\[ C \frac{dV}{dt} + g_{\text{leak}} (V - V_{\text{leak}}) + g_c (V - V_c) + g_i (V - V_i) + g_{Na} m^3 h (V - V_{Na}) + g_k n^4 (V - V_k) + ... = 0 \]

Are we done yet?

**Vision is an unconscious inference**

**Visual inference: motion perception**
Two guiding principles

Functional specialization

Computational theory

Neural circuits perform computations

~50,000 neurons per cubic mm
~6,000 synapses per neuron
~10 billion neurons & ~60 trillion synapses in cortex

Computational theory: how do neurons compute motion?

Wednesday, February 1, 2012
V1 orientation tuning

Hubel & Wiesel (1968)

Orientation selectivity model

No stimulus in receptive field: no response

Preferred stimulus: large response

Non-preferred stimulus: no response

Rectification and spiking threshold

Complementary receptive fields

Rectification and squaring
Rectification approximates relationship between membrane potential and spiking

Responses of each of several orientation tuned neurons. Peak (distribution mean) codes for stimulus orientation.

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

Direction selectivity

Orientation in space-time

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).

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Impulse response

Space-time receptive field

Ohzawa, DeAngelis, & Freeman (1995)

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Strong response to preferred direction

Note: negative responses not seen in neural firing rates

Weak response to opposite direction

‘On’ and ‘off’ responses

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Response saturation and phase advance

Carandini, Heeger & Movshon, J Neurosci, 1997

Failure of invariance with saturation?

Can no longer discriminate orientations near vertical

Masking

Carandini, Heeger & Movshon, J Neurosci, 1997

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Normalization model

\[
\text{normalized response} = \frac{\text{unnormalized response}}{\sum \text{unnormalized responses} + \sigma}
\]

Heeger, Vis Neurosci, 1992

Contrast invariance

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

Tolhurst & Dean (1980)

Response saturation

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

Carandini, Heeger & Movshon, J Neurosci, 1997
**Masking**

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

Carandini, Heeger & Movshon, J Neurosci, 1997

**Surround suppression & normalization**

Cavanaugh, Bair and Movshon, J Neurophysiol, 2002

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Surround suppression & contrast appearance

Chubb, Sperling and Solomon, PNAS, 1989

Surround suppression & contrast discrimination

Zenger-Landolt & Heeger, J Neurosci, 2003

Surround suppression & contrast discrimination

Zenger-Landolt & Heeger, J Neurosci, 2003

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Normalization in other brain areas

Normalization in MT

Computational theory explains the responses of V1 & MT neurons and motion perception

Normalization in MT

Snowden et al. (1991) Model

Number of dots in anti-preferred direction
- spontaneous rate
- 0
- 16
- 64
- 256

Simoncelli & Heeger, Vis Res, 1998

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Normalization in fruit fly olfaction

Also...

- Normalization in the visual system: light adaptation in the retina; contrast adaptation in the retina; normalization in inferotemporal cortex (involved in object recognition).
- Normalization in other sensory modalities: auditory cortex; multisensory integration (visual motion and vestibular system) in MST.
- Normalization and the encoding of value in posterior parietal cortex.
- Attention...
- Possible dysfunction of normalization underlying schizophrenia, epilepsy, and other developmental and neurological disorders.

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).
From circuits & mechanisms to behavior

Computation

Circuits & cellular/molecular mechanisms

Behavior

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