V1 Computational Theory

Stimulus drive & response selectivity

V1 orientation tuning

![Graph showing neural response (spikes/sec) vs stimulus orientation (deg).]
Orientation selectivity model

No stimulus in receptive field: no response

Preferred stimulus: large response

Non-preferred stimulus: no response

Distributed representation of orientation

Stimulus: vertical bar

Responses of each of several orientation tuned neurons.

Peak (distribution mean) codes for stimulus orientation.

Broad tuning can code for small changes

Stimulus: vertical bar

Stimulus: diagonal bar

Response (spikes/sec) vs Preferred orientation (deg)
Neural code depends on multiple factors

Hubel & Wiesel (1968)

Motion is like orientation in space-time and spatiotemporally oriented filters can be used to detect and measure it.

Motion is orientation in space-time

Direction selectivity model

Strong response for motion in preferred direction.

Weak response for motion in non-preferred direction.

Distributed representation of speed

Each spatiotemporal filter computes something like a derivative of image intensity in space and/or time. “Perceived speed” is the orientation corresponding to the gradient in space-time (max response).
Impulse response

Rectification and squaring

Rectification approximates relationship between membrane potential and spiking
Space-time receptive field

Ohzawa, DeAngelis, & Freeman (1995)

Strong response to preferred direction

Note: negative responses not seen in neural firing rates
Weak response to opposite direction

Stimulus

Off response

On response

'On' and 'off' responses

Complex cells: theory
Complex cells & position invariance

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

![Diagram of oriented stimulus and subunits](image)

Normalization in monkey V1

Response saturation and phase advance
Failure of invariance with saturation?

Can no longer discriminate orientations near vertical.

Masking

Normalization model

normalized response = \frac{(unnormalized response)^2}{\sum (unnormalized response)^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

\[ r = \alpha \frac{c^3}{c^3 + \beta c_t^2 + \sigma^2} \]

\[ 0 < \beta < 1 \quad \text{surround suppression} \]
Surround suppression

Surround suppression & contrast appearance

Contrast adaptation
Canonical computation hypothesis: normalization in other brain areas

Light adaptation in the retina (revisited)

Normalization in fruit fly olfaction
Also...

- Visual cortical areas V4 (pattern), MT (motion perception), and IT (object recognition).
- Other sensory modalities: auditory cortex; multisensory integration (visual motion and vestibular 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).
- 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).

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?

Possible mechanism for normalization deficit

MR spectroscopy

Yoon et al, J Neurosci, 2010

Dakin, Carlin & Hemsley, Curr Biol, 2005