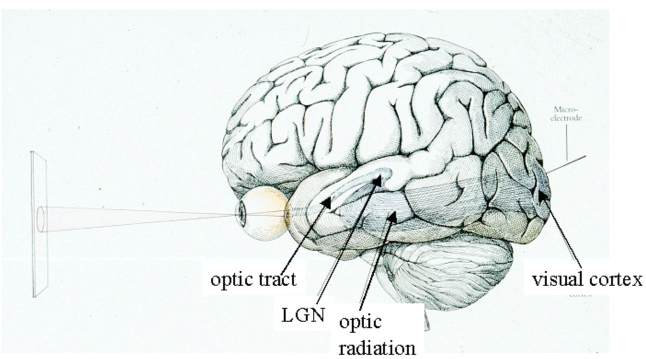
V1 Computational Theory

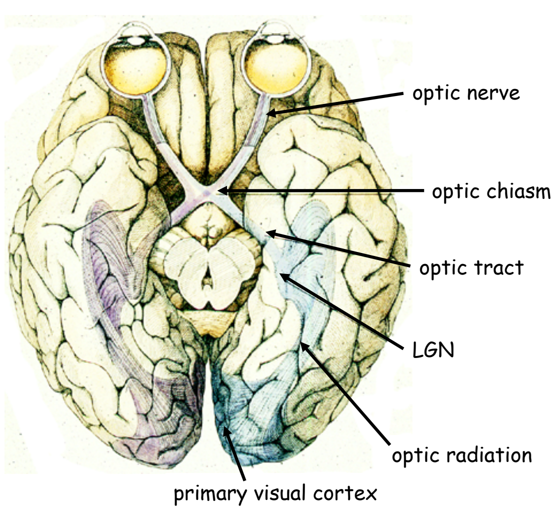
Retinogeniculate visual pathway



Lateral view

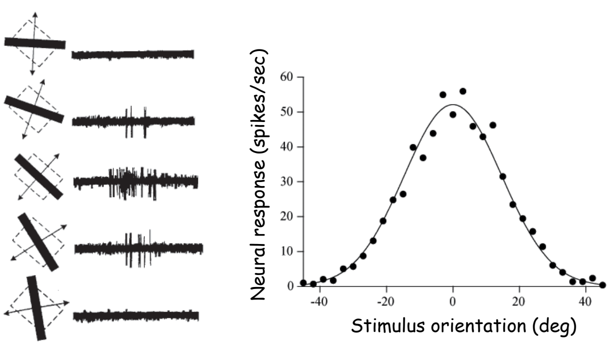
Retinogeniculate visual pathway

Ventral view

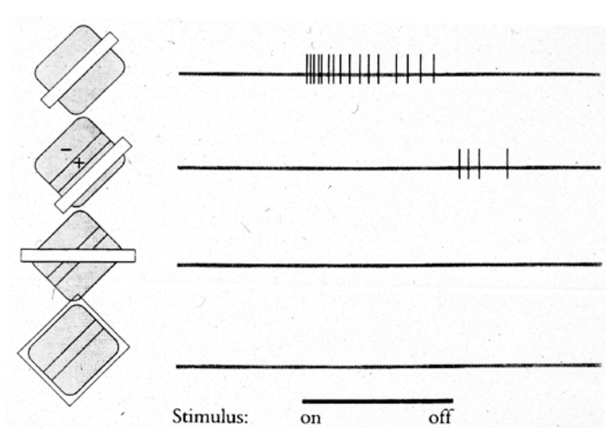


Stimulus drive & response selectivity

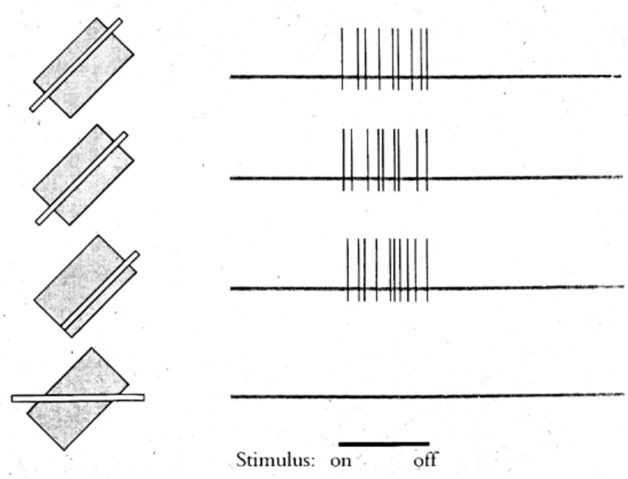
V1 orientation tuning



Simple cell



Complex cell



Hubel & Wiesel movie

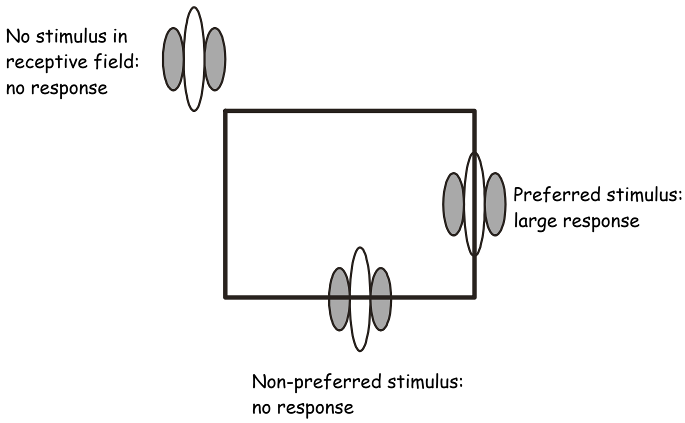
V1 physiology

Simple cells:
- orientation selective
- some are direction selective
- some are disparity selective
- monocular or binocular
- separate ON and OFF subregions
- length summation (best response to long bar)

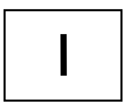
Complex cells:
- orientation selective
- some are direction selective
- some are disparity selective
- nearly all are binocular
- no separate ON and OFF subregions
- length summation

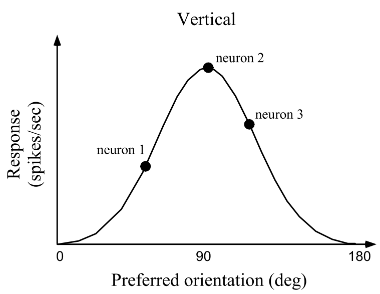
Hypercomplex cells:
end-stopping (best response to short bar)

Orientation selectivity model



Distributed representation of orientation

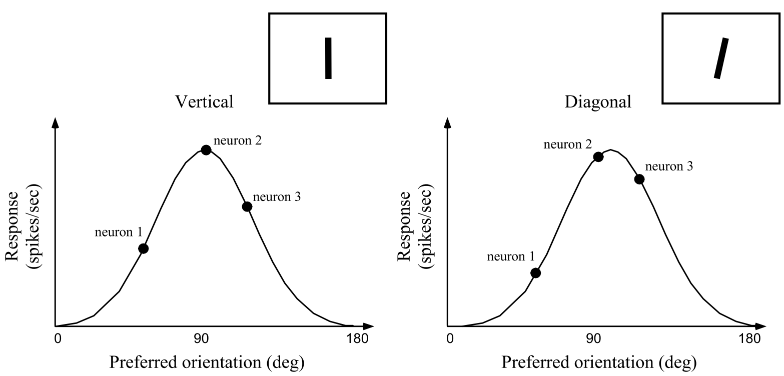




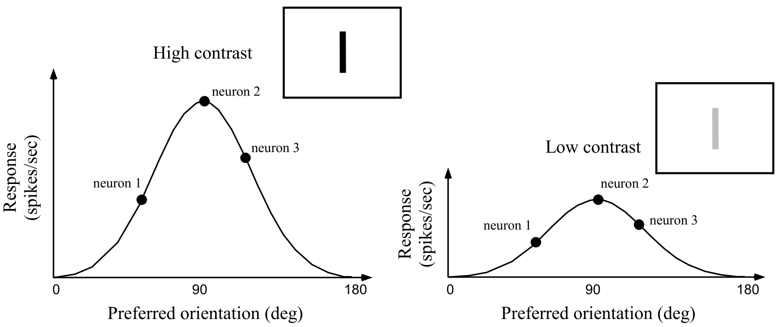
Responses of each of several orientation tuned neurons.

Peak (distribution mean) codes for stimulus orientation.

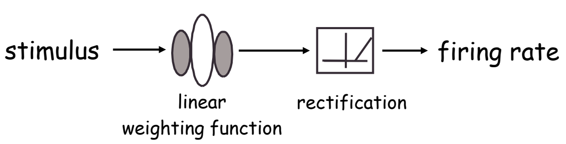
Broad tuning can code for small changes



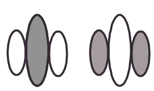
Neural code depends on multiple factors



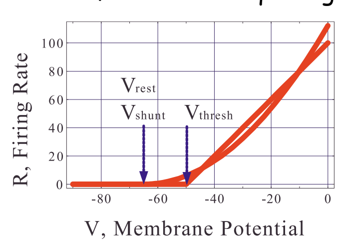
Rectification and squaring



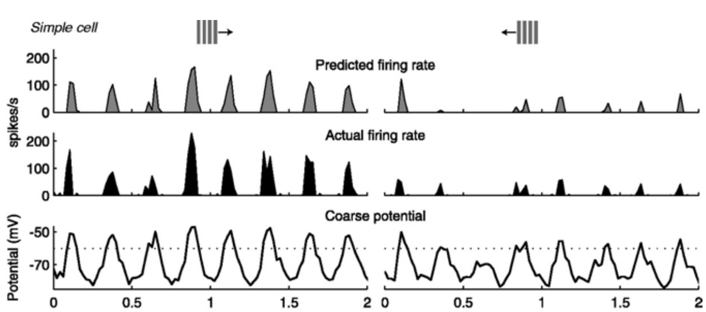
Complementary receptive fields

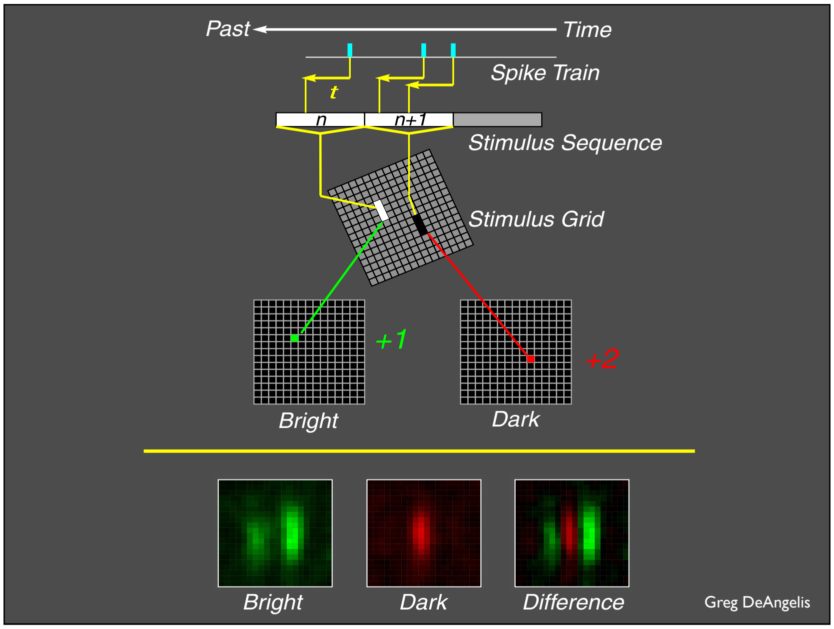


Rectification and squaring

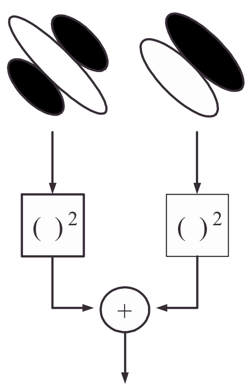


Rectification approximates relationship between membrane potential and spiking



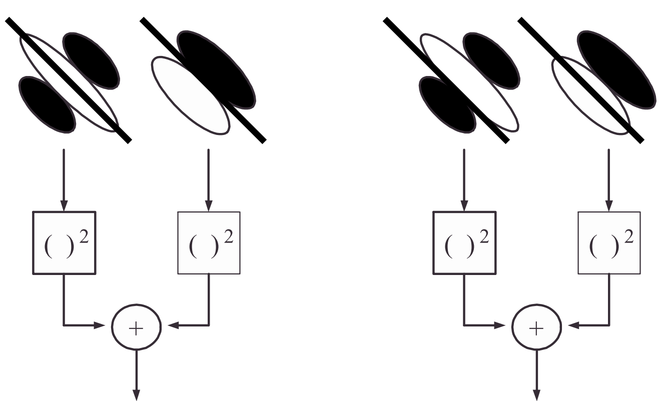


Complex cells: theory



Complex cells & position invariance

Oriented stimulus as seen by both subunits at two different locations:

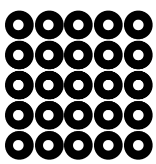


Theory of spatial pattern analysis by the visual system

Neural image: retinal ganglion cell responses

Input image
(cornea)

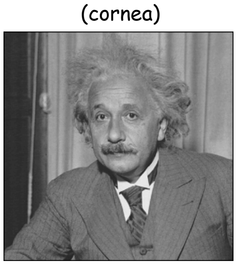
Array of center-surround
receptive fields



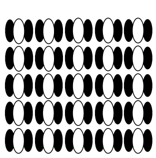
"Neural image"
(retinal ganglion cells)

Neural image: simple cell responses

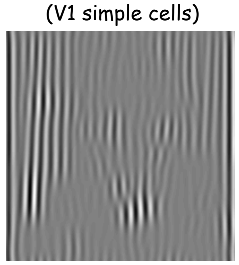
Input image
(cornea)



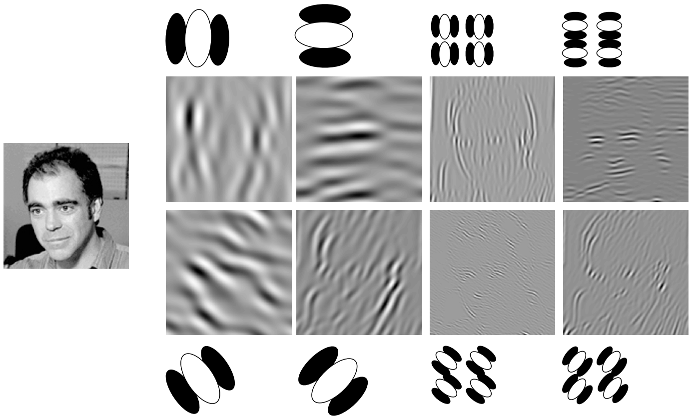
Array of orientation-
selective receptive fields



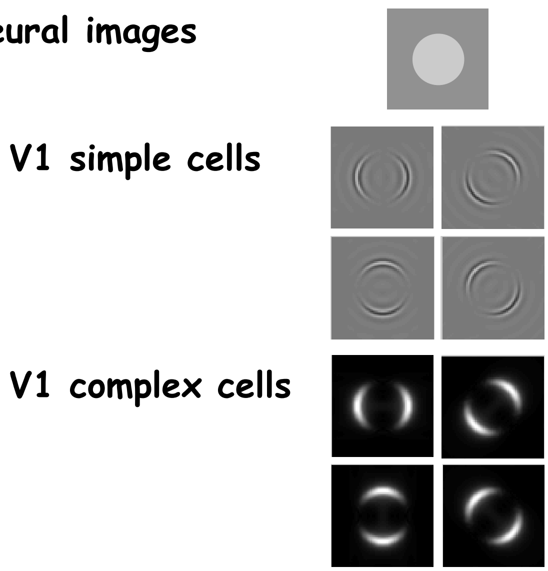
"Neural image"
(V1 simple cells)



Lots of neural images: V1 simple cells

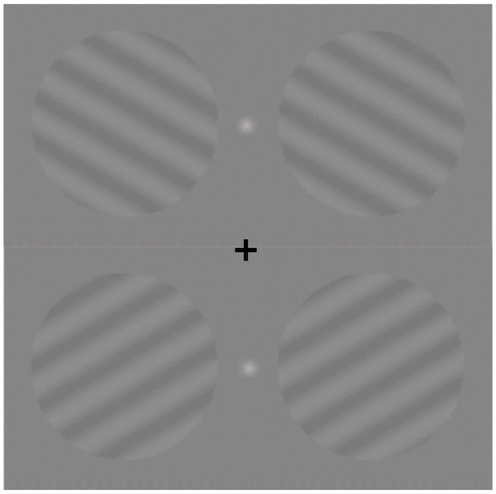


Lots of neural images

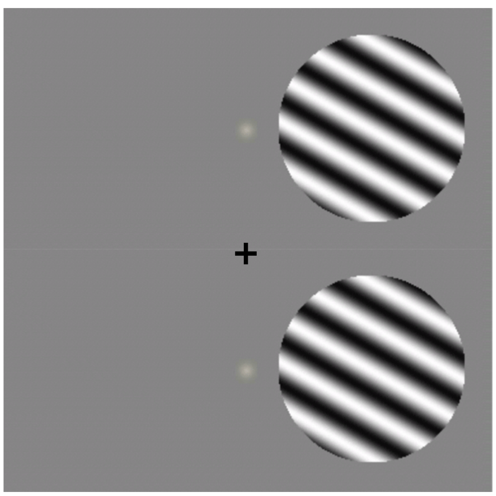


Psychophysical/perceptual evidence for spatial-frequency and orientation selective channels

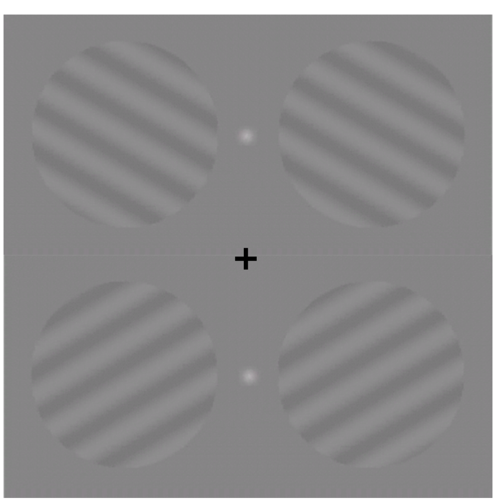
Orientation selective adaptation



Orientation selective adaptation

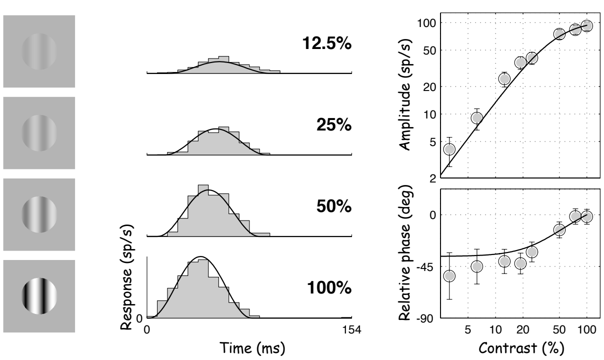


Orientation selective adaptation

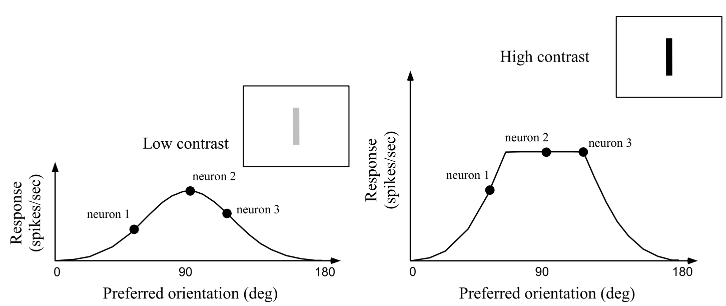


Normalization in monkey V1

Response saturation and phase advance

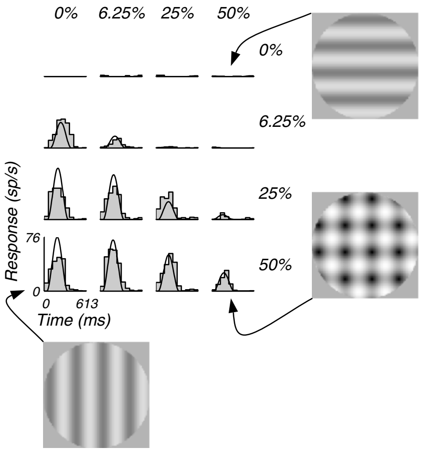


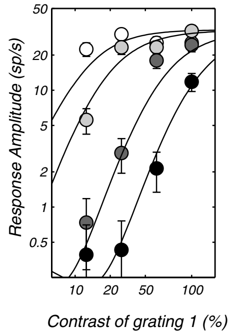
Failure of invariance with saturation?



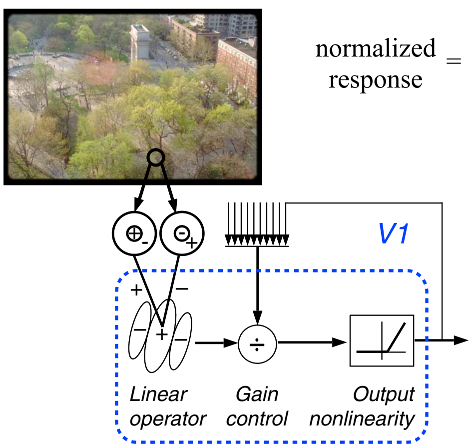
Can no longer discriminate orientations near vertical

Masking



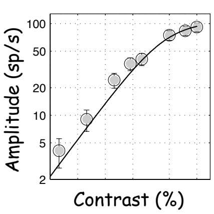


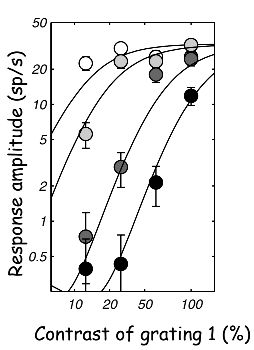
Normalization model



$$\text{normalized response} = \frac{(\text{unnormalized response})^2}{\sum\left(\text{unnormalized responses}\right)^2 + \sigma^2}$$

Response saturation and cross-orientation suppression





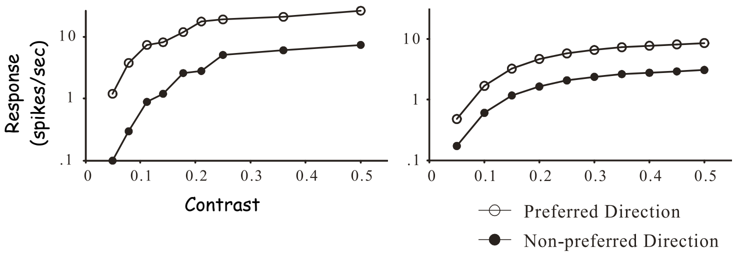
$$r = \alpha \frac{c^2}{c^2 + \sigma^2}$$

$$r = \alpha \frac{c_t^2}{c_t^2 + c_m^2 + \sigma^2}$$

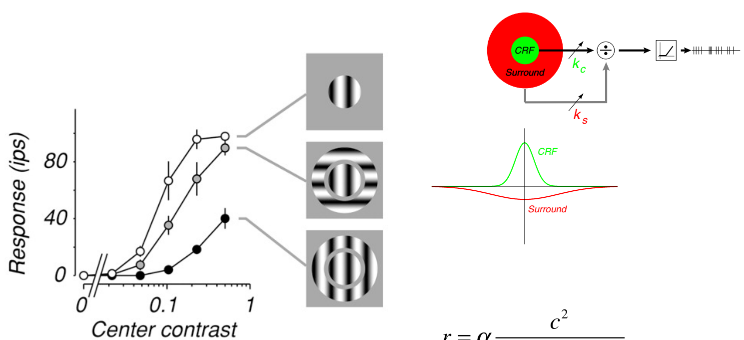
Contrast invariance

Ratio of responses to pref and non-pref directions constant over full range of contrasts.

Tolhurst & Dean (1980) | Model



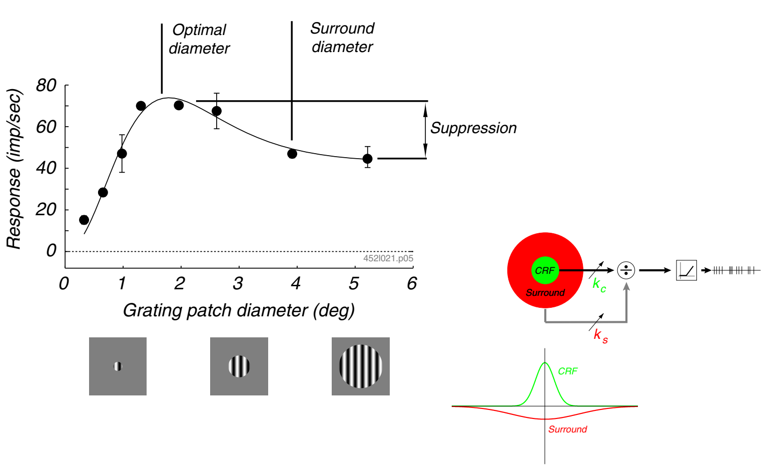
Surround suppression



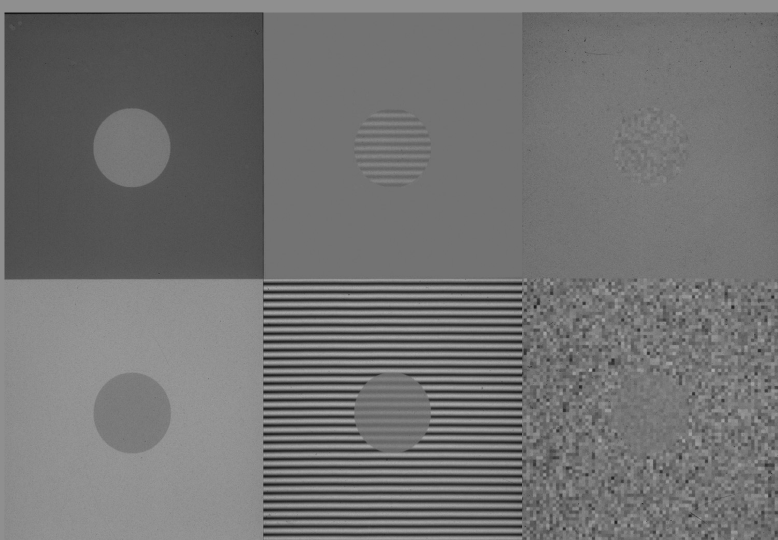
$$r = \alpha \frac{c^2}{c^2 + \beta c_s^2 + \sigma^2}$$

$0 < \beta < 1$ surround suppression

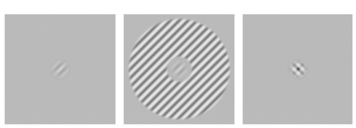
Surround suppression



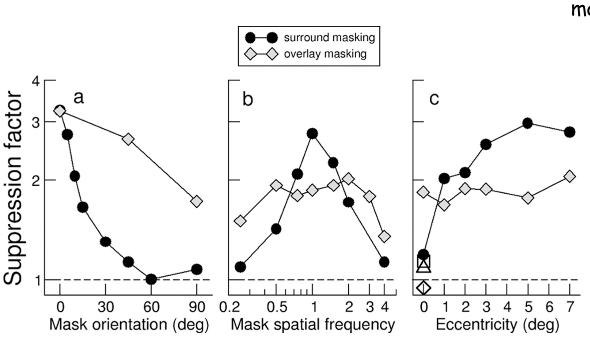
Psychophysical/perceptual evidence for normalization



Masking

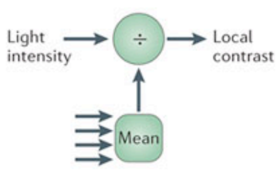


Target Surround masking Overlay masking

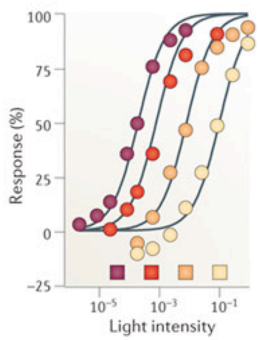


Canonical computation hypothesis: normalization in other brain areas

Light adaptation in the retina (revisited)

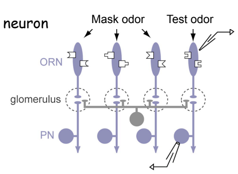


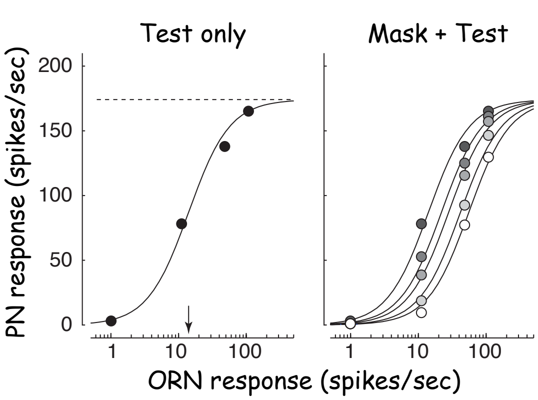
$$R = \alpha \frac{I_t}{I_t + I_b + \sigma}$$



Normalization in fruit fly olfaction

ORN: olfactory receptor neuron
PN: projection neuron





$$R = \alpha \frac{I_t^n}{I_t^n + I_m^n + \sigma^n}$$

Also...

- Visual cortical areas V4 (pattern), MT (motion perception), and IT (object recognition).
- Other sensory modalities: auditory cortex; multisensory integration (visual motion and vesibular system) in MST.
- Encoding of value in posterior parietal cortex.
- Superior colliculus: saccade averaging.
- Attention: modulation of activity in visual cortex.

Why normalize?

- Limited dynamic range (Heeger, Vis Neurosci, 1992).
- Simplify read-out, thinking of population code as a probability density (Simoncelli & Heeger, Vis Res, 1998; Simoncelli, in The Visual Neurosciences, 2003; Beck, Latham & Pouget, J Neurosci, 2011).
- Invariance w.r.t. one or more stimulus dimensions, e.g., contrast, odorant concentration (Heeger, Vis Neurosci, 1992; Heeger, Simoncelli & Movshon, PNAS, 1996; Simoncelli & Heeger, Vis Res, 1998; Ringach, Vis Res, 2009; Olsen, Bhandawat & Wilson, Neuron, 2010).
- Averaging vs. winner-take-all (Busse, Wade & Carandini, Neuron, 2009).
- Decorrelation & statistical independence (Schwartz & Simoncelli, Nat Neurosci, 2001; Lyu & Simoncelli, Neural Comput, 2009; Olsen, Bhandawat & Wilson, Neuron, 2010; Lyu, Axel & Abbott, PNAS, 2010).

Possible circuits & mechanisms

- Might be feedforward, feedback, or a combination of the two (Heeger, J Neurophysiol, 1993)
- Shunting inhibition (Carandini & Heeger, Science, 1994; Carandini, Heeger & Movshon, J Neurosci, 1997)
- Synaptic depression (Carandini, Heeger & Senn, J Neurosci, 2002)
- Presynaptic inhibition (Olsen & Wilson, Nature 2008)
- Balanced amplification (Murphy & Miller, Neuron, 2009)
- Background synaptic activity (Chance, Abbott & Reyes, Neuron, 2002)
- Saturation of the inputs combined with spike threshold and spike-rate rectification (Priebe & Ferster, Neuron, 2008)
- Etc.

From circuits & mechanisms to behavior

Computation

Circuits & cellular/ molecular mechanisms

Behavior

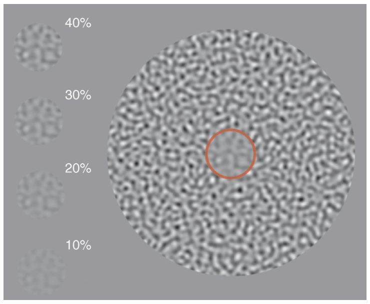
Carandini, Nat Neurosci (2012)

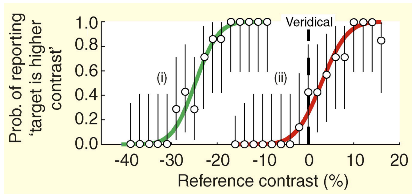
Mechanism?

Canonical computation deficit hypothesis

Possible dysfunction of normalization underlying schizophrenia, epilepsy, and other developmental and neurological disorders.

Schizophrenia: a dysfunction of normalization?

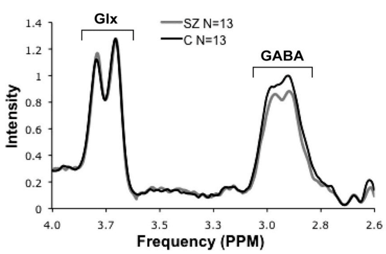


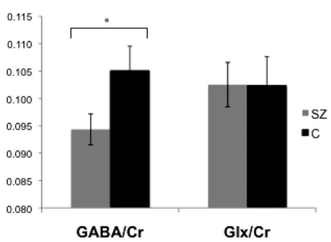


Dakin, Carlin & Hemsley, Curr Biol, 2005

Possible mechanism for normalization deficit

MR spectroscopy





Yoon et al, J Neurosci, 2010