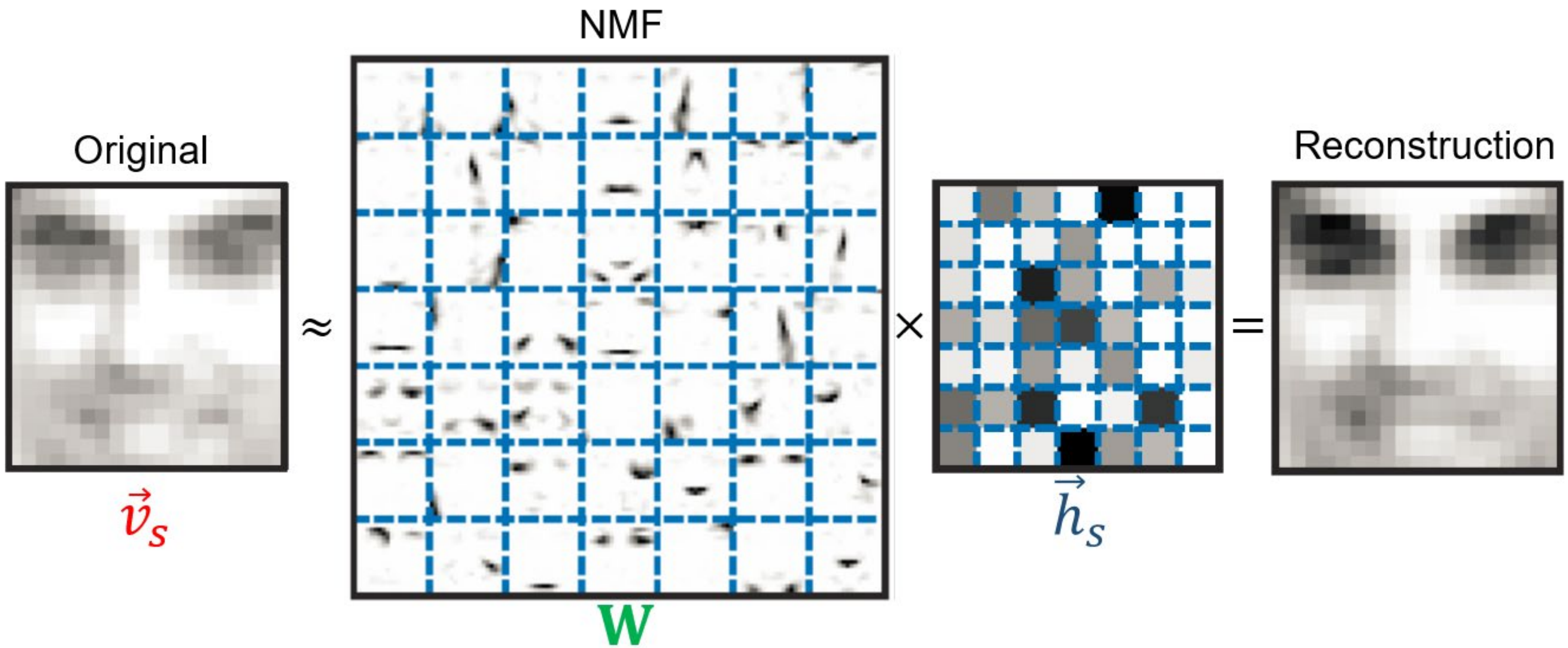
B <<< *S*

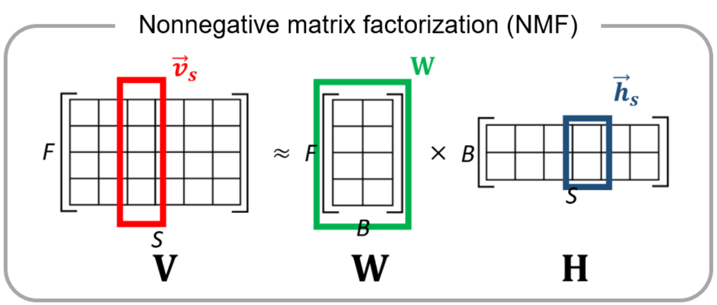
- Linear decomposition: $\mathbf{V} \approx \mathbf{WH}$
- NMF minimizes the following cost function:

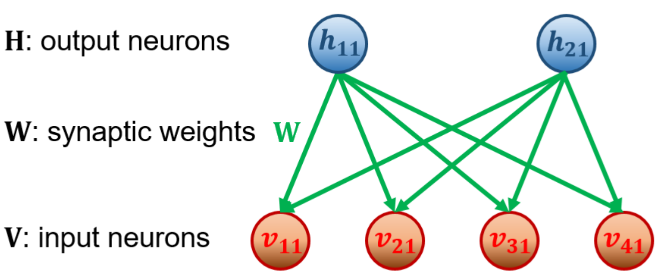
$$c(\mathbf{W},\mathbf{H}) = \|\mathbf{V} - \mathbf{WH}\|^2$$
$$\forall ij: W_{ij} \geq 0, H_{ij} \geq 0$$

(Paatero & Tapper, *Environmetrics*, 1994; Lee & Seung, *Nature*, 1999)

NMF applied to face images





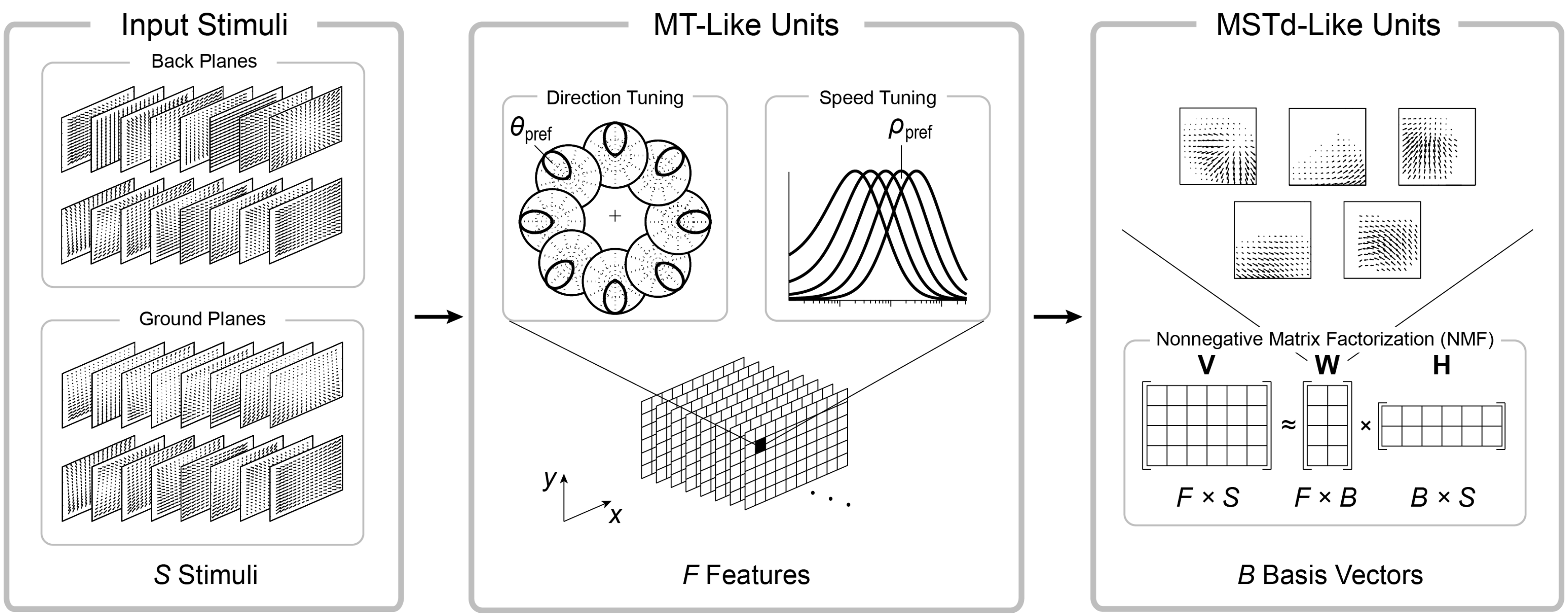


$$\vec{v}_s = \mathbf{W}\,\vec{h}_s$$

(Lee & Seung, *Nature*, 1999)

Sparse decomposition model of MSTd

- Input stimuli: All naturally occurring optic flow fields
- MT-like units: local motion sensors (direction / speed)
- MSTd-like units: small basis set of complex motion templates



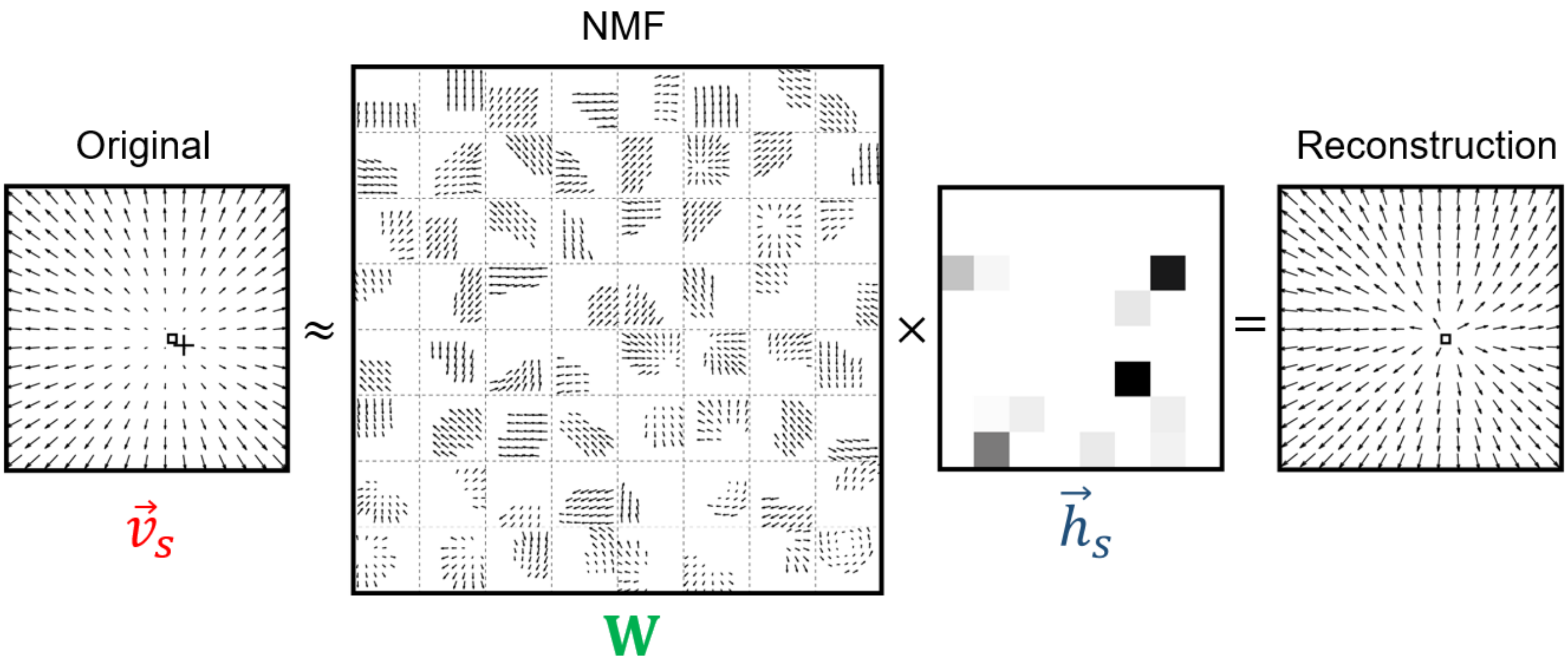
$S = 6000$ virtual flow fields

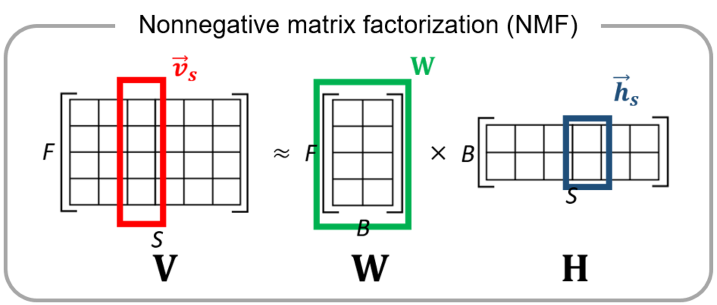
$F = 15 \times 15 \times 8 \times 5 = 9000$ virtual flow fields

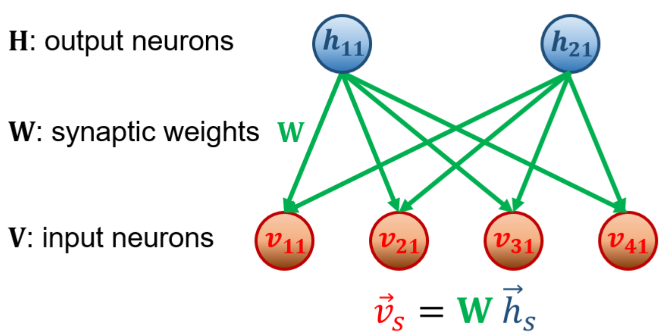
$B = 64$ basis vectors

(Beyeler et al., *J Neurosci*, 2016)

NMF applied to optic flow

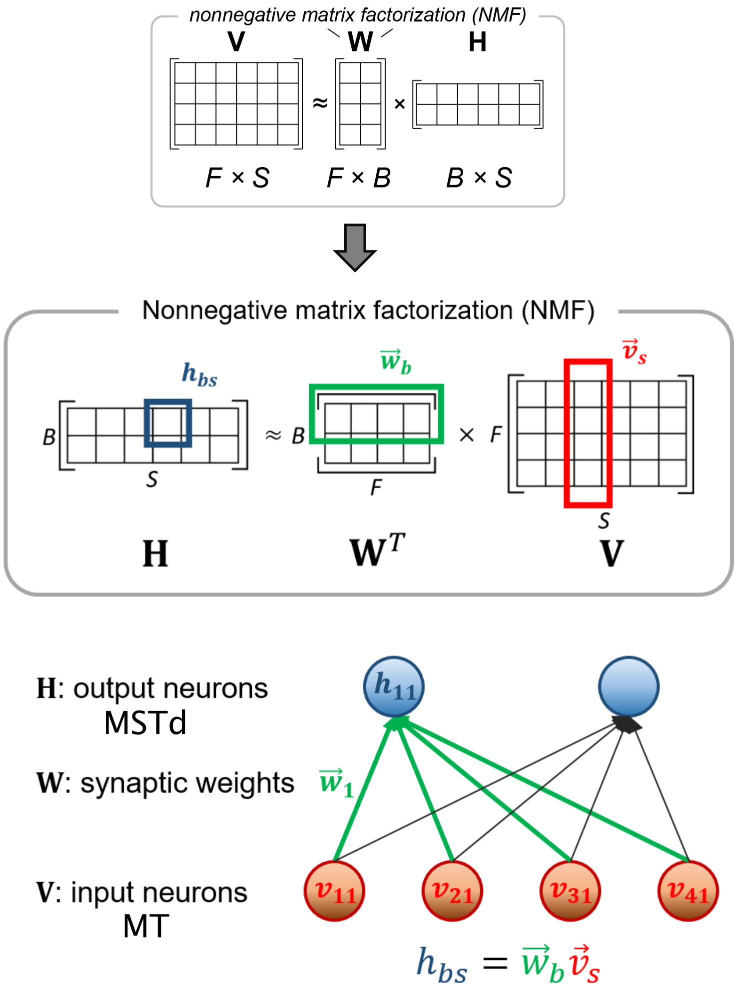




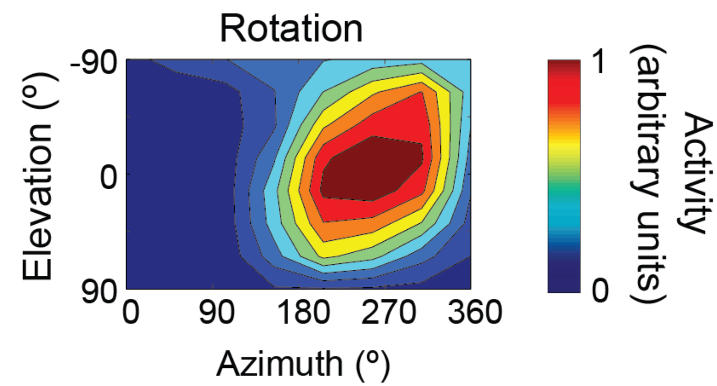


(Beyeler et al., *J Neurosci*, 2016)

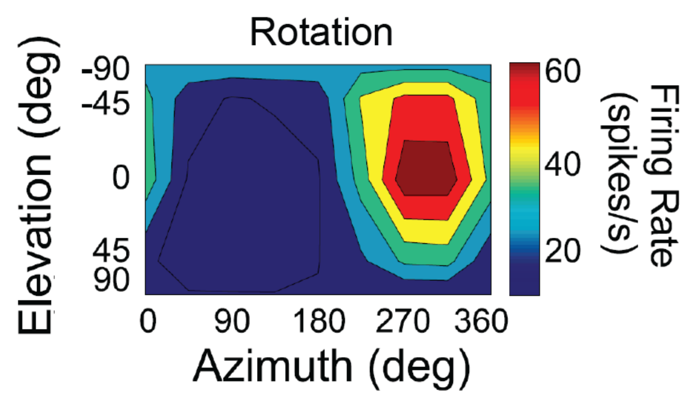
Using NMF to model neuronal response properties



Sparse decomposition model



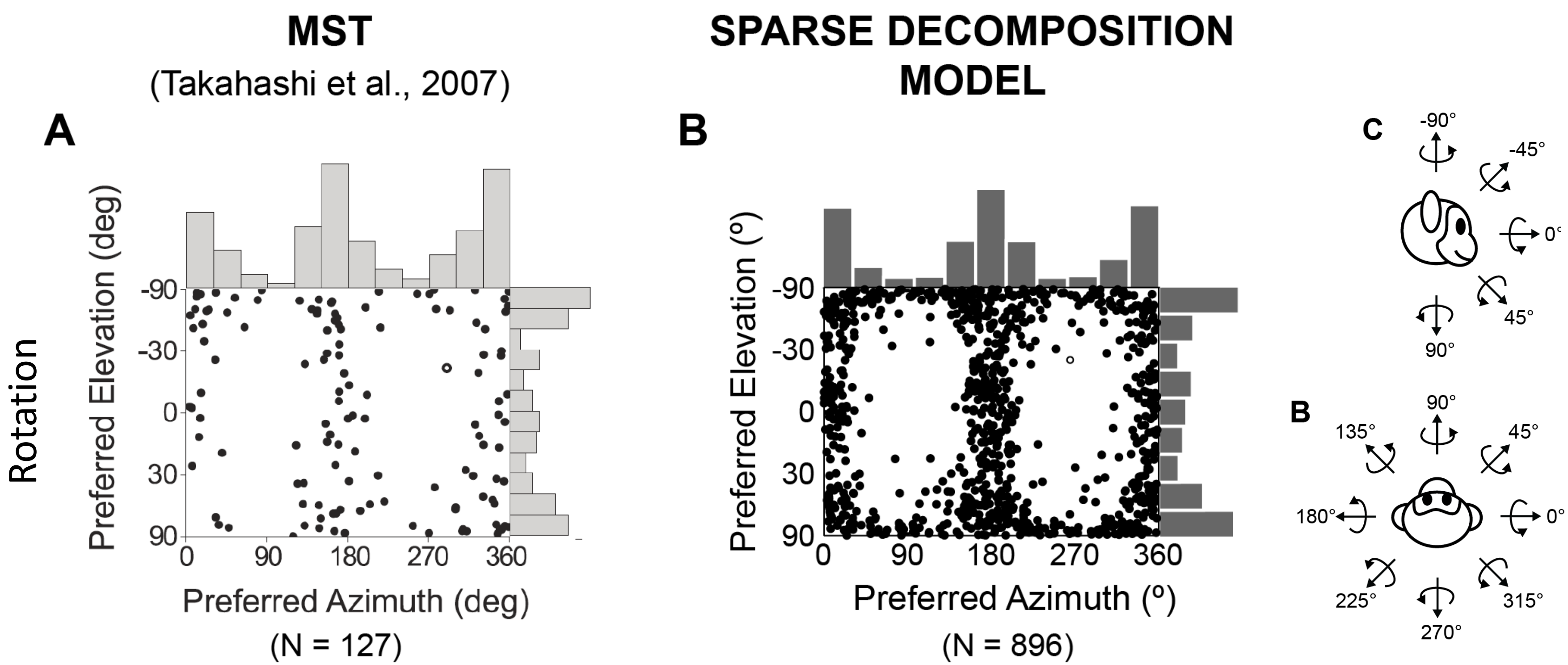
Takahashi et al., JNeurosci, 2007



(Beyeler et al., *J Neurosci*, 2016)

3D translation / rotation selectivity

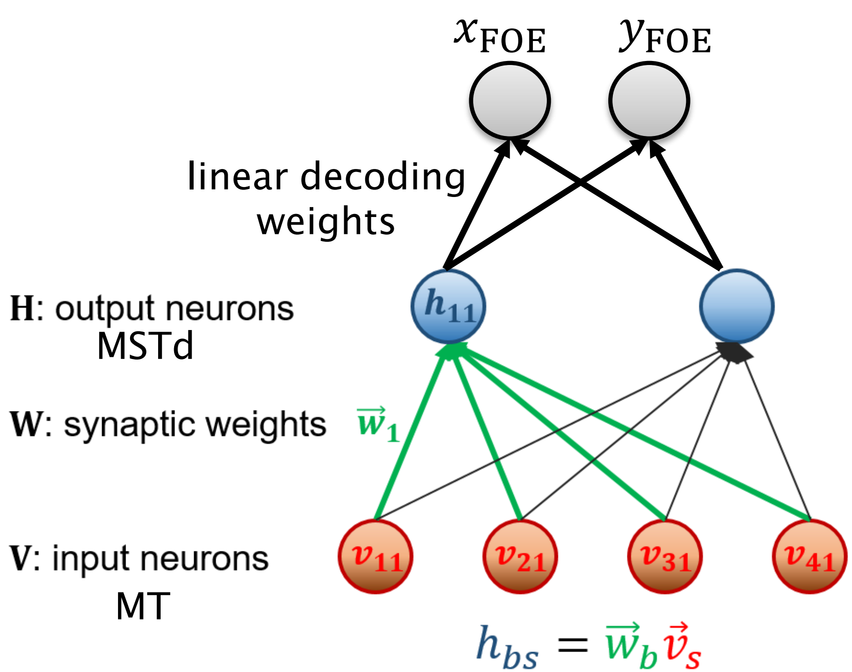
- All 3D directions are represented
- Bias towards lateral headings
  - Only few neurons respond to straight-ahead headings
  - Only few neurons respond to roll rotation



(Beyeler et al., *J Neurosci*, 2016)

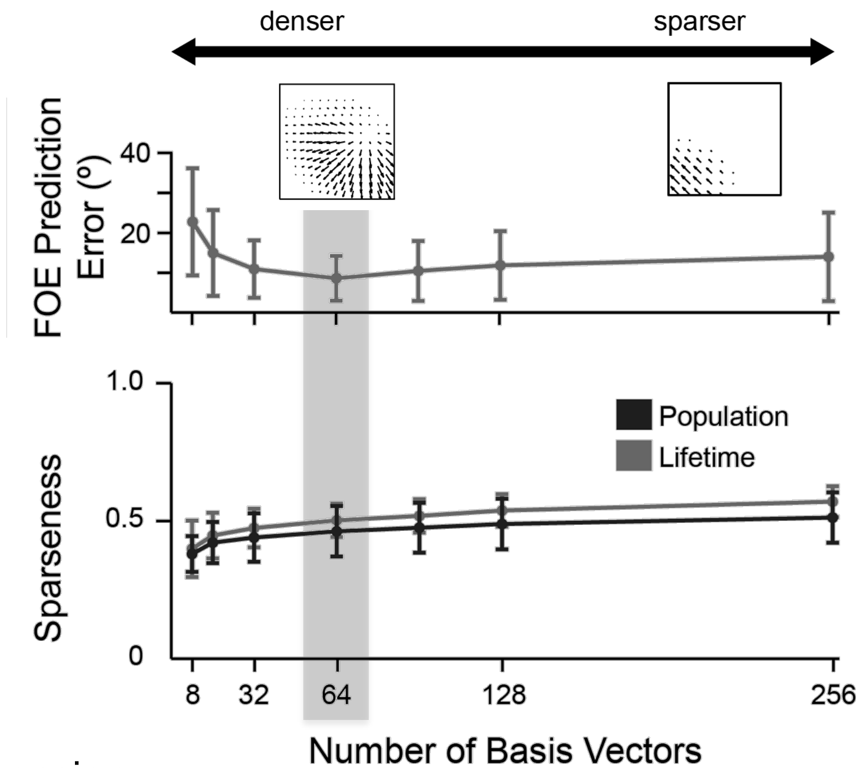
Decoding heading from the population response

- Decode $(x_{\mathrm{FOE}}, y_{\mathrm{FOE}})$ of arbitrary expansive flow fields from a population of N MSTd-like model units
  - linear regression, cross-validated
  - randomly sampled 10,000 flow fields
  - azimuth between $[45°, 135°]$, elevation between $[-45°, +45°]$
  - learn a set of $N \times 2$ linear decoding weights



Sparse population code for heading

Translation	FOE (x, y)
Ben Hamed et al. (2003)	$(3.62° \pm 6.78°, 3.87° \pm 4.96°)$
Sparse decomposition model	$(5.75° \pm 5.62°, 6.02° \pm 5.51°)$



s=1: maximal sparseness

s=0: minimal sparseness

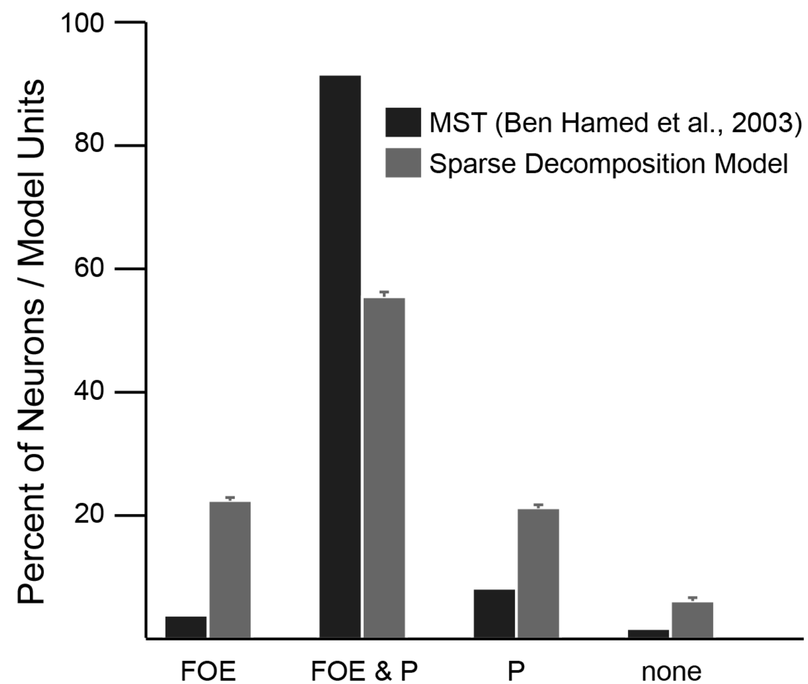
FOE = focus of expansion

(Beyeler et al., *J Neurosci*, 2016)

Encoding of multiple perceptual variables

Translation	FOE (x, y)	Eye velocity (ω_x, ω_z)
Ben Hamed et al. (2003)	$(3.62° \pm 6.78°, 3.87° \pm 4.96°)$	$(1.39° \pm 3.69°, 1.38° \pm 3.02°)$
Sparse decomposition model	$(5.75° \pm 5.62°, 6.02° \pm 5.51°)$	$(0.82° \pm 0.89°, 0.92° \pm 0.99°)$

- A strong decoding weight suggests a neuron contributes strongly to the decoding
  - most model units involved in encoding both FOE and P
  - same is true for neurons in MSTd
- These neurons are generalists, not specialists

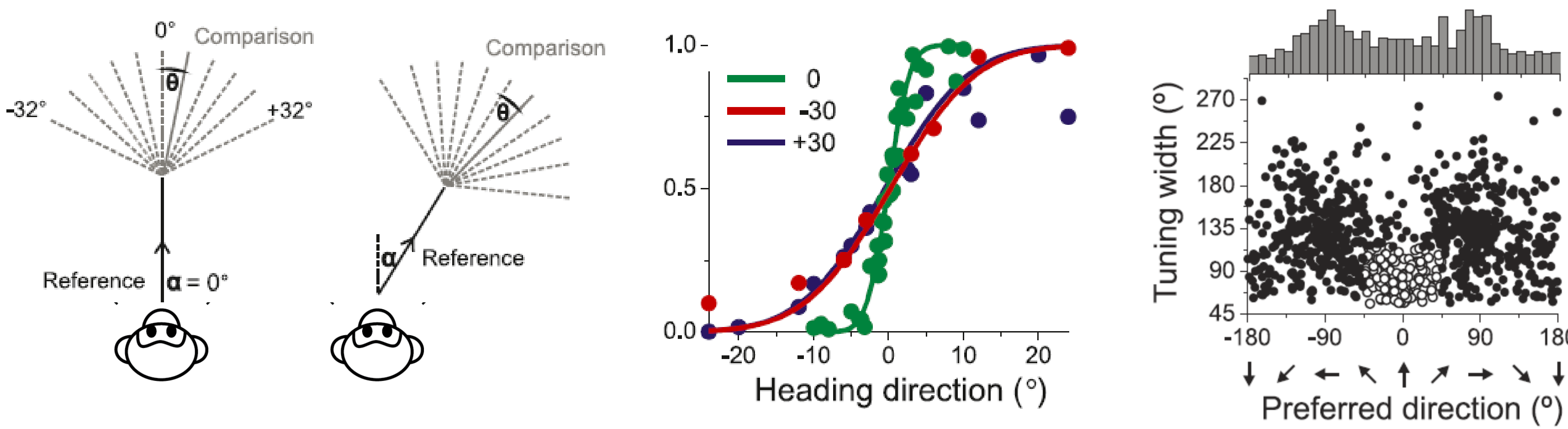


FOE = focus of expansion
P = pursuit (eye movement velocity)

(Beyeler et al., *J Neurosci*, 2016)

Heading discrimination

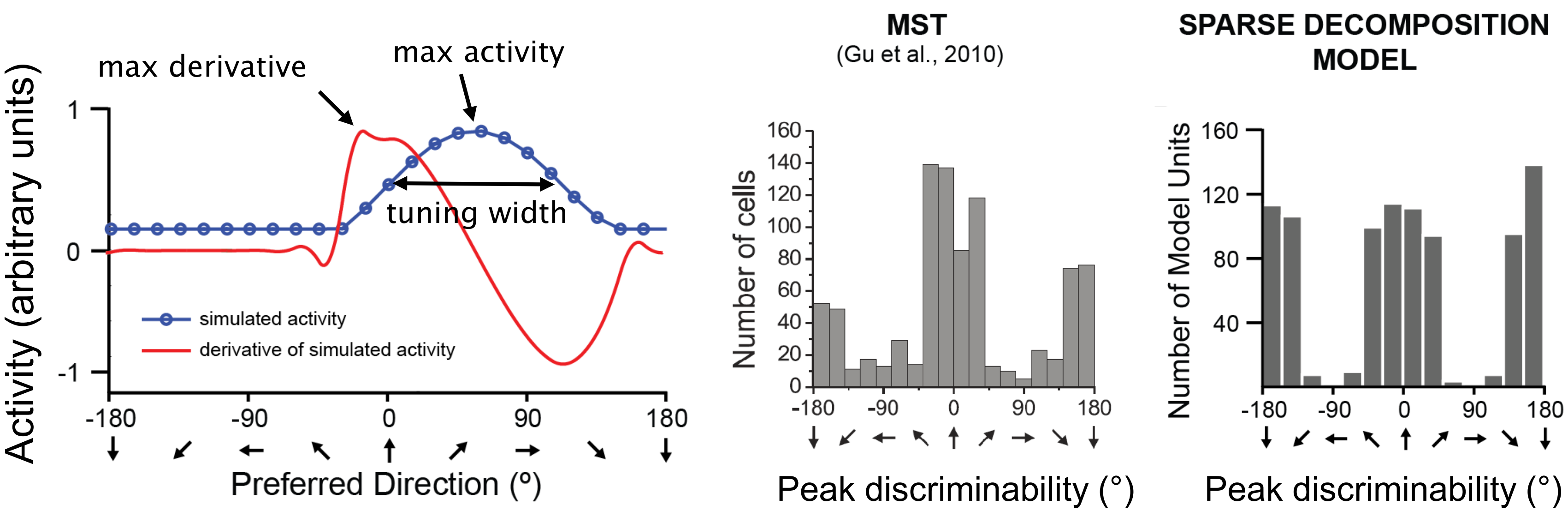
- Heading discrimination is best around straight-ahead headings
- MSTd is causally linked to heading perception
  - behavioral performance due to neurons preferring straight-ahead headings with sharp tuning curves? (Duffy & Wurtz, 1995)
- But most MSTd neurons prefer lateral headings!



(Gu et al., *Neuron*, 2010)

Population code underlying heading discrimination

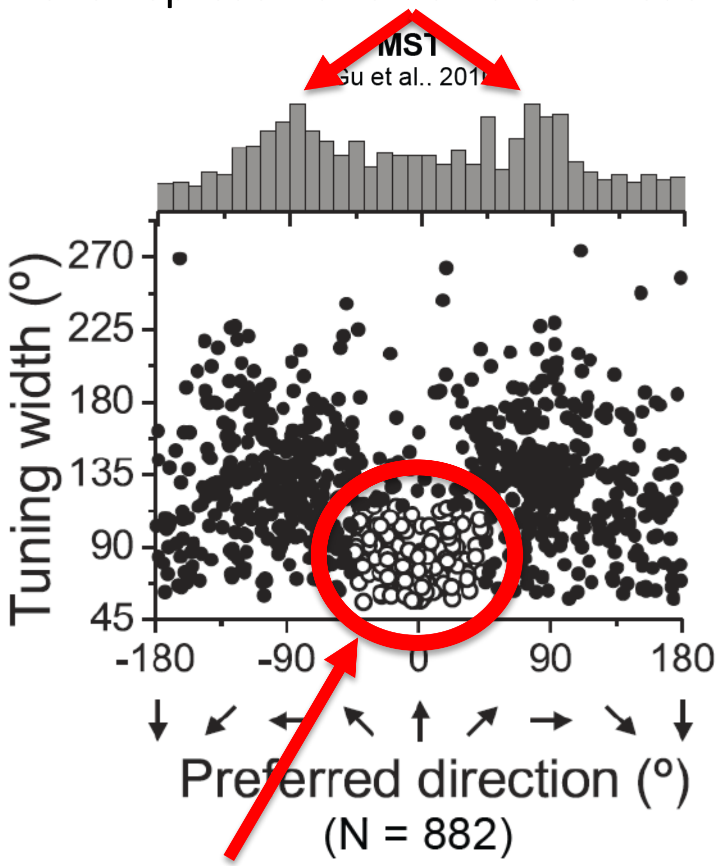
- Calculate tuning curves:
  - Preferred direction: Heading where neuronal activity is maximal (peak of tuning curve)
  - Tuning width: Spread of tuning curve at half-maximum
  - Peak discriminability: Heading where derivative of tuning curve is maximal

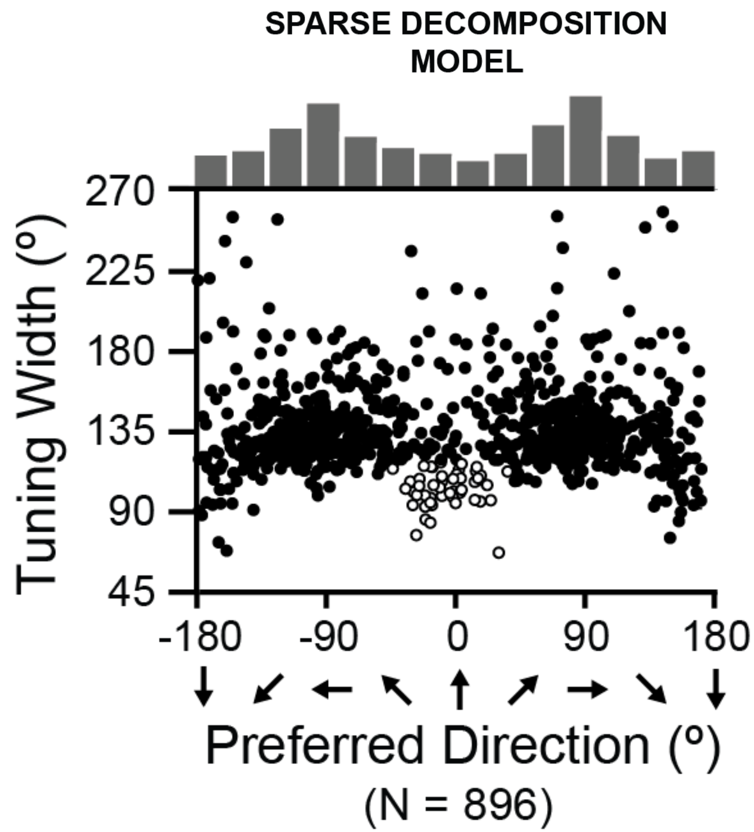


(Beyeler et al., *J Neurosci*, 2016)

Population code underlying heading discrimination

overrepresentation of lateral headings





subset of MSTd neurons preferring
forward headings with sharp tuning curve

(Beyeler et al., *J Neurosci*, 2016)

Conclusion

- Sparse decomposition model of MSTd
  - Offers a biologically plausible account of a wide range of visual response properties ranging from single-unit selectivity to population statistics
  - Suggests that most visual response properties are a by-product of MSTd neurons performing dimensionality reduction on their inputs
  - Provides a further step towards a scientific understanding of nonintuitive MSTd response properties

Sparseness

- Sparseness metric s for a signal r with N sample points (Vinje & Gallant, 2000):

$$s = \left(1 - \frac{1}{N} \frac{(\sum_i r_i)^2}{\sum_i r_i^2}\right) \Big/ \left(1 - \frac{1}{N}\right)$$

- Sparseness: $s \in [0,1]$
  - $s = 0$: minimal sparseness (dense code)
  - $s = 1$: maximal sparseness (local code)

- Population sparseness:
  - How many MSTd-like model units were activated by any given stimulus
  - r_i: response of i–th neuroto a particular stimulus
  - N: number of model units
- Lifetime sparseness:
  - How many stimuli any given MSTd-like model unit responded to
  - r_i: response of i–th stimulus
  - N: number of stimuli

Population Fisher Information

- Provides an upper limit on the precision with which an unbiased estimator can discriminate small variations in a variable (x) around a reference value (x_{ref}):

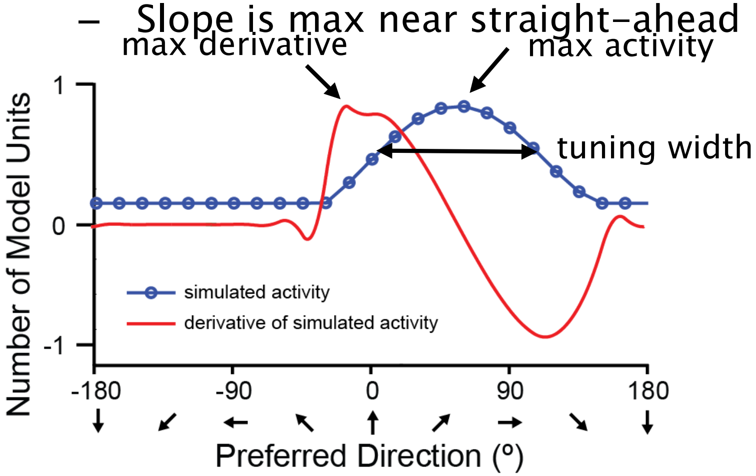
$$I_{\mathrm{F}}(x_{\mathrm{ref}}) = \sum_{i=1}^{N} \frac{\left(R_i'(x_{\mathrm{ref}})\right)^2}{\left(\sigma_i(x_{\mathrm{ref}})\right)^2}$$

- N: number of neurons in the population
- $R_i'(x_{\mathrm{ref}})$: derivative of tuning curve for the i–th neuron at x_{ref}
- $\sigma_i(x_{\mathrm{ref}})$: variance of i–th neuron's response at x_{ref}

(Pouget et al., *Neural Comput*, 1998; Seung & Sompolinsky, *PNAS*, 1993)

Population Code for Heading Discrimination

- Discrimination best around straight-ahead headings
- Traditional view: Performance due to neurons tuned to straight-ahead headings
- Gu et al. (2010): Performance due to neurons tuned to lateral headings
  - Broad tuning curves
  - Slope is max near straight-ahead



- Consider two input stimuli with similar headings (e.g., 0°, 4°)
- Neurons with preferred direction (peak response) near 0° will contribute little to discrimination
  - Small heading deviations do not significantly alter response amplitude => not informative
  - Derivative ≈ 0
- Neurons whose tuning curve slope is steepest near 0° will contribute a lot to discrimination
  - Near steepest slope, small heading deviations cause large changes in response amplitude
  - Derivative is max
  - => "Peak discriminability"

(Beyeler et al., *J Neurosci*, 2016)

Nonnegative sparse coding (NSC)

- Combination of dimensionality reduction and sparse coding
  - represents observed data **V** with a small number of dictionary elements in **W**
    - such that all dictionary elements are nonnegative
    - such that elements are sparsely activated (**H**)

$$\min_{\mathbf{W},\mathbf{H}} \frac{1}{2}\|\mathbf{V}-\mathbf{WH}\|^2 + \lambda \sum_{ij} f(H_{ij})$$

nonnegative matrix factorization (NMF)

$$\forall ij: W_{ij} \geq 0, H_{ij} \geq 0$$

sparsity constraints

V: Observed data

W: Basis vectors

H: Hidden coefficients

- can explain response properties in V1, V2
- shown to be equivalent to spike-timing dependent plasticity (STDP) and homeostatic synaptic scaling

(Hoyer, *NNSP*, 2002; Hoyer, *JMLR*, 2004; Carlson et al., *IJCNN*, 2013)

Nonnegative sparse coding (NSC)

- Sparse and (potentially) parts-based representations have been found throughout the brain
- Could NSC be a general principles to which neuronal computations adhere?

Table 1: Nonnegative sparse coding in the brain

Area	Sparse	Parts-based	Experimental evidence	Modeled by NSC	Computational support
Retina	X	X	[27]	X	[27]
Early visual cortex	X	X	[17, 19, 28, 29]	X	[17, 19, 30, 31]
Ventral visual stream	X	X	[20]	X	[14, 32]
Dorsal visual stream	X	X	[33–35]	X	[22]
Auditory cortex	X	?	[36]	?	?
Olfactory cortex	X	?	[37]	?	[38]
Retrosplenial cortex	X	X	[26]	X	present paper
Motor cortex	X	?	[39, 40]	?	[41]
Basal ganglia	X	?	[3, 42]	X	[3], advanced RDDR
Barrel cortex	X	?	[43]	?	?

(Beyeler et al., *bioRxiv*, 2017