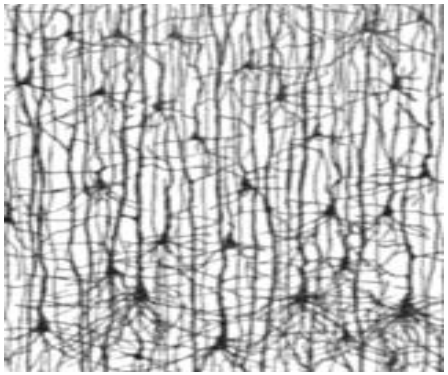
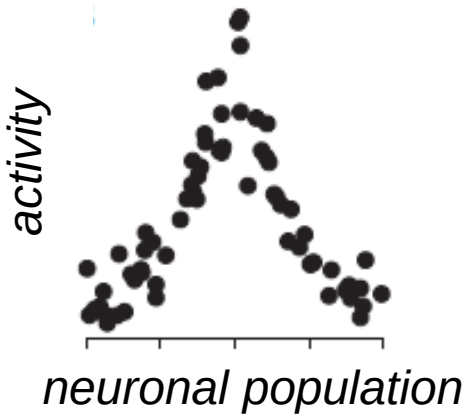
Filtering and normalization in the visual system (and in a few other systems)

Matteo Carandini
UCL Institute of Ophthalmology

circuits



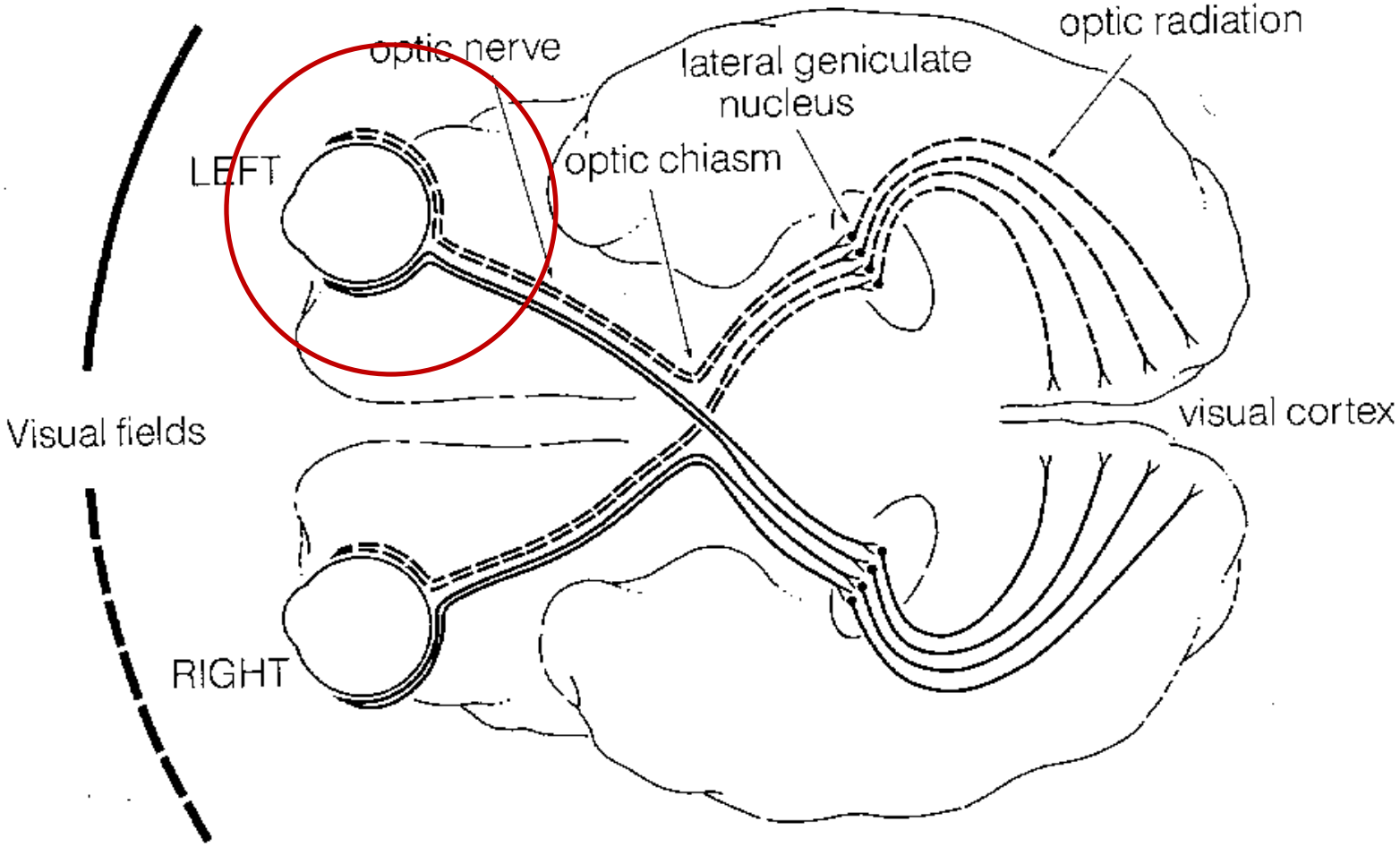
computations



behavior

how is it computed? ⟷ what is computed? ⟷ why is it computed?

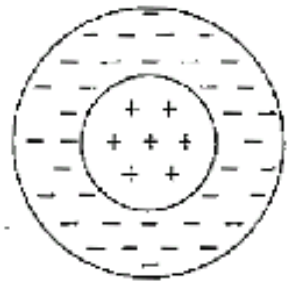
Carandini, *Nature Neuroscience*, 2012



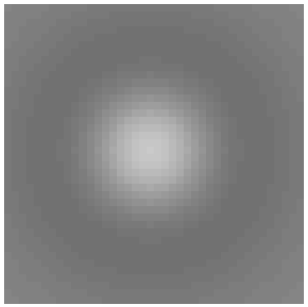
Dowling, 1987 (Fig 1.2)

A model of the ganglion cell receptive field

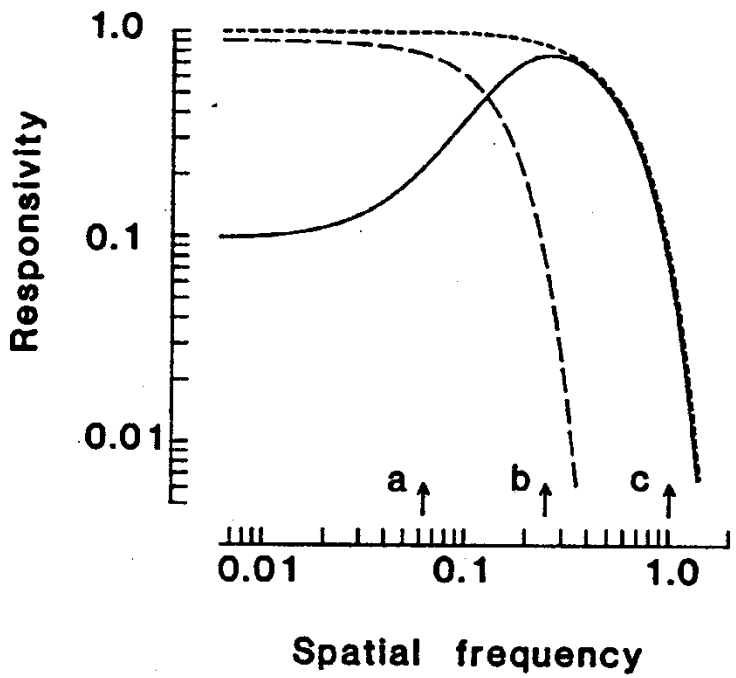
ON-center
receptive field

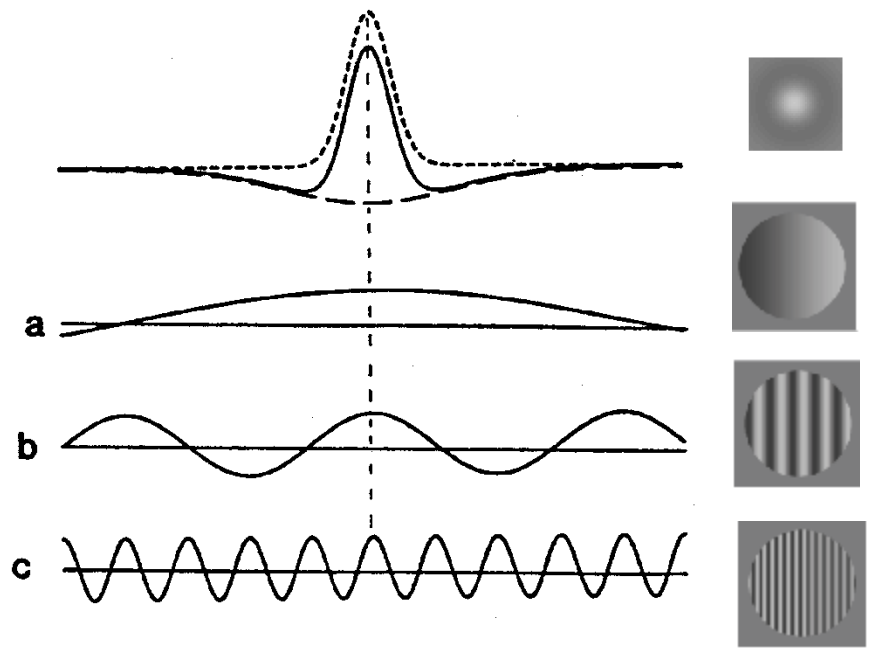


“Difference of
gaussians” model



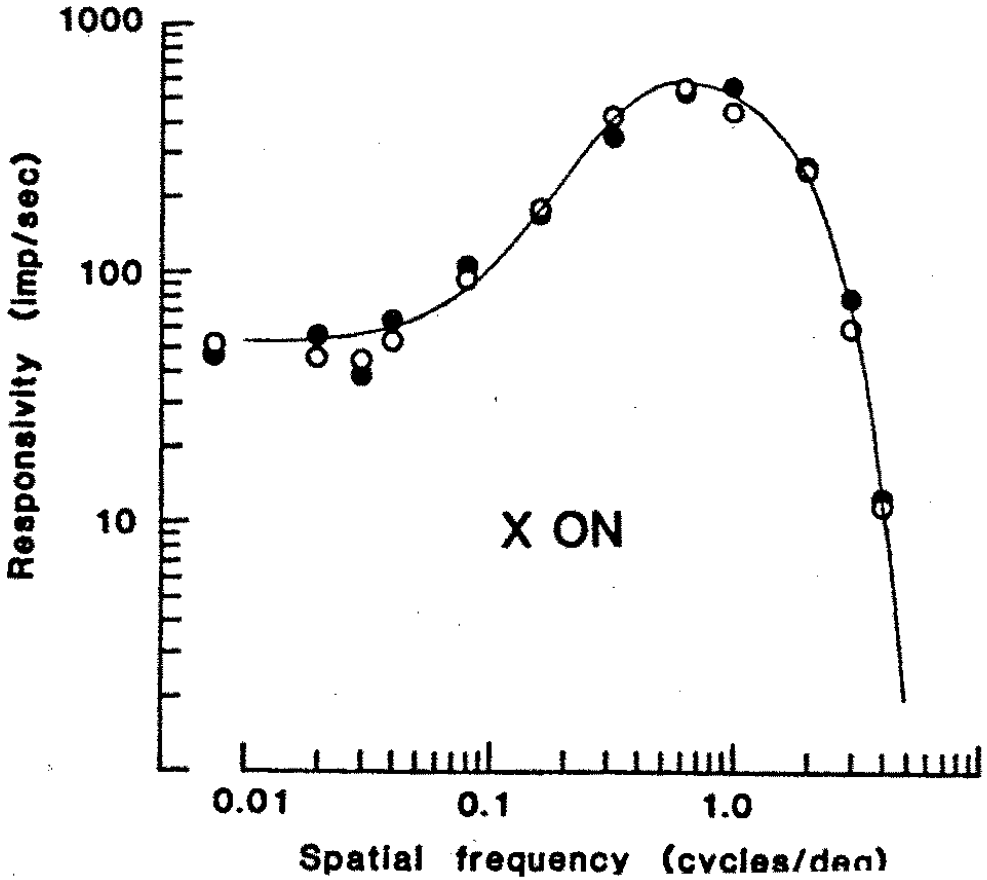
Predictions of the “difference of gaussians” model





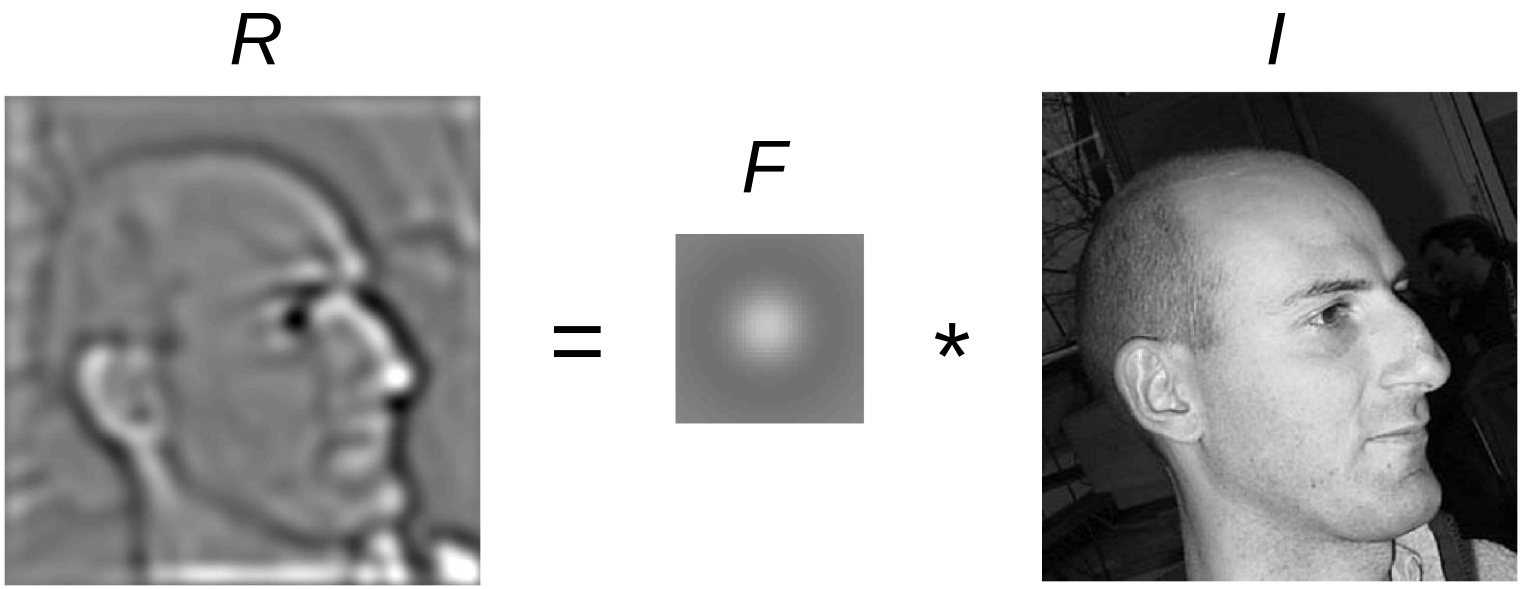
Enroth-Cugell and Robson (1984)

Fitting the model to the data



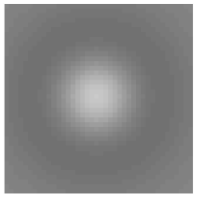
Enroth-Cugell et al. (1983)

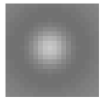
Responses are weighted sums: linear filtering

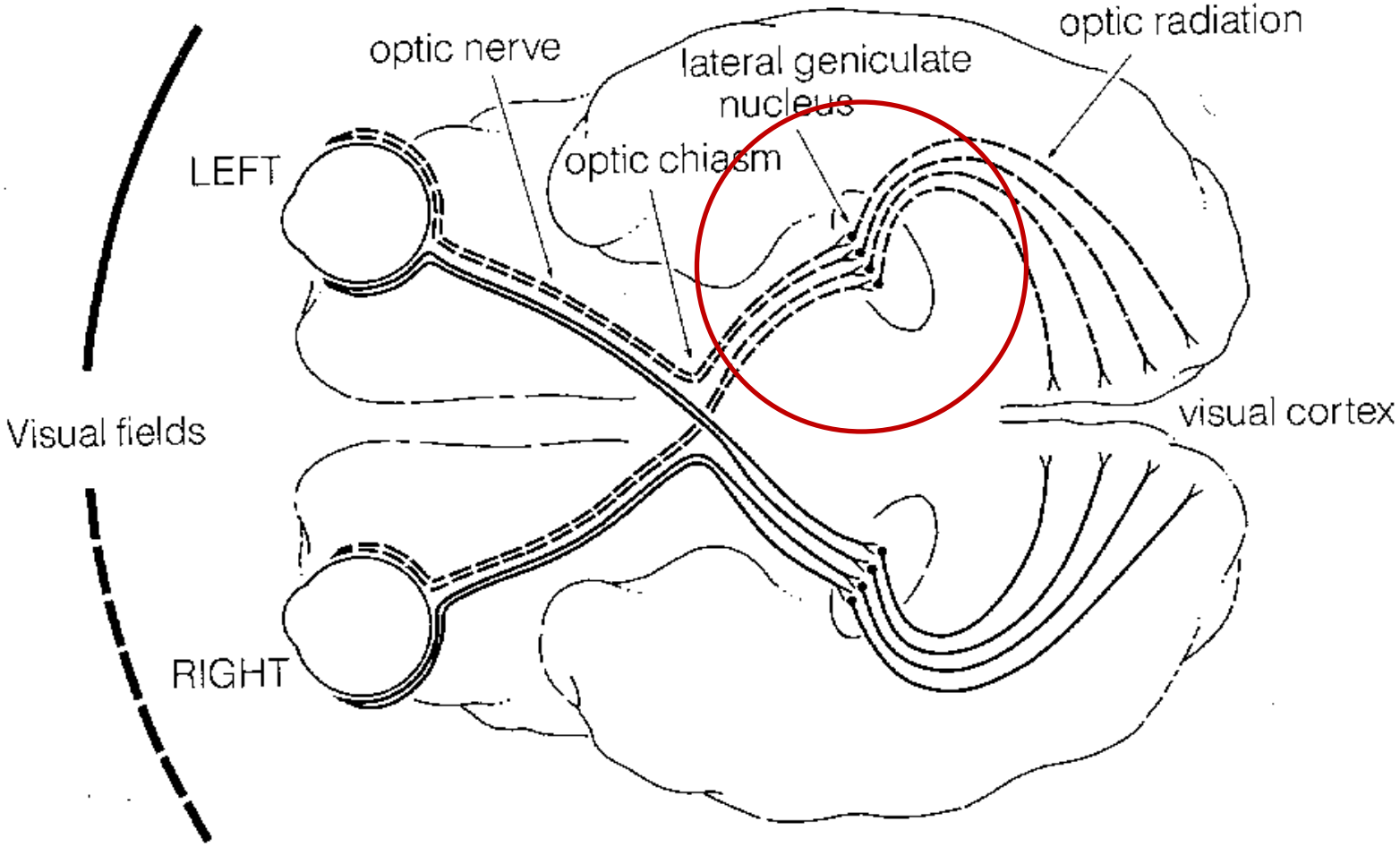


$$R_{i,j} = \sum_{u,v} F_{u,v} I_{i+u,j+v}$$

Center-surround receptive fields enhance edges

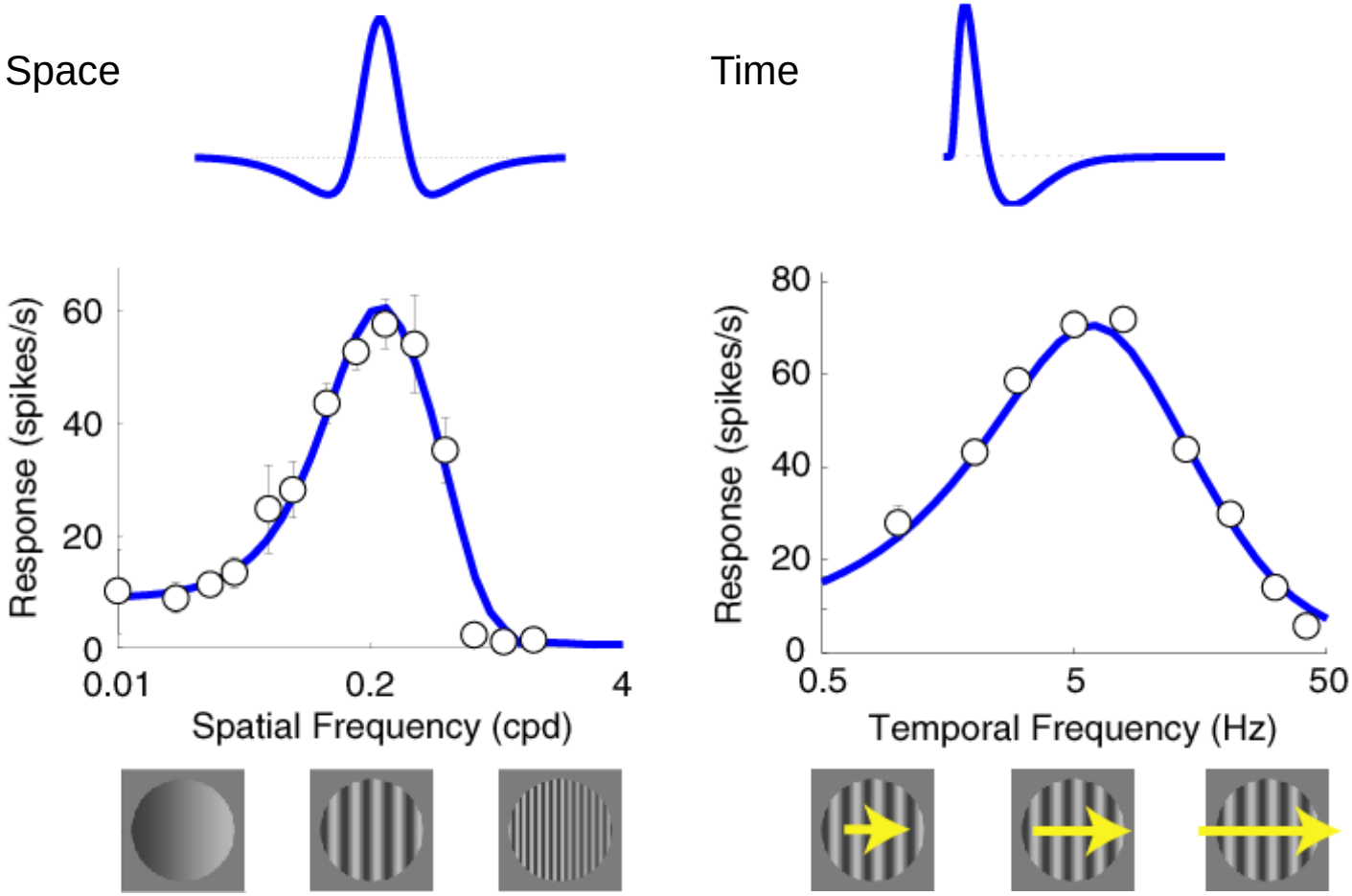




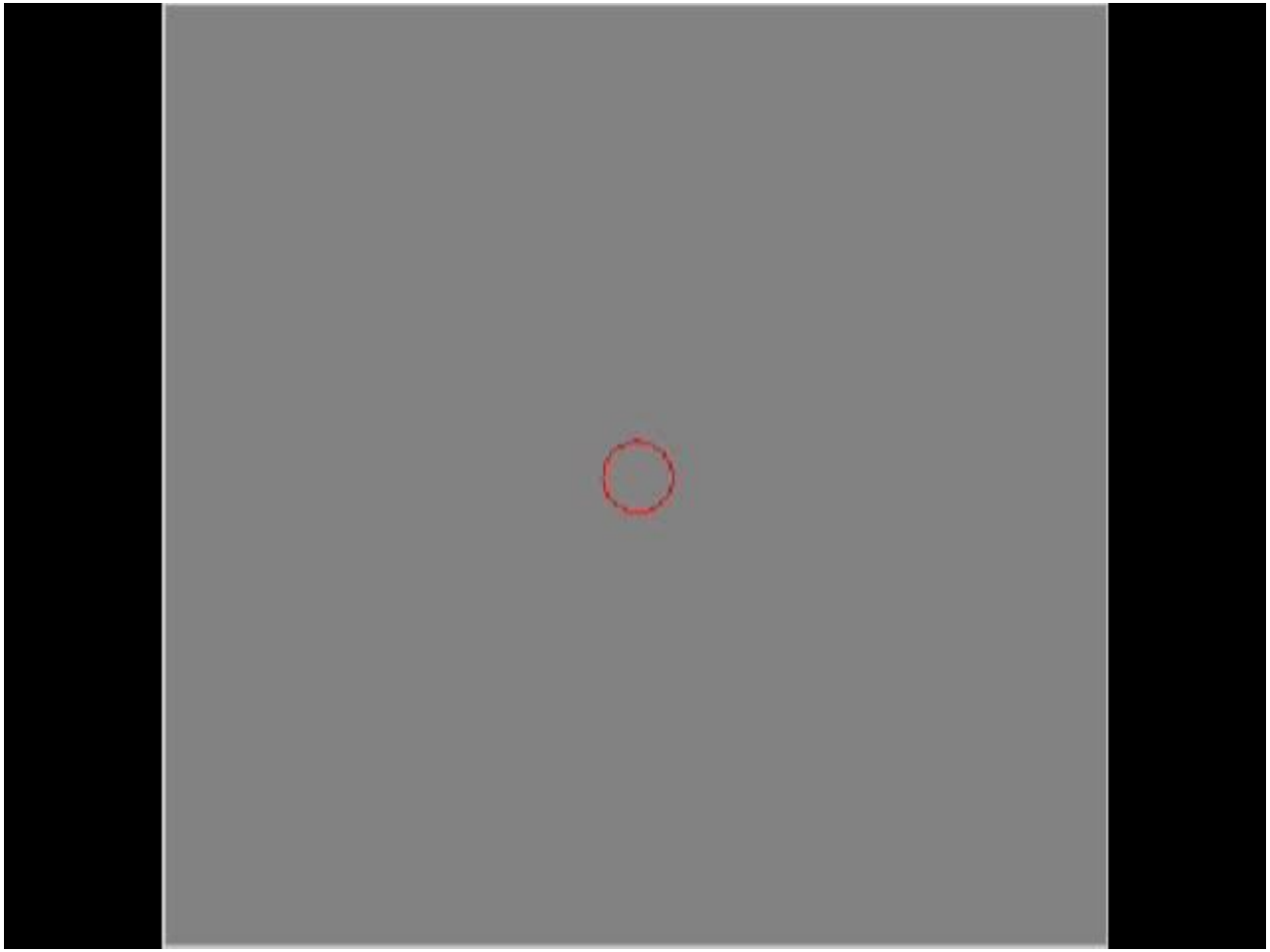


Dowling, 1987 (Fig 1.2)

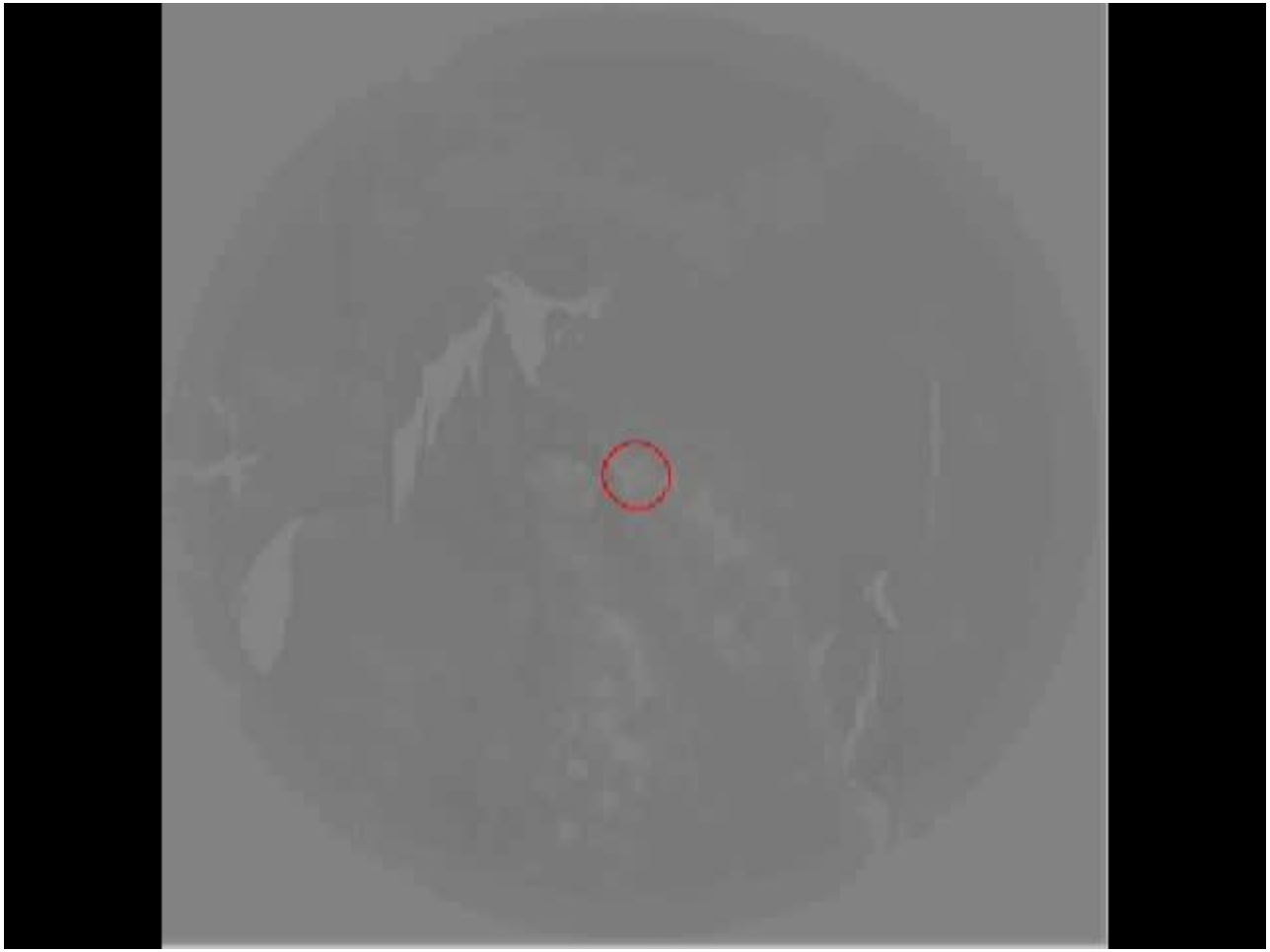
Receptive field explains LGN responses to gratings



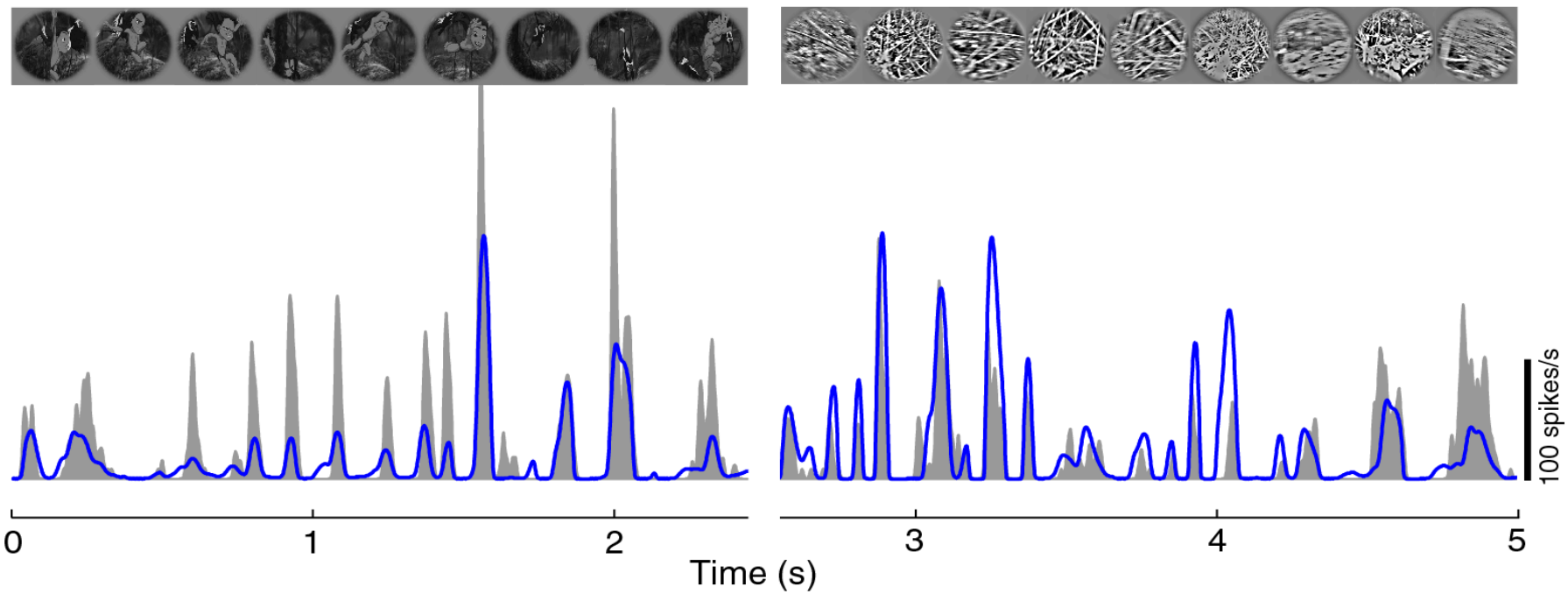
Cat-cam



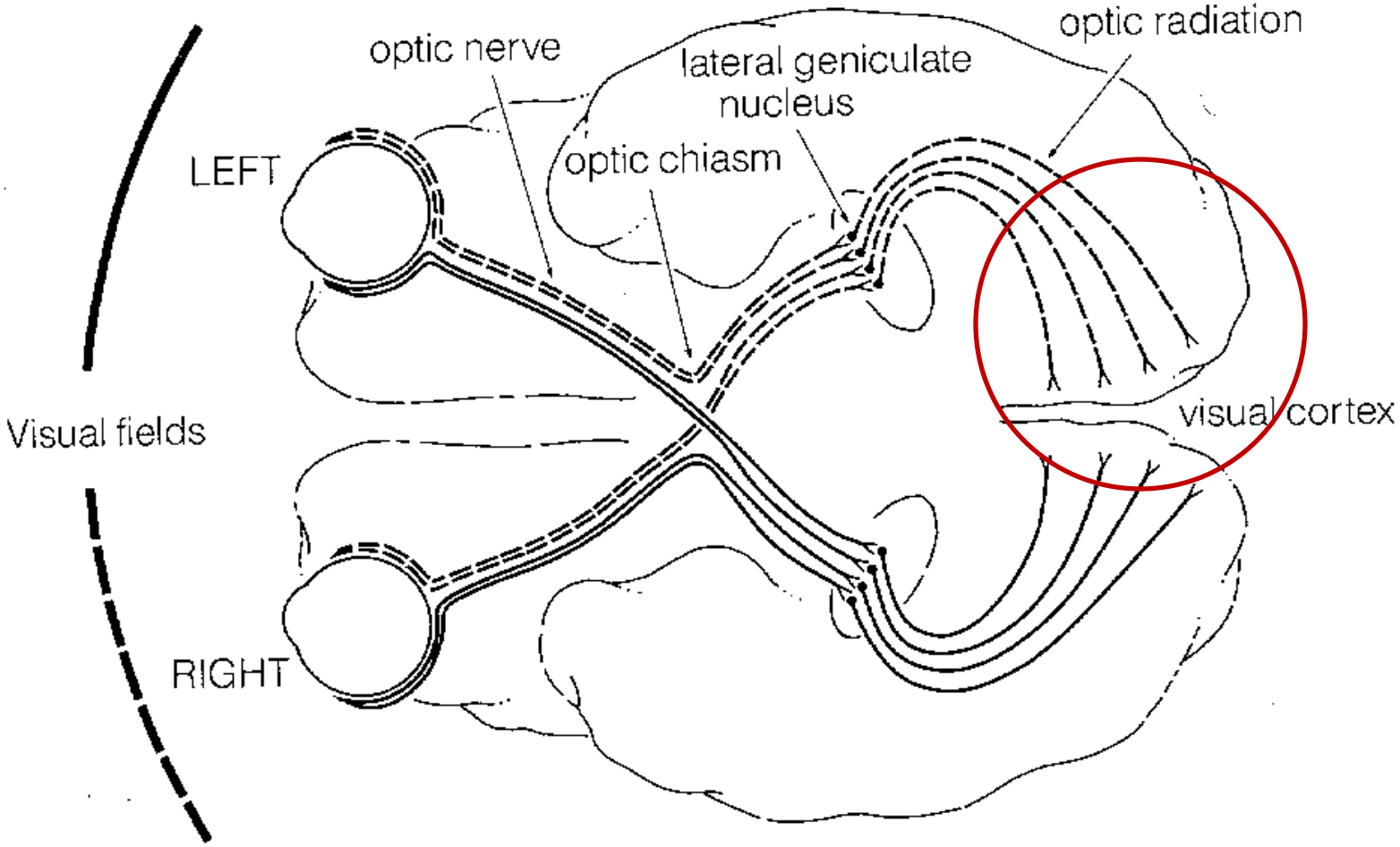
Tarzan



Predictions based on the receptive field

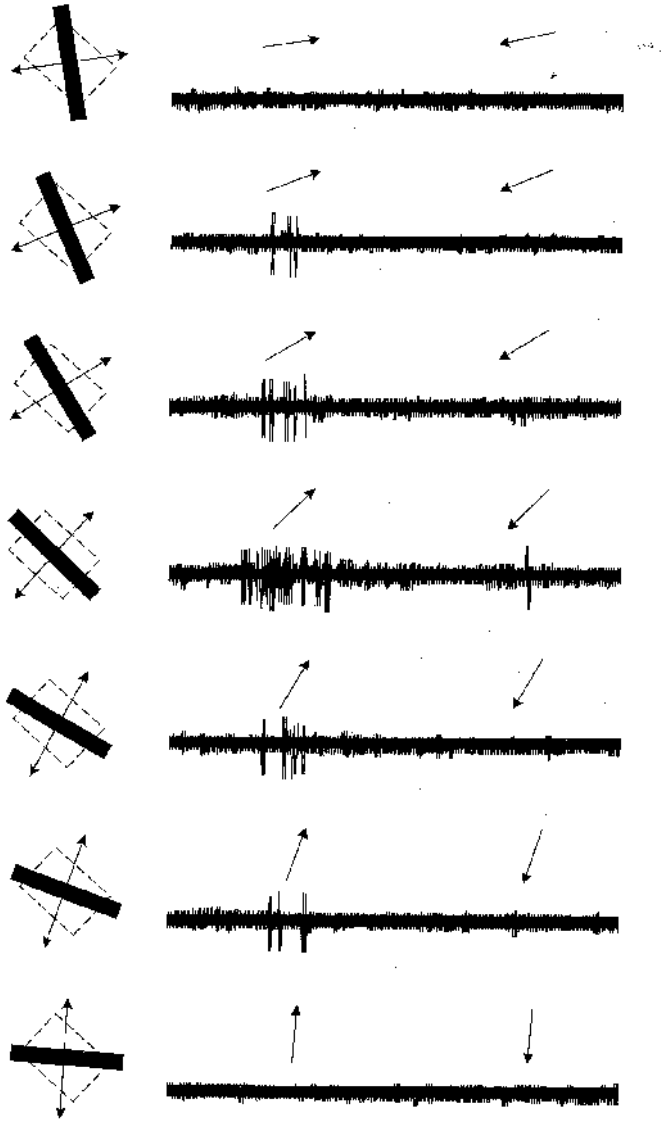


Mante, Bonin & Carandini (2007)
See also: Dan, Atick & Reid, *J Neurosci*, 1996



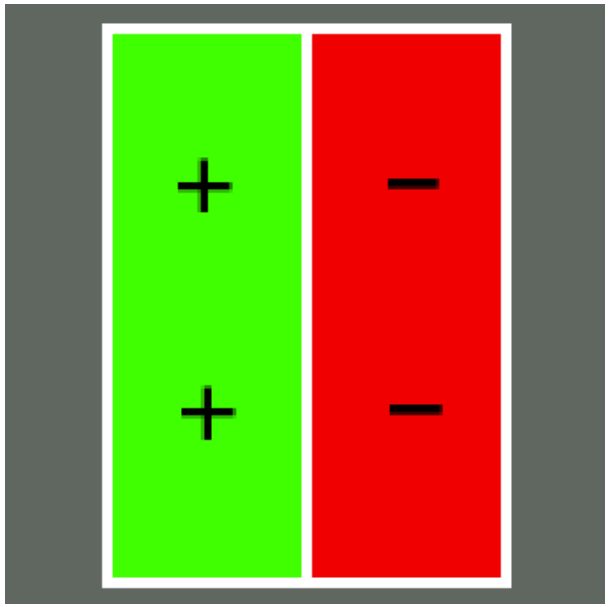
Dowling, 1987 (Fig 1.2)

Selectivity for stimulus orientation and direction

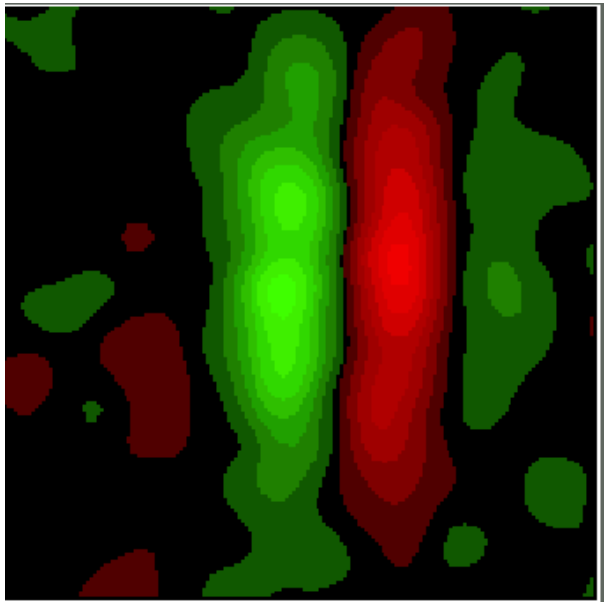


Hubel and Wiesel (1968)
in Wandell (1995)

Receptive field of a simple cell



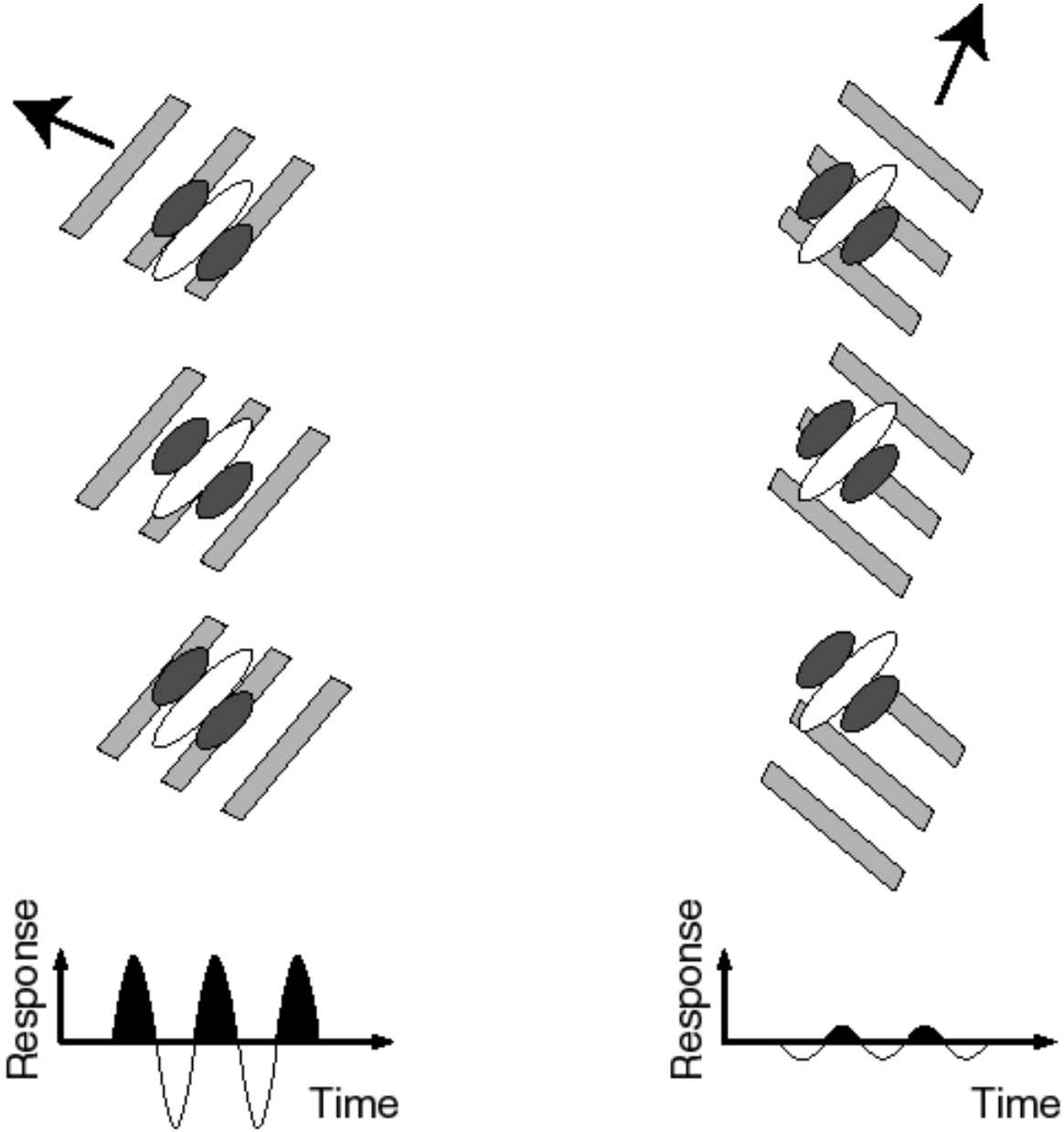
Schematic of the receptive field



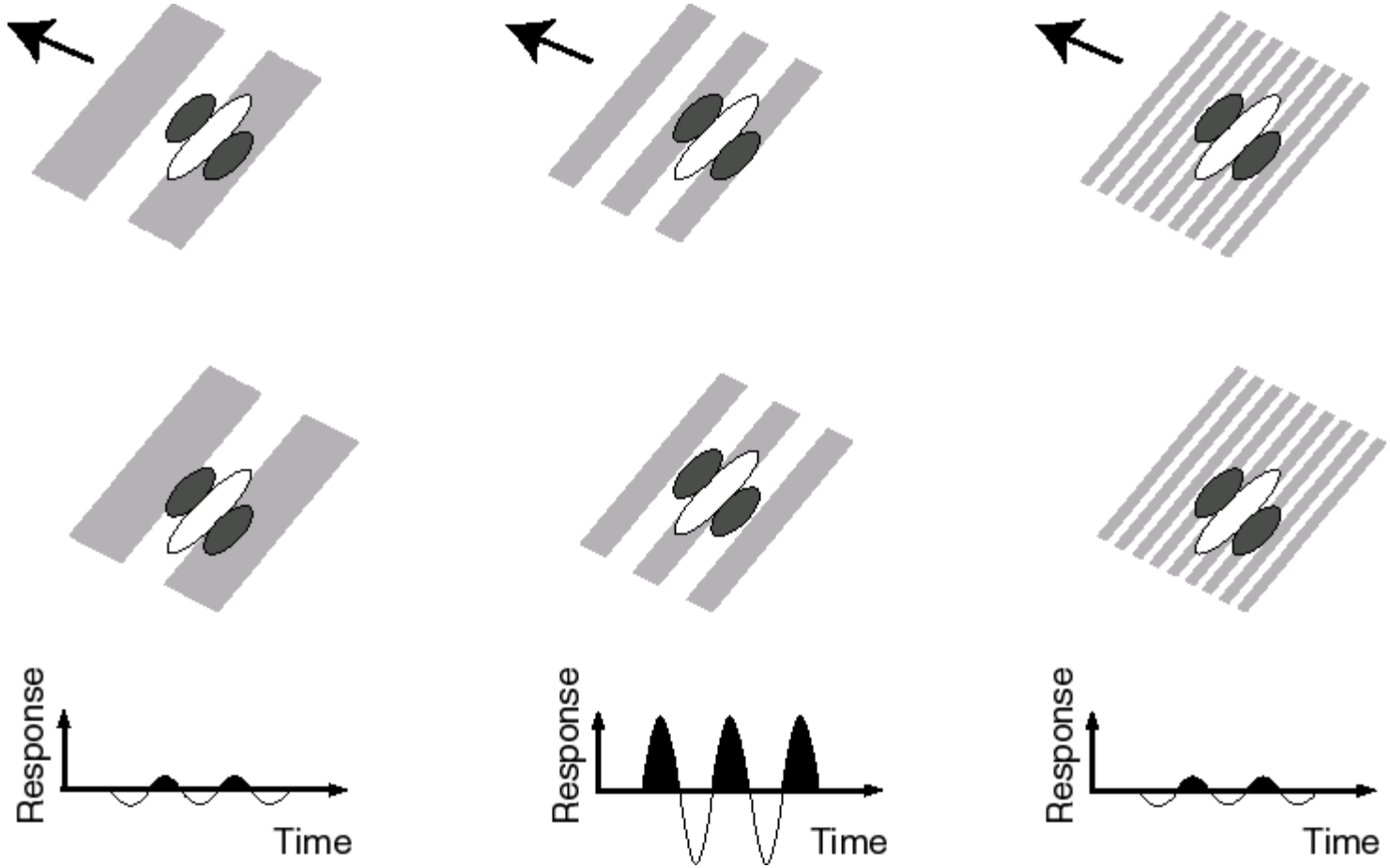
Responses to white dots - responses to black dots

DeAngelis, Ohzawa & Freeman (1995

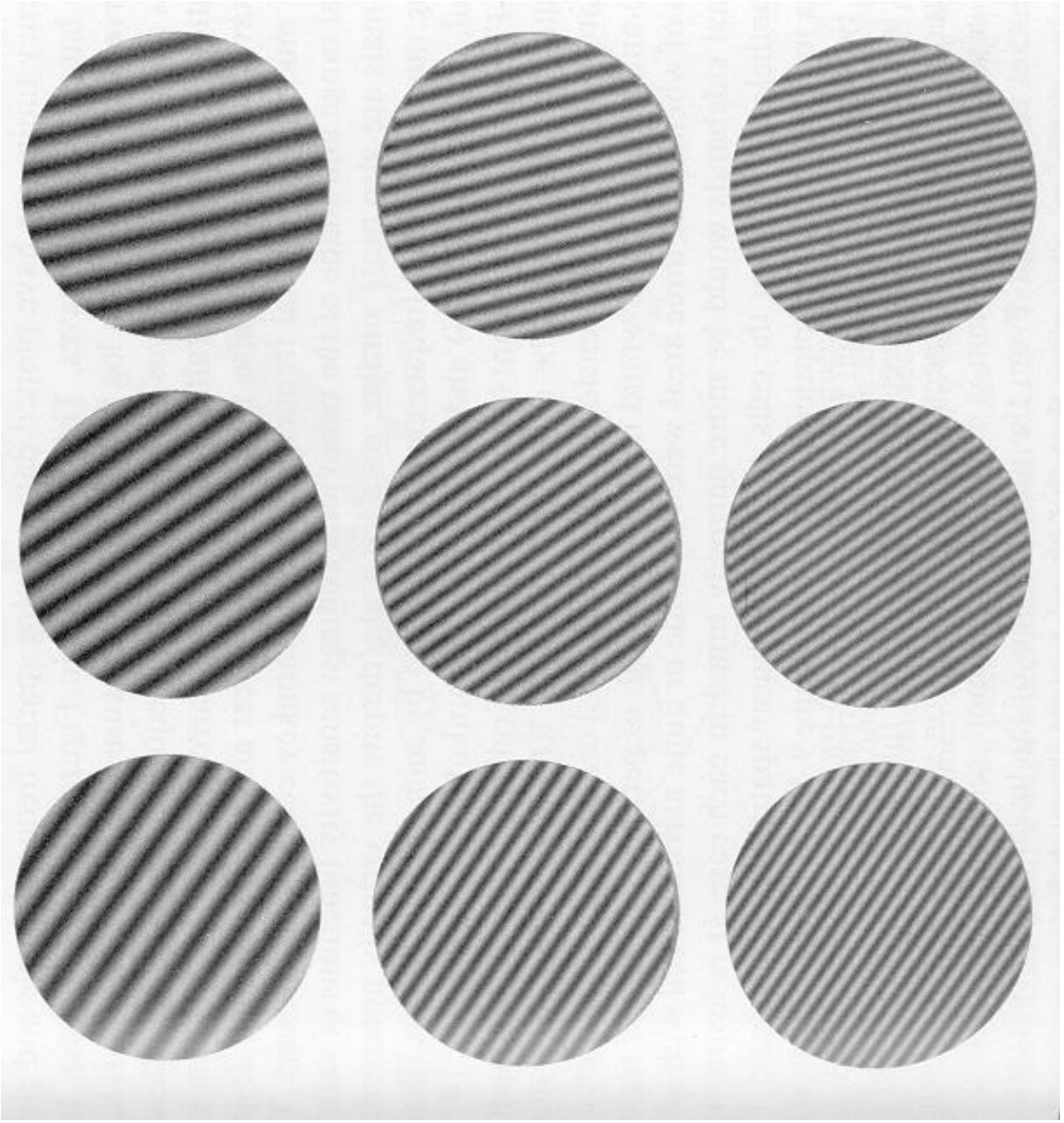
Dependence of responses on orientation



Dependence of responses on spatial frequency

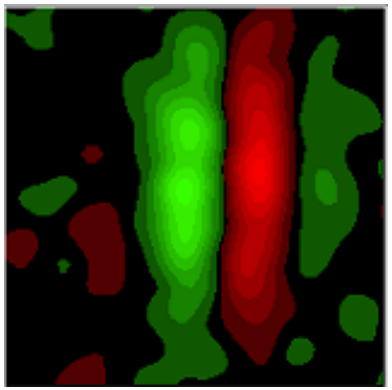


Selectivity in V1 is extremely sharp

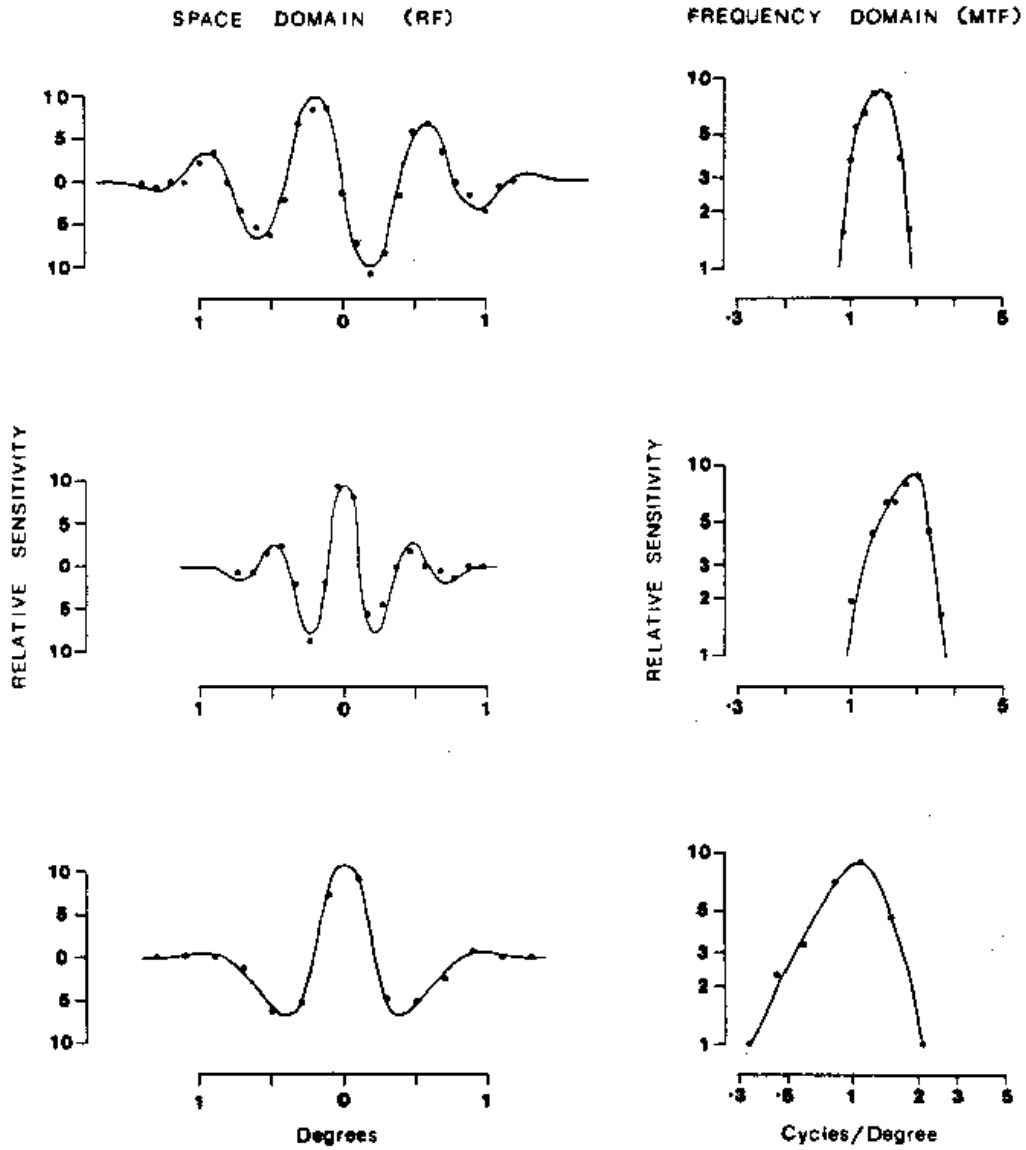


De Valois & De Valois (1990)

Receptive field predicts spatial selectivity

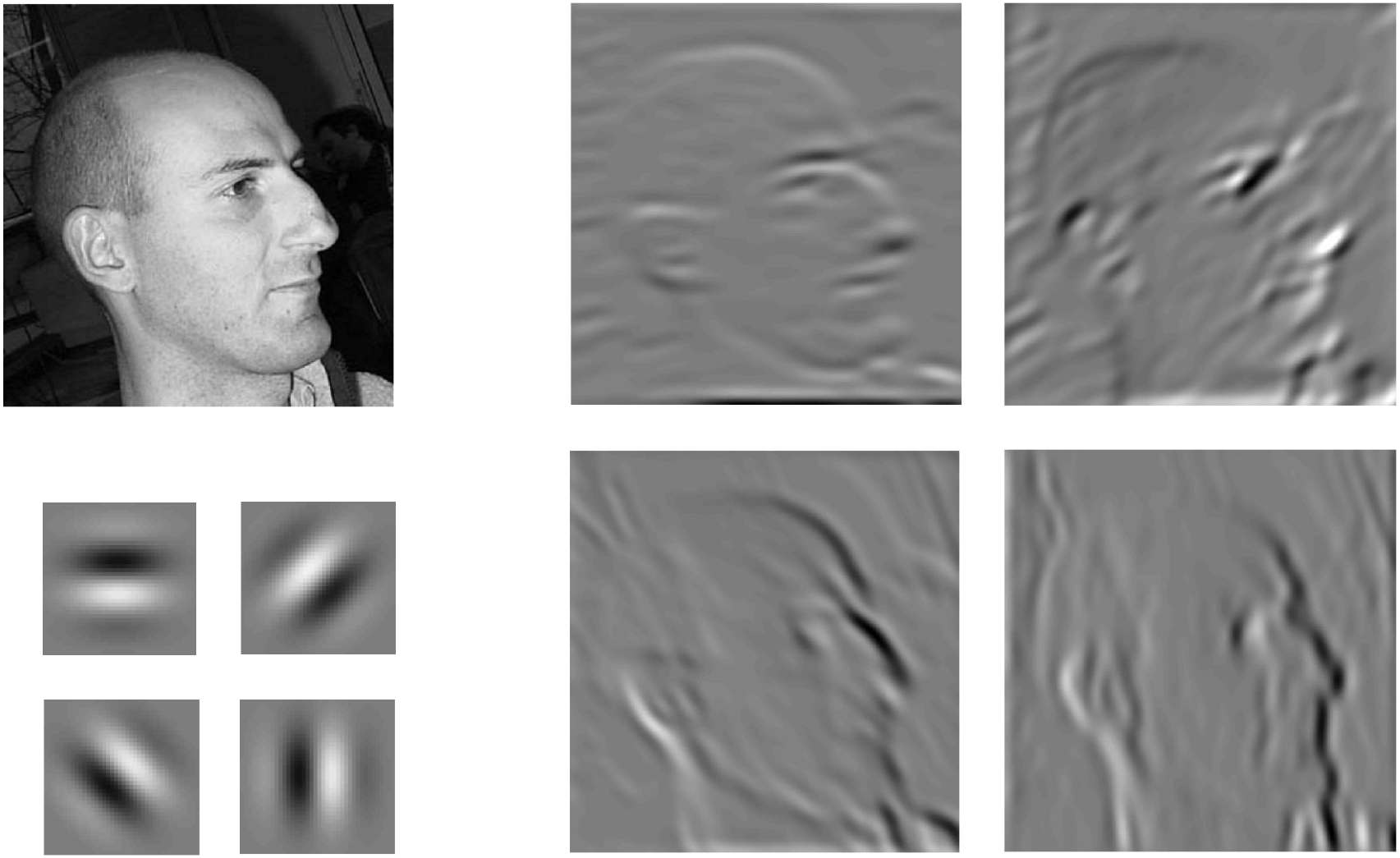


DeAngelis, Ohzawa & Freeman, 1995



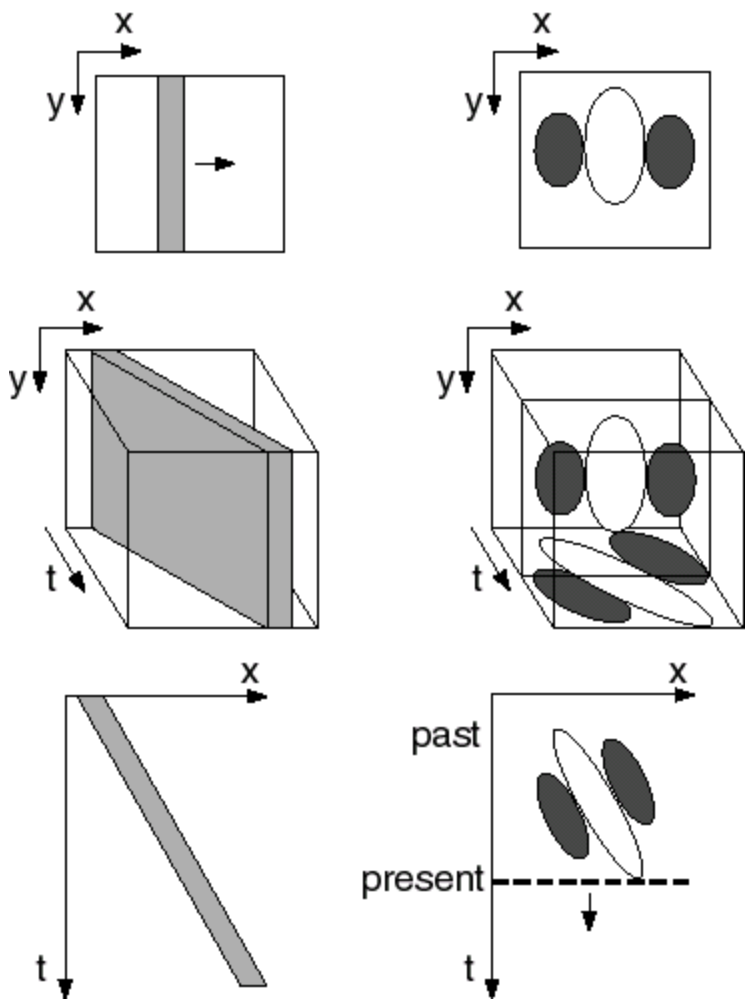
Albrecht (1978); Movshon, Thompson & Tolhurst (1978)

V1 receptive fields enhance oriented edges

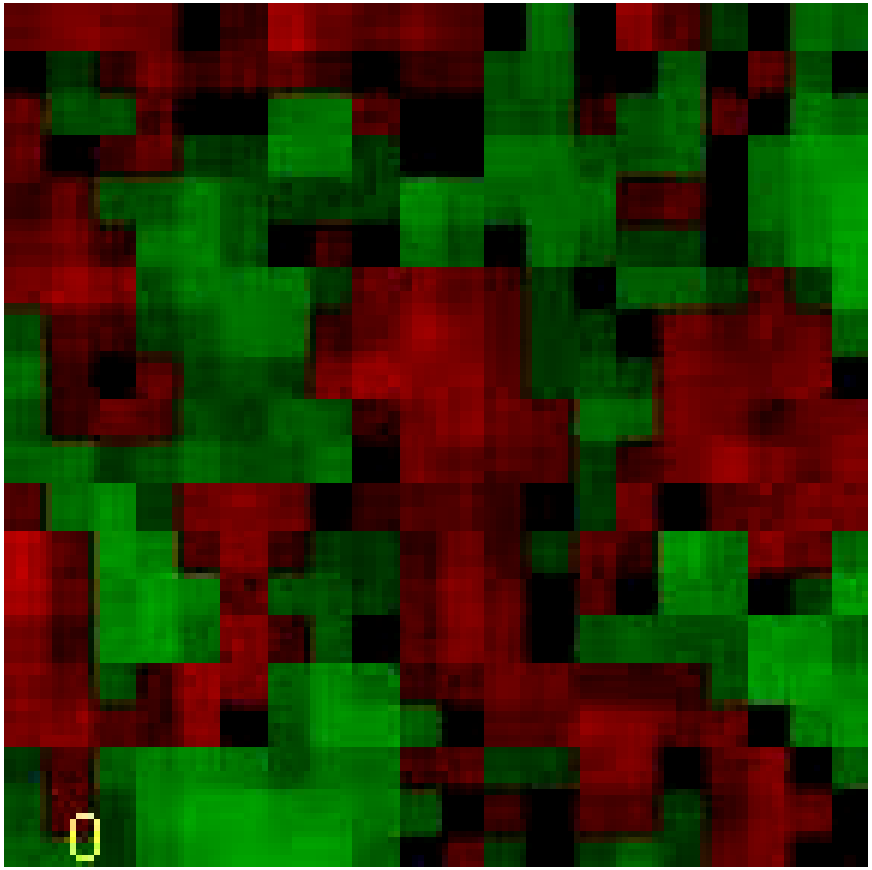


receptive fields in space-time

Stimuli and receptive fields in space-time



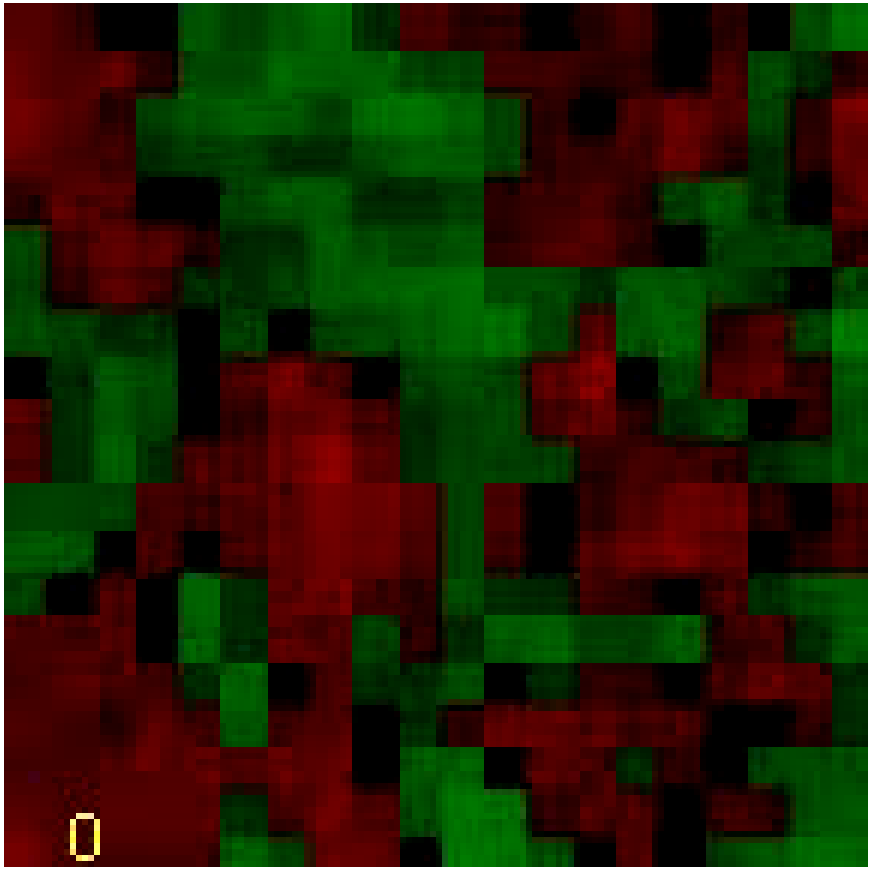
V1 simple cell, separable



www.bpe.es.osaka-u.ac.jp/ohzawa-lab/

Ohzawa, DeAngelis & Freeman, 1996

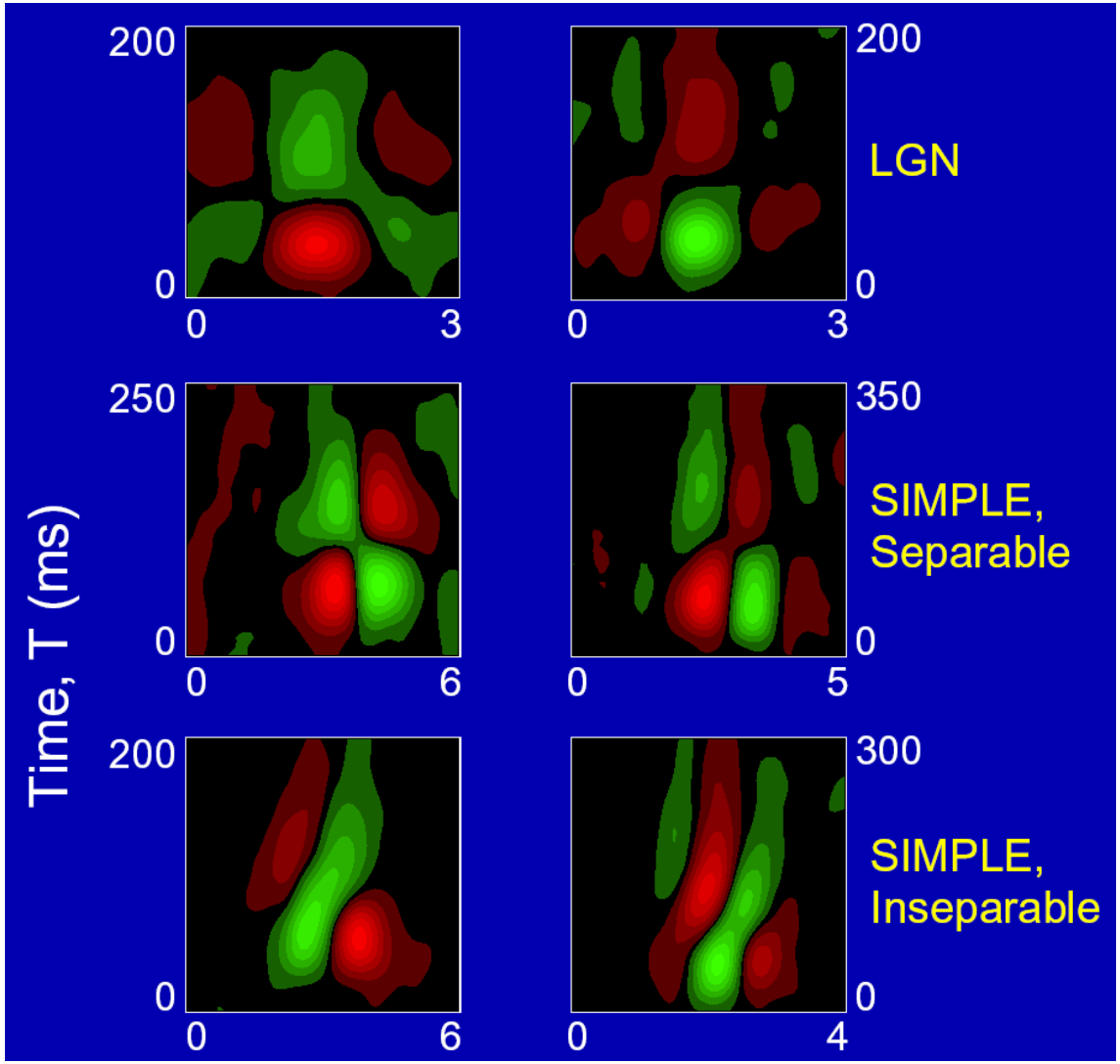
V1 simple cell, inseparable



www.bpe.es.osaka-u.ac.jp/ohzawa-lab/

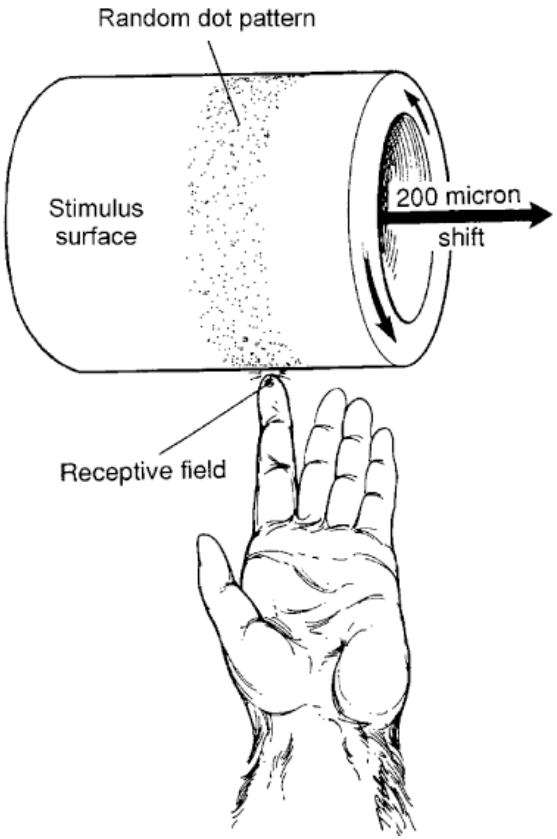
Ohzawa, DeAngelis & Freeman, 1996

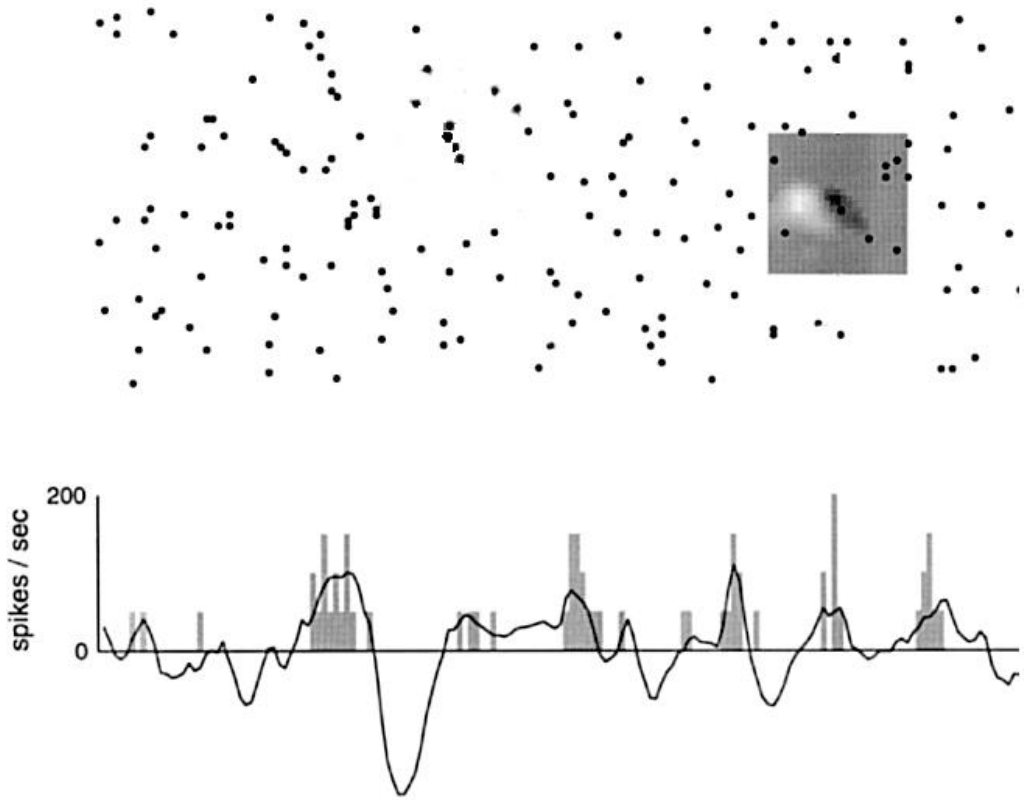
Space-time receptive fields



DeAngelis, Ohzawa & Freeman, 1995

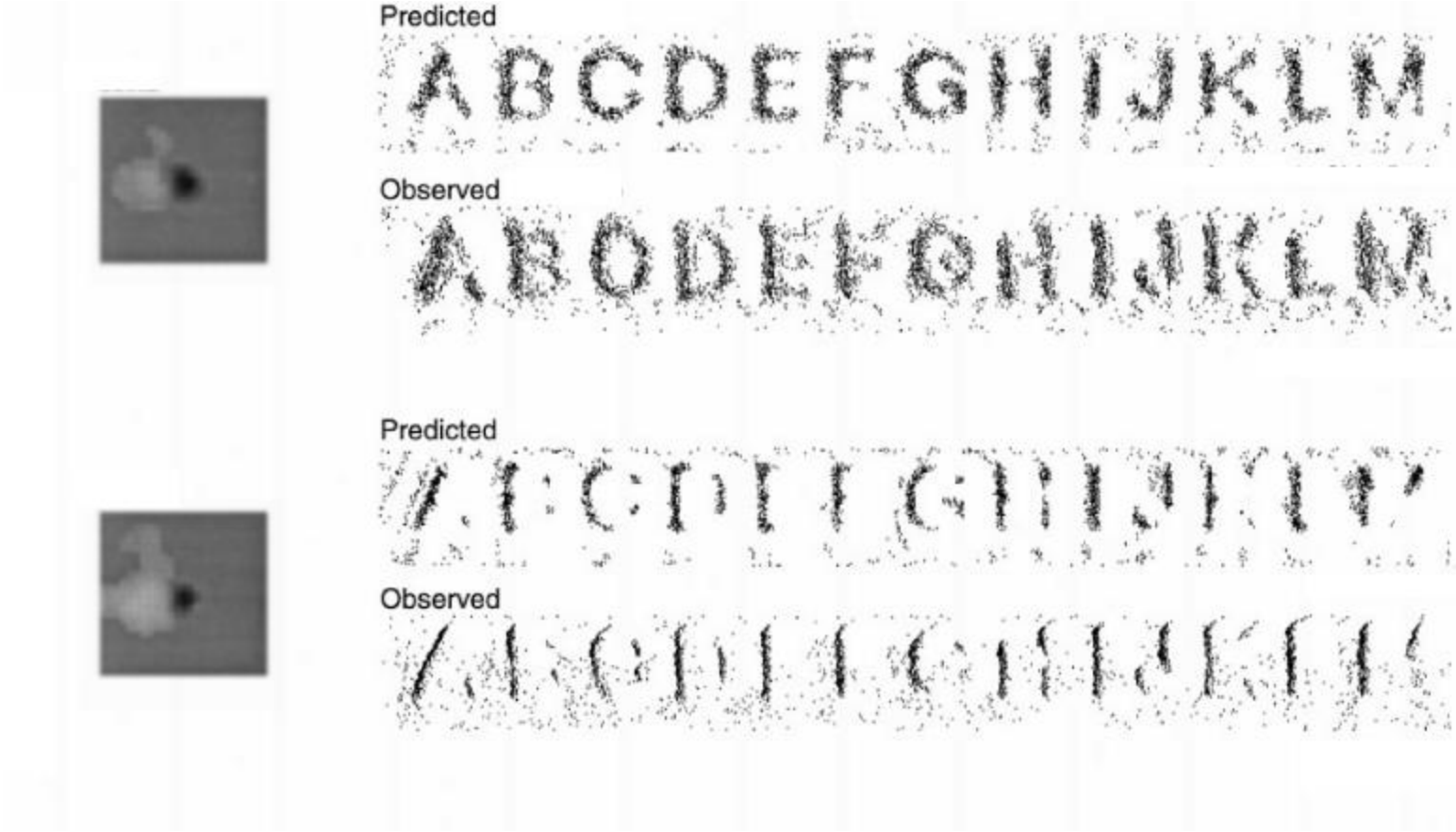
Receptive field in somatosensory cortex





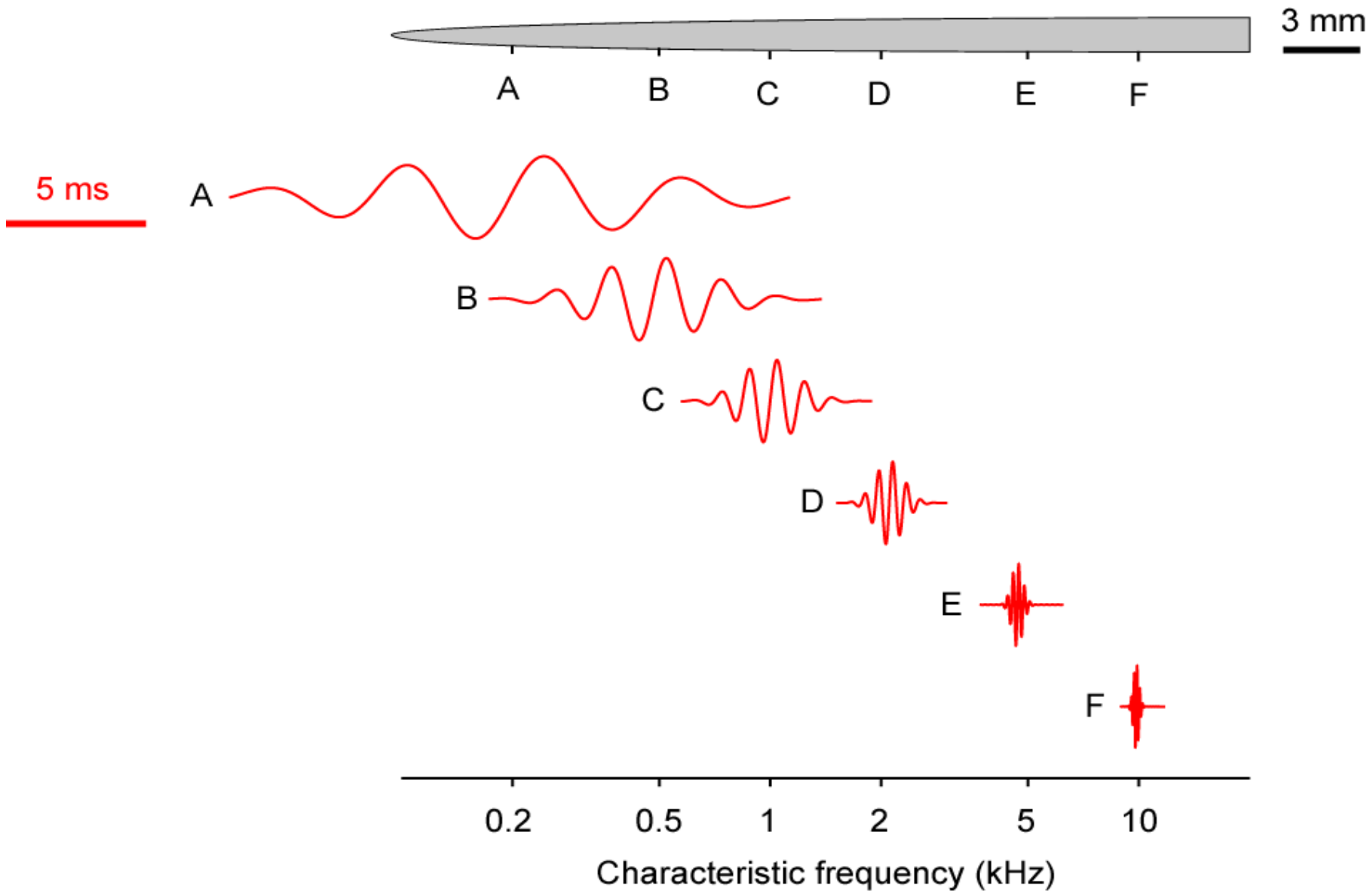
DiCarlo, Johnson & Hsiao (1998)

A linear model predicts responses

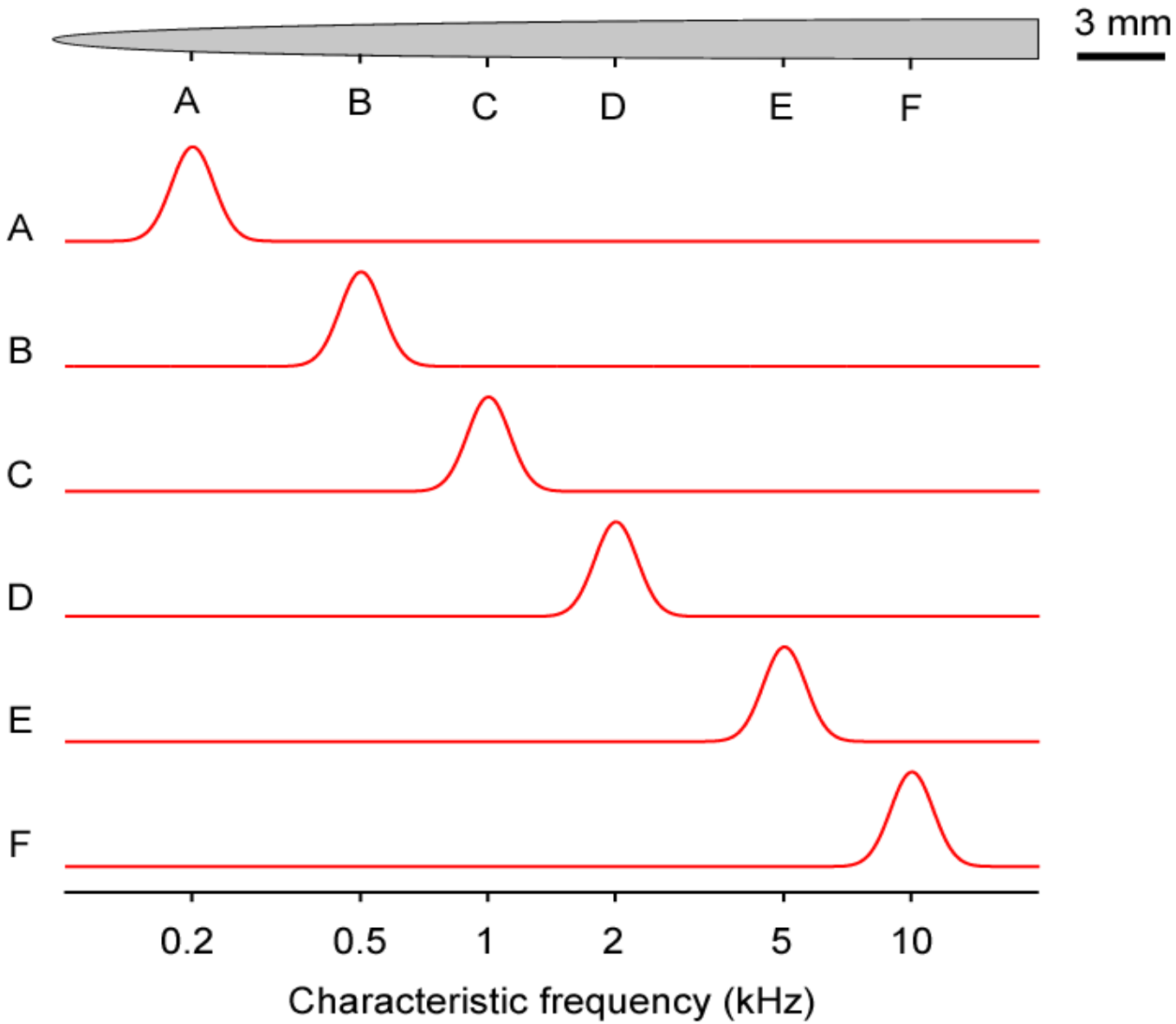


DiCarlo, Johnson & Hsiao (1998)

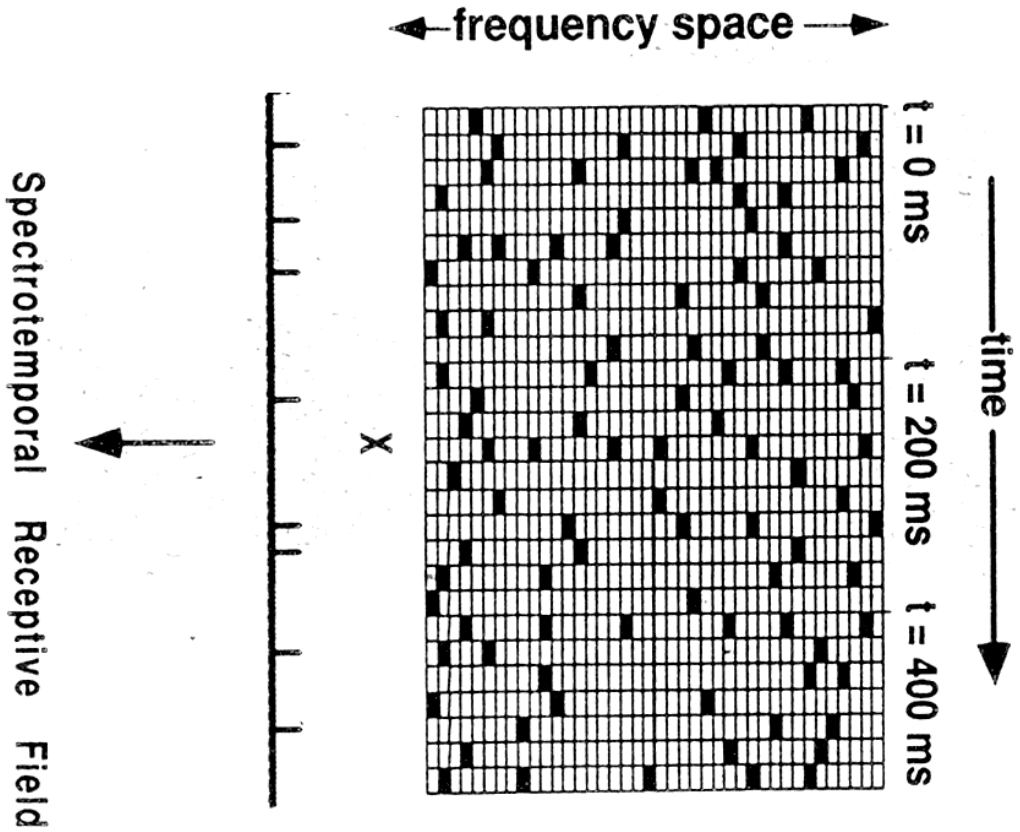
Unrolling the cochlea



Receptive fields in frequency space

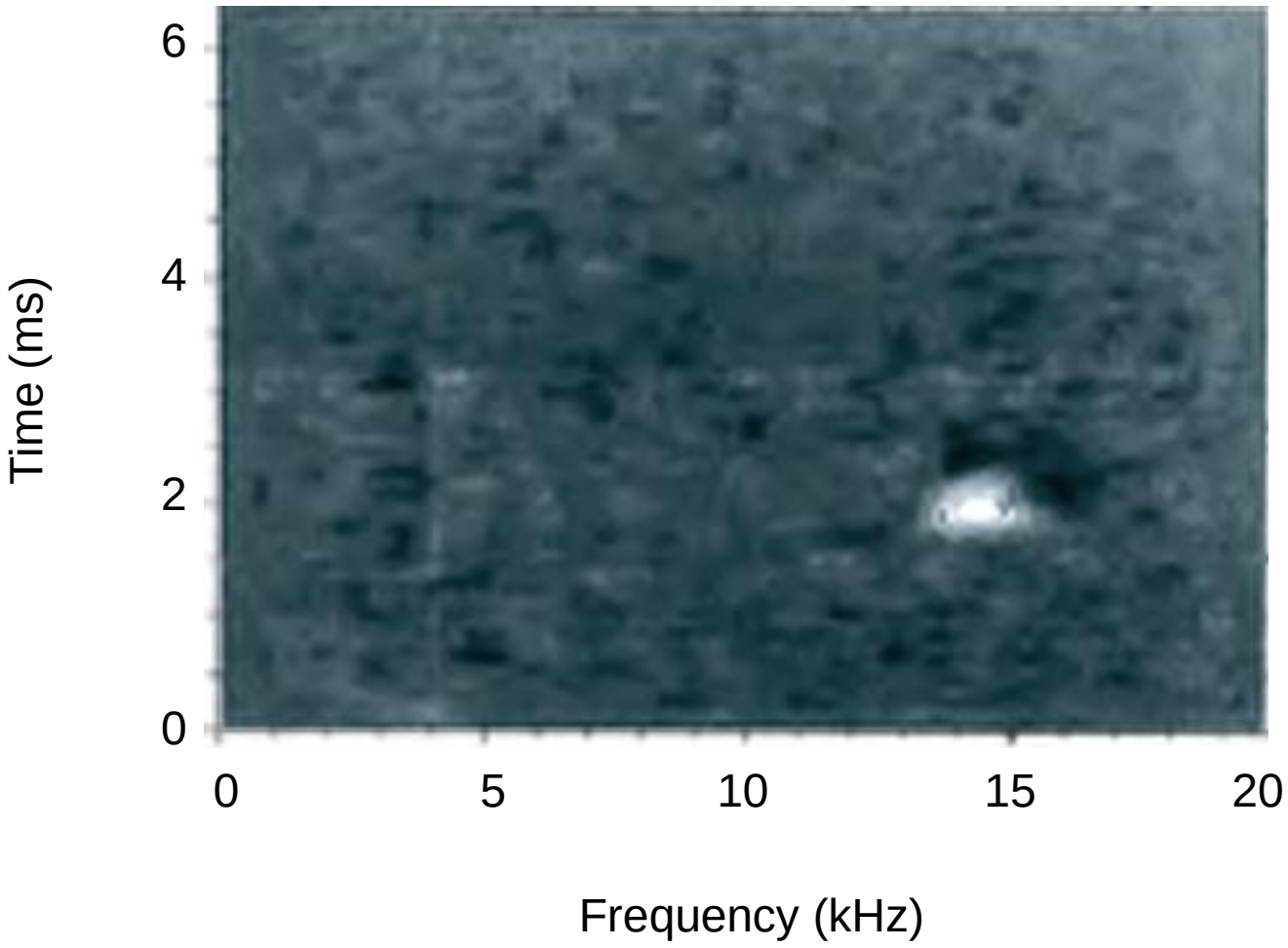


Measuring a spectro-temporal receptive field



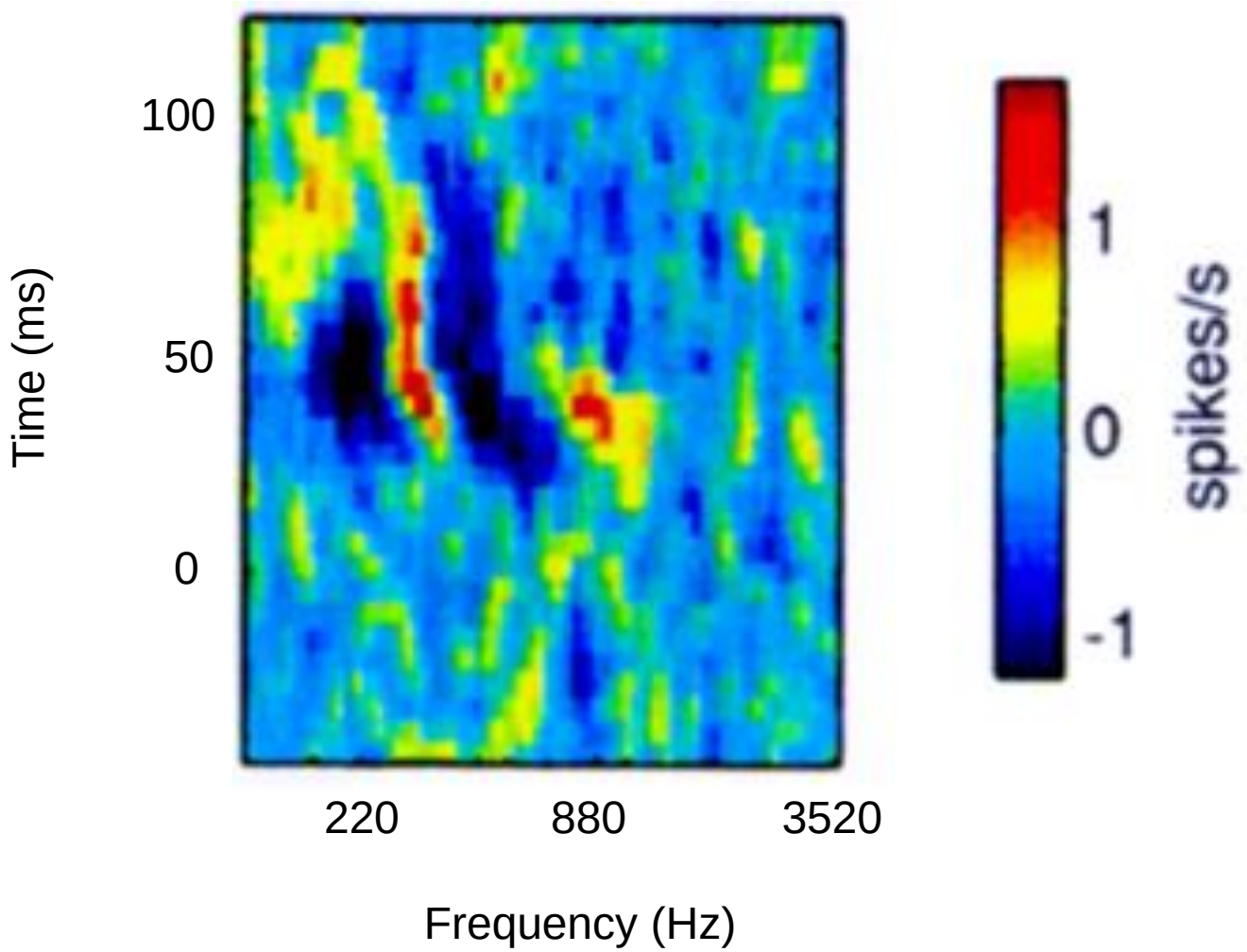
deCharms, Blake & Merzenich (1998)

Spectro-temporal receptive field in auditory nerve



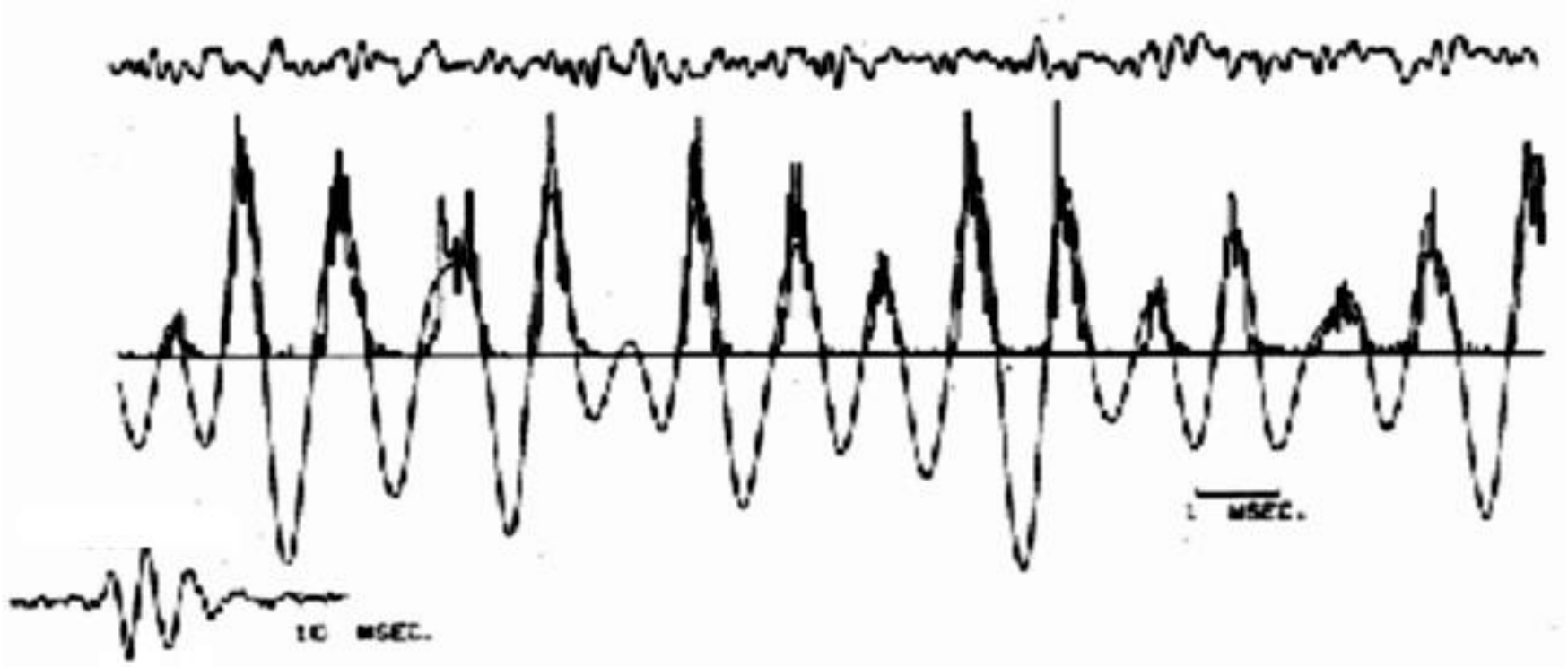
Kim & Young (1994)

Spectro-temporal receptive field in auditory cortex



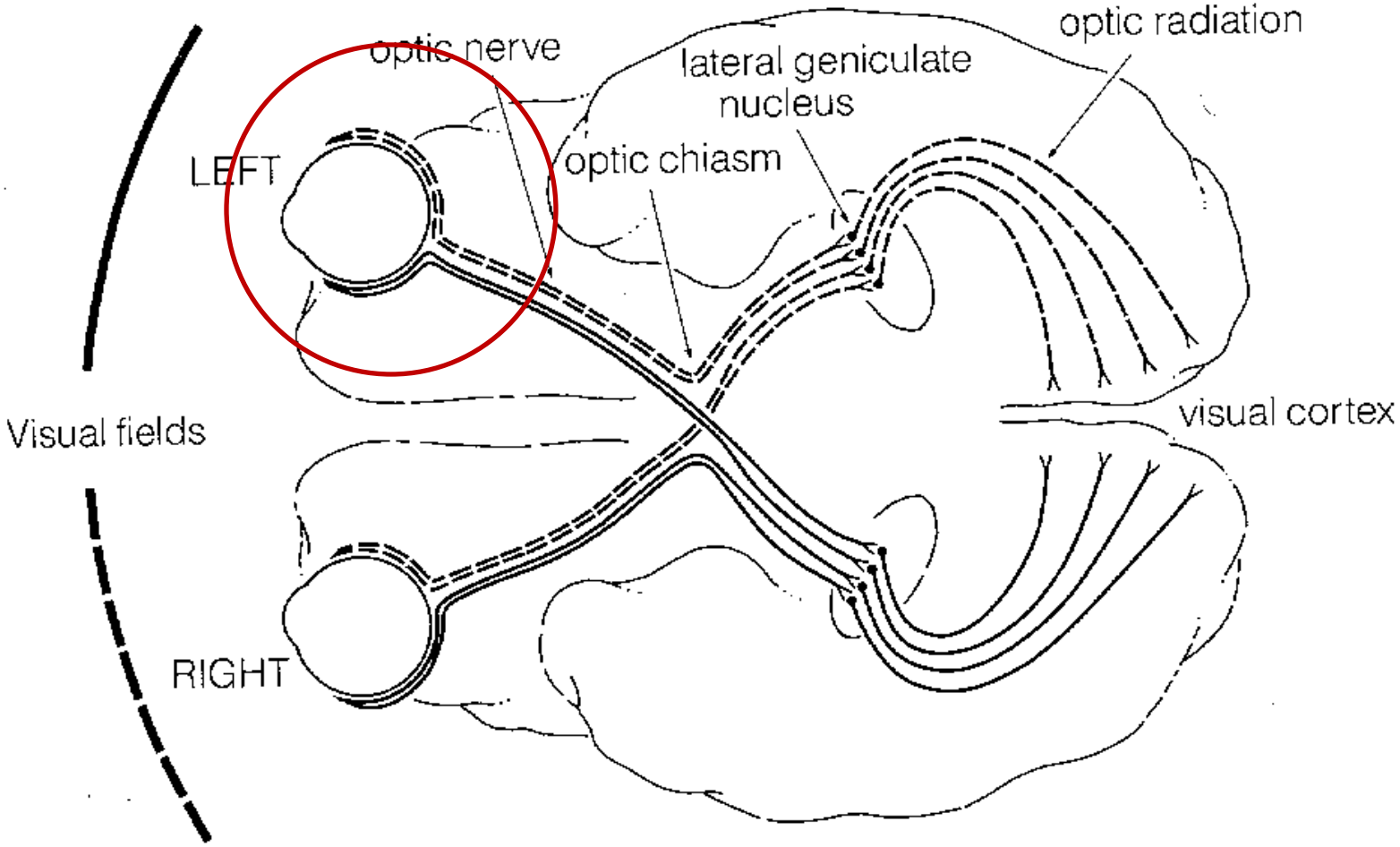
deCharms, Blake & Merzenich (1998)

Responses to noise in auditory nerve



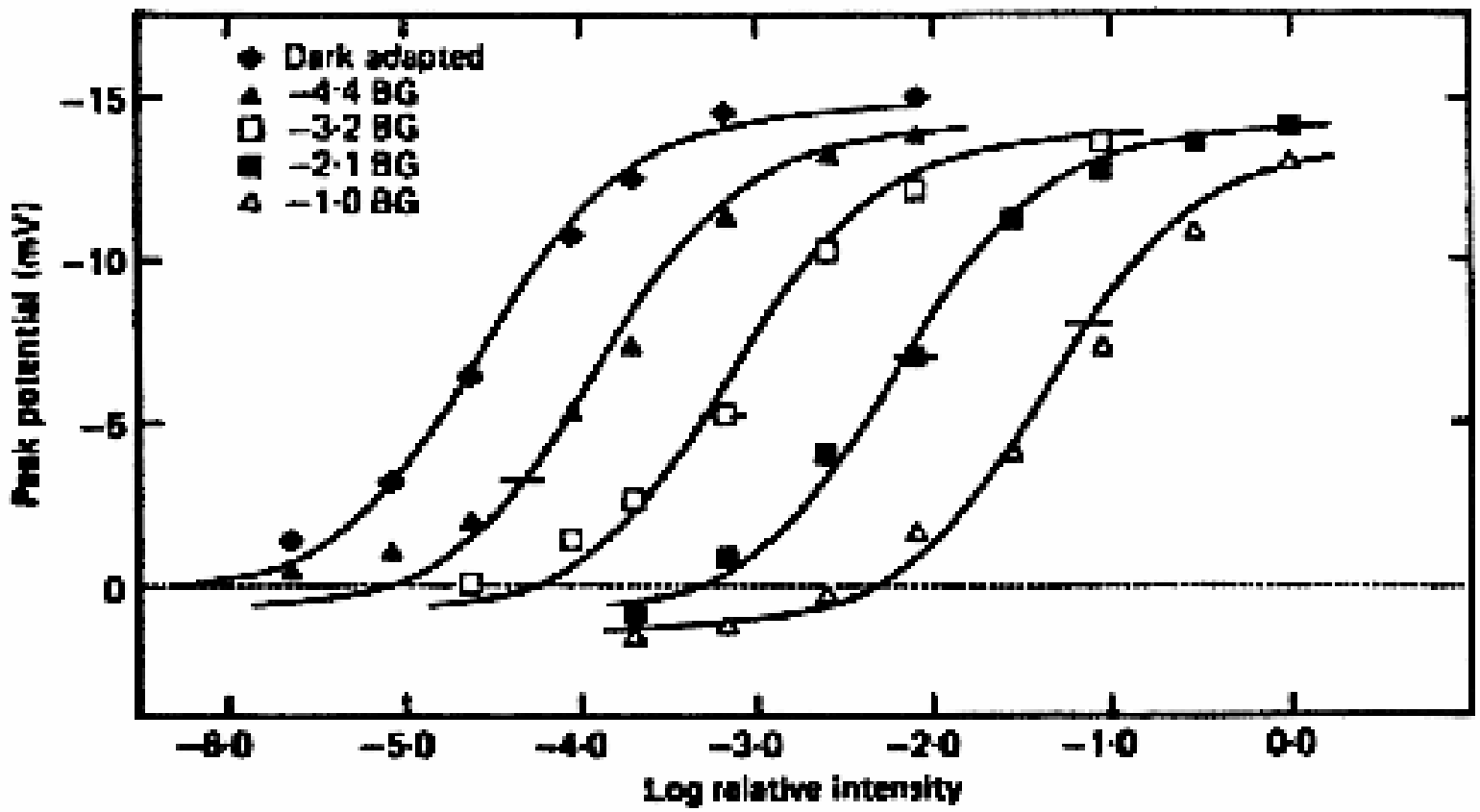
Linear model predictions are good.
But only if characteristic frequency is low.

de Boer & de Jongh (1978)

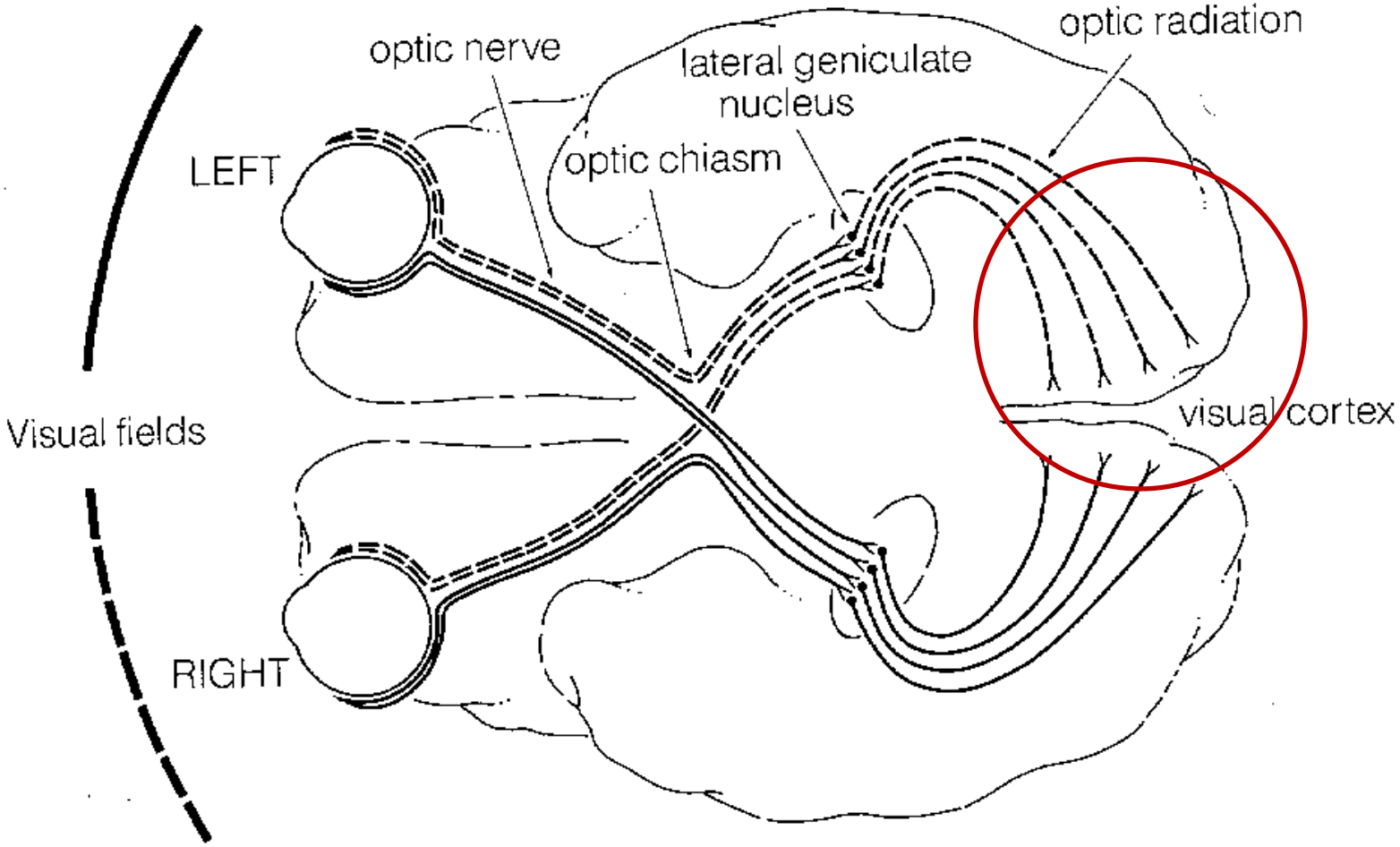


Dowling, 1987 (Fig 1.2)

Light adaptation in photoreceptors

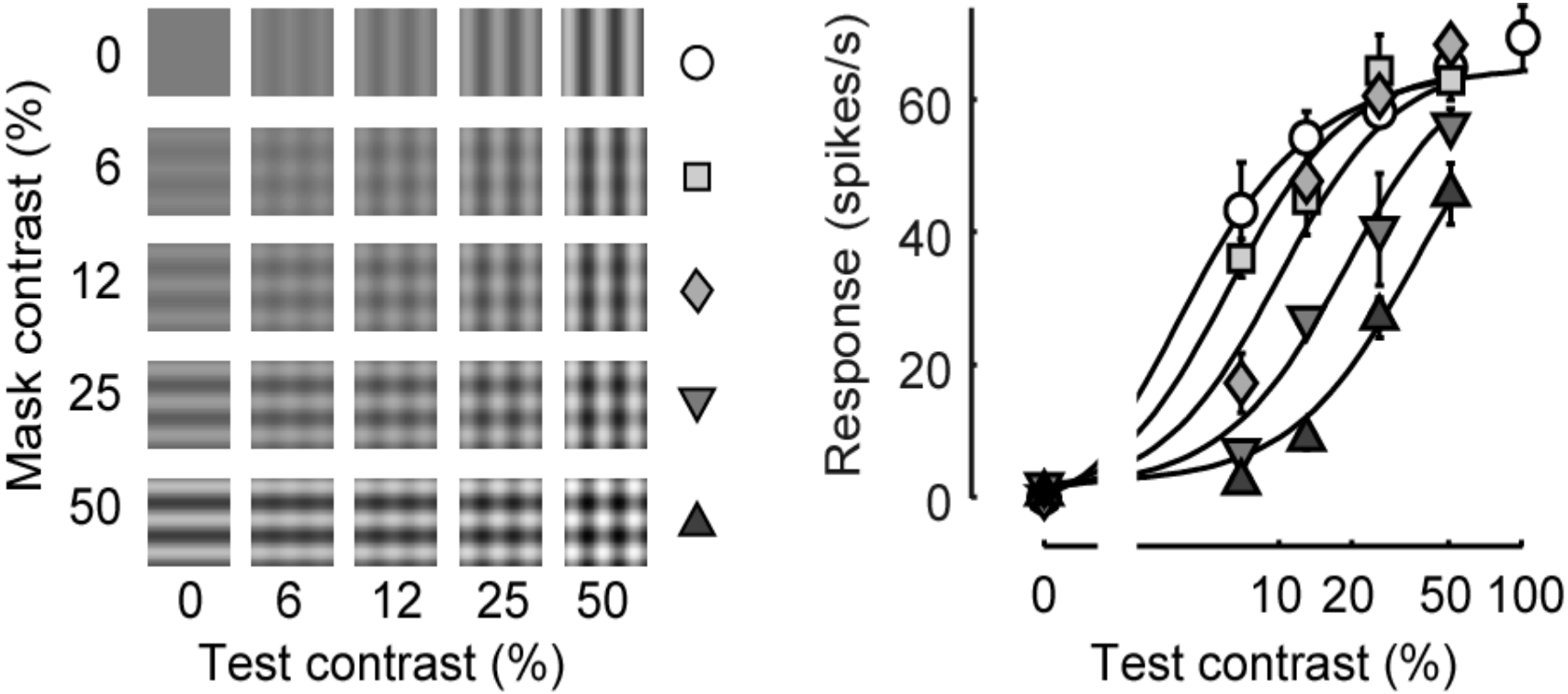


Norman & Perlmann (1979)



Dowling, 1987 (Fig 1.2)

Cross-orientation suppression



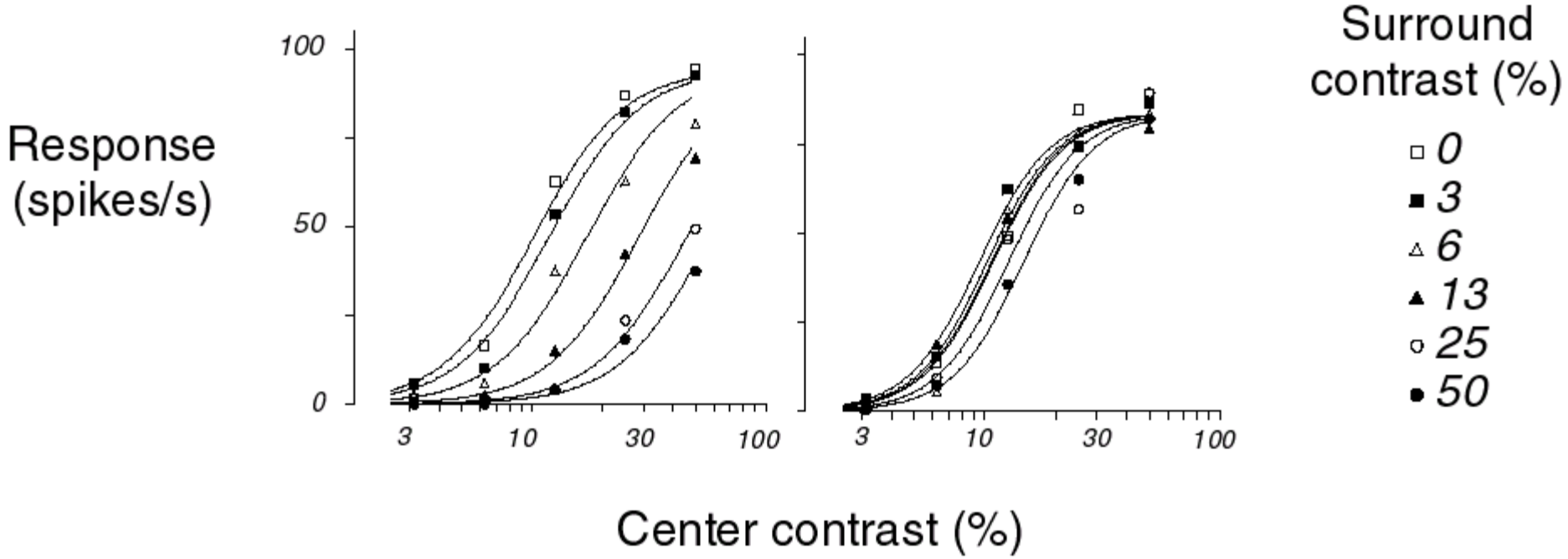
Freeman, Durand, Kiper & Carandini (2002)

Nonlinearities in V1 responses

$$R = \frac{Lc}{c_{50} + c_{local}}$$

Albrecht & Geisler (1991)
Heeger (1991)

Surround suppression

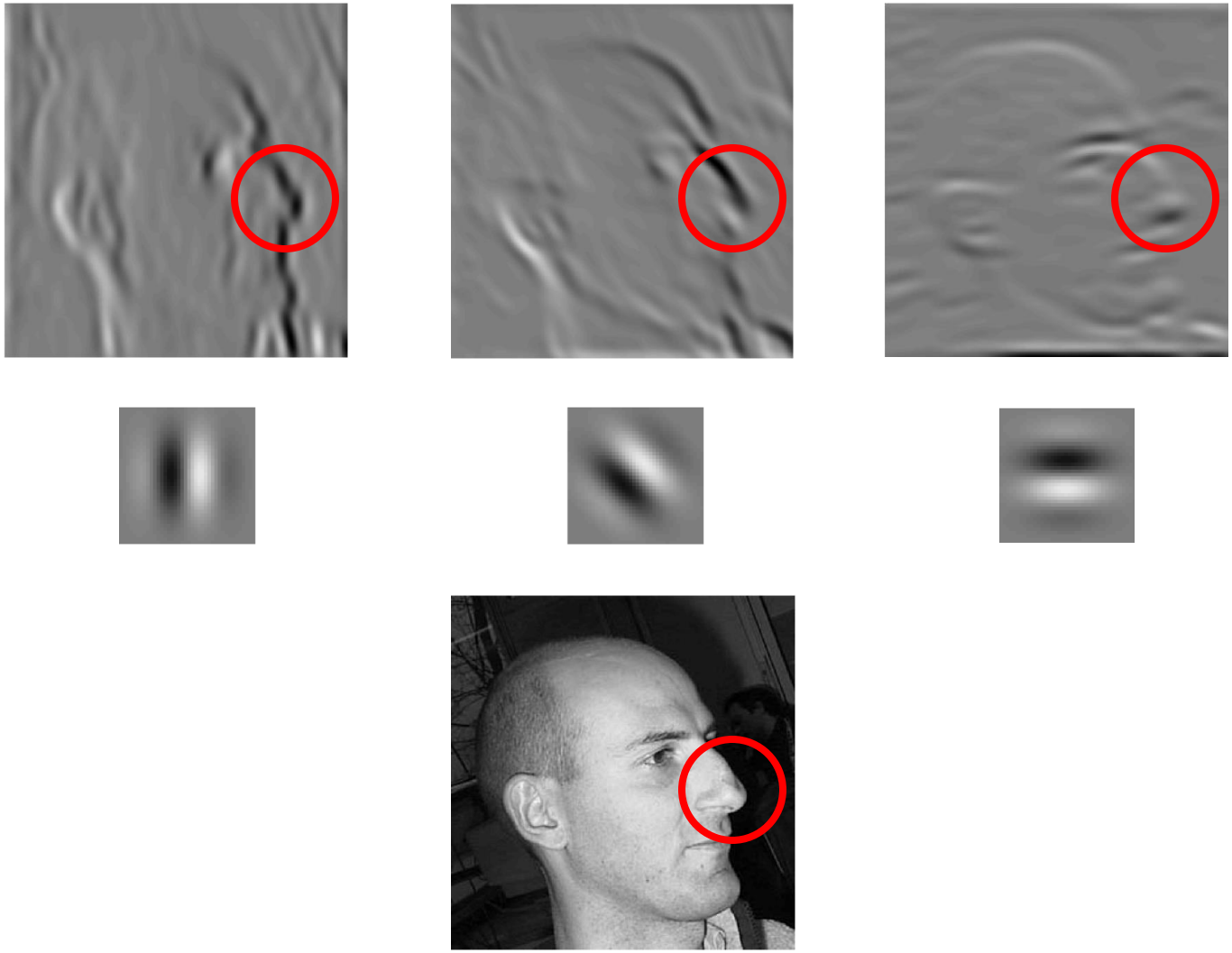


Cavanaugh, Blair & Movshon (1997)

Blakemore & Tobin (1972)

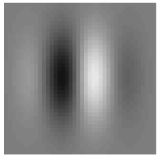
A possible role for normalization

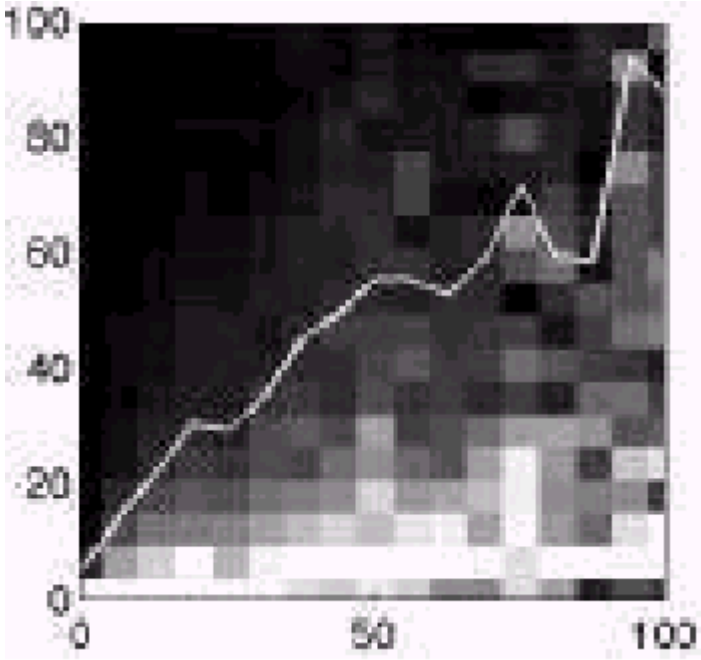
Three orientations in one location

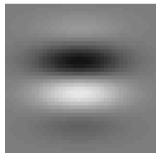


Contours with different orientations overlap often

Conditional probability

Output of 

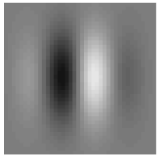


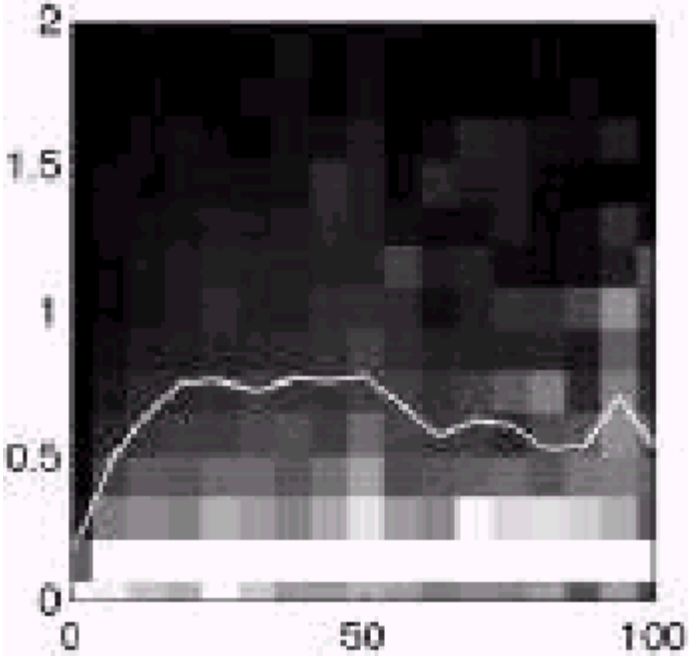
Output of 

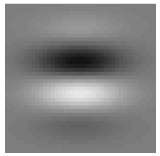
Simoncelli and Schwartz, 1997

Normalization enhances V1 neuron independence

Conditional probability

Output of 



Output of 

Simoncelli and Schwartz, 1997