Implications of single-neuron gain control for information transmission in networks

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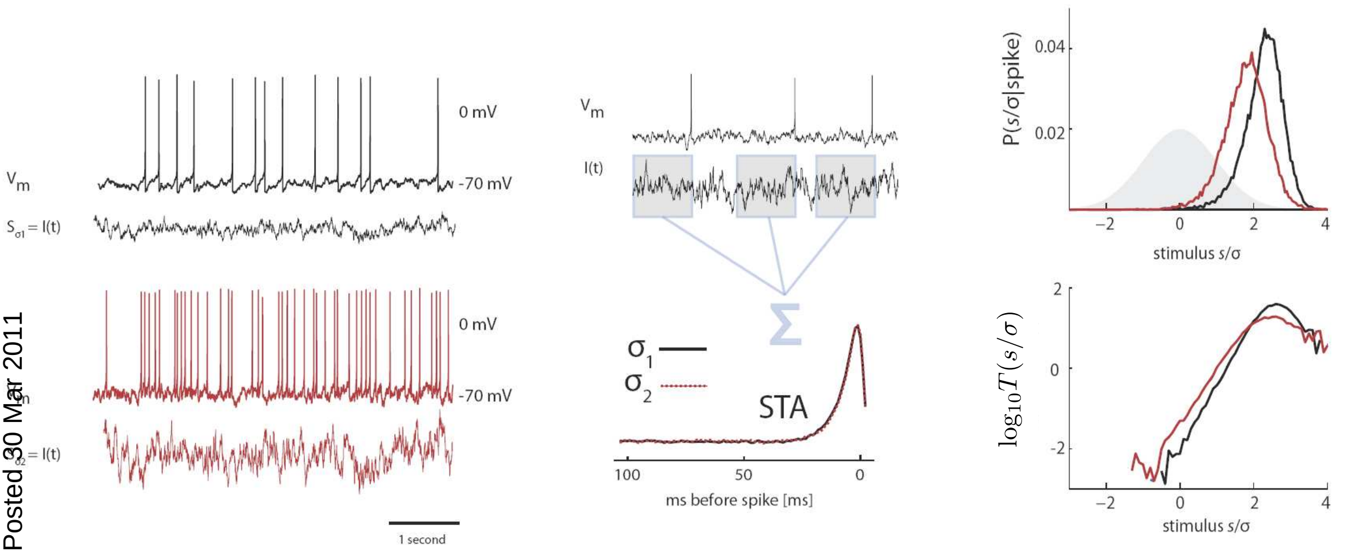
Introduction

Many neural systems are equipped with mechanisms to efficiently encode sensory information. To represent natural stimuli with time-varying statistical properties, neural systems should adjust their gain to the inputs' statistical distribution. Such matching of dynamic range to input statistics has been shown to maximize the information transmitted by the output spike trains (Brenner et al., 2000, Fairhall et al., 2001). Gain scaling has not only been observed as a system response property, but also in single neurons in developing somatosensory cortex stimulated with currents of different amplitude (Mease et al., 2010). We examine the implications of single-neuron gain control for information transmission in feed-forward neural networks. In particular, we distinguish between two regimes:

- networks with gain scaling produce responses which capture the original signal in the presence of background noise
- networks without gain scaling respond synchronously to large-amplitude features of the signal

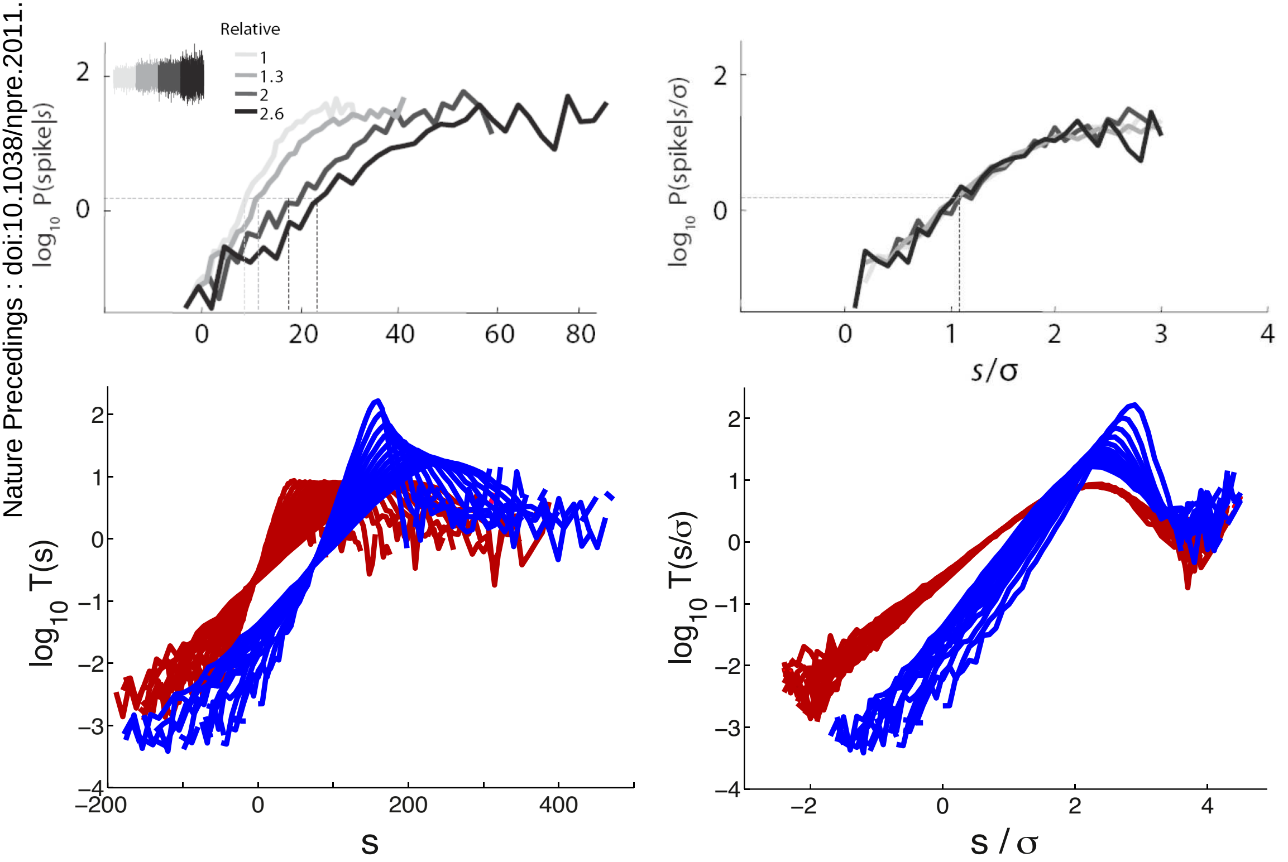
Gain scaling in single neurons



We use white noise analysis to determine a linear-nonlinear model which describes the computation performed by a single neuron for a stimulus with fixed statistics

$$T(s) = \frac{p(s|\text{spike})p(\text{spike})}{p(s)}, \text{ where } s = \text{STA} * \text{I(t)}$$

Neurons with **perfect gain scaling** have response functions whose form is the same for all Gaussian stimuli with constant mean, when the stimulus is scaled by its standard deviation.



In early development (P0), cortical neurons do not scale the amplitude of their response to incoming stimuli (Mease et al. 2010).

By P7, cortical neurons acquire the ability to gain-scale their outputs. This coincides with the disappearance of spontaneous waves emergent in developing cortex (Conheim et al. 2010).

A conductance-based model can reproduce the presence or absence of gain scaling depending on the choice of ion channel parameters.

$$C\frac{\mathrm{d}V}{\mathrm{d}t} = -G_{\mathrm{L}}(V - E_{\mathrm{L}}) - G_{\mathrm{Na}}m^3h(V - E_{\mathrm{Na}}) - G_{\mathrm{K}}n(V - E_{\mathrm{K}}) + I(t)$$

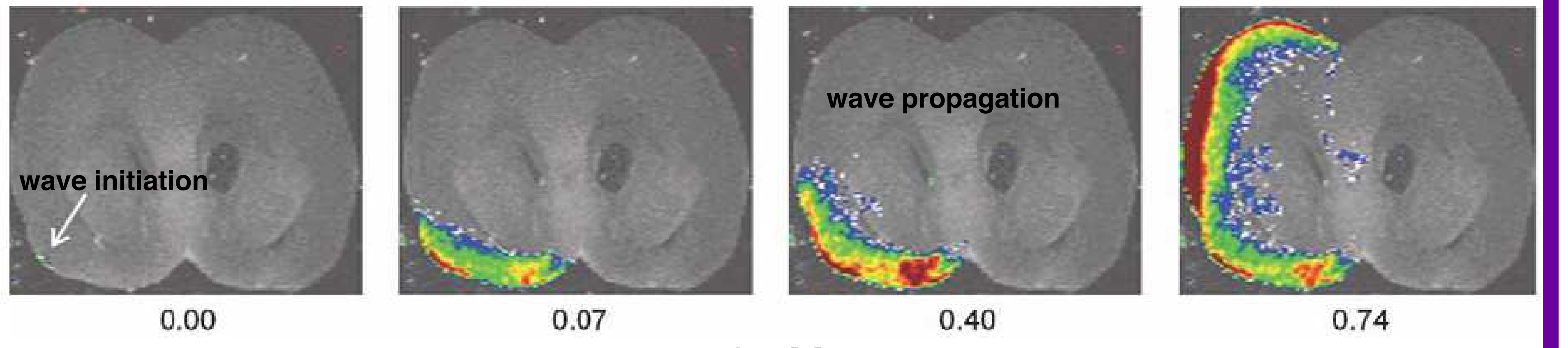
Gain scaling: $R = G_{Na}/G_{\mathrm{K}} = 1.5$

Non-gain scaling: $R = G_{Na}/G_{\mathrm{K}} = 0.6$

Spontaneous waves in developing cortex

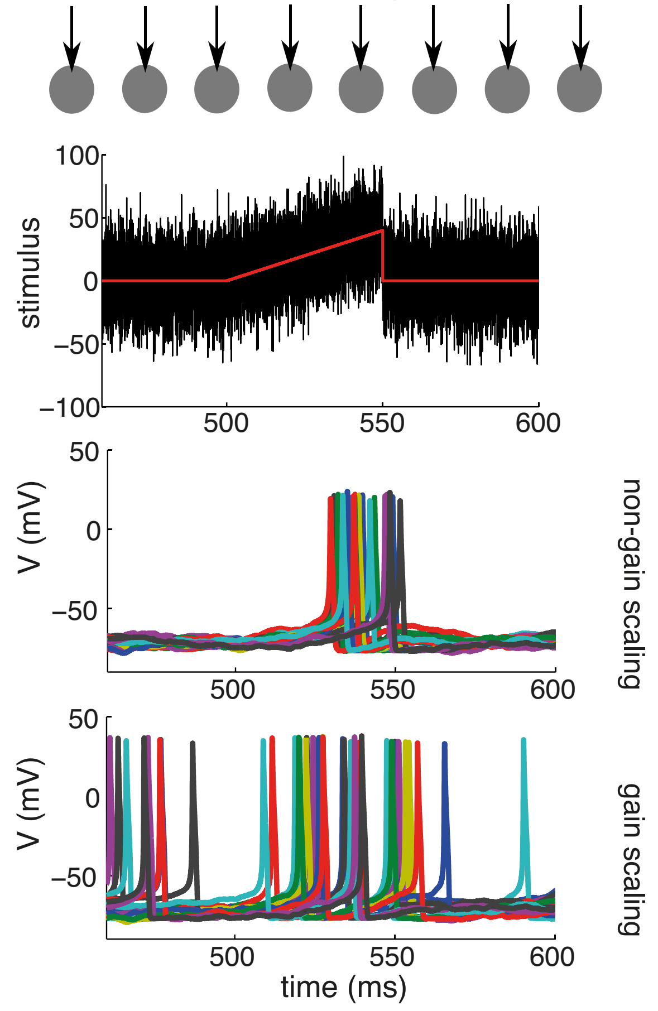
Spontaneous activity in the developing cortex occurs in the form of propagating waves. Waves are triggered by pacemaker cells which are thought to regulate the spatio-temporal extend of the waves at different ages.

We studied how individual cells, with and without the ability to scale their gain, respond to incoming synaptic input as might occur during a wave of activity: a large correlated input summed with uncorrelated activity.



time [s]

Gain scaling desynchronizes neural responses



We examined the response of gain scaling and non-gain scaling neurons receiving feedforward ramp-like input.

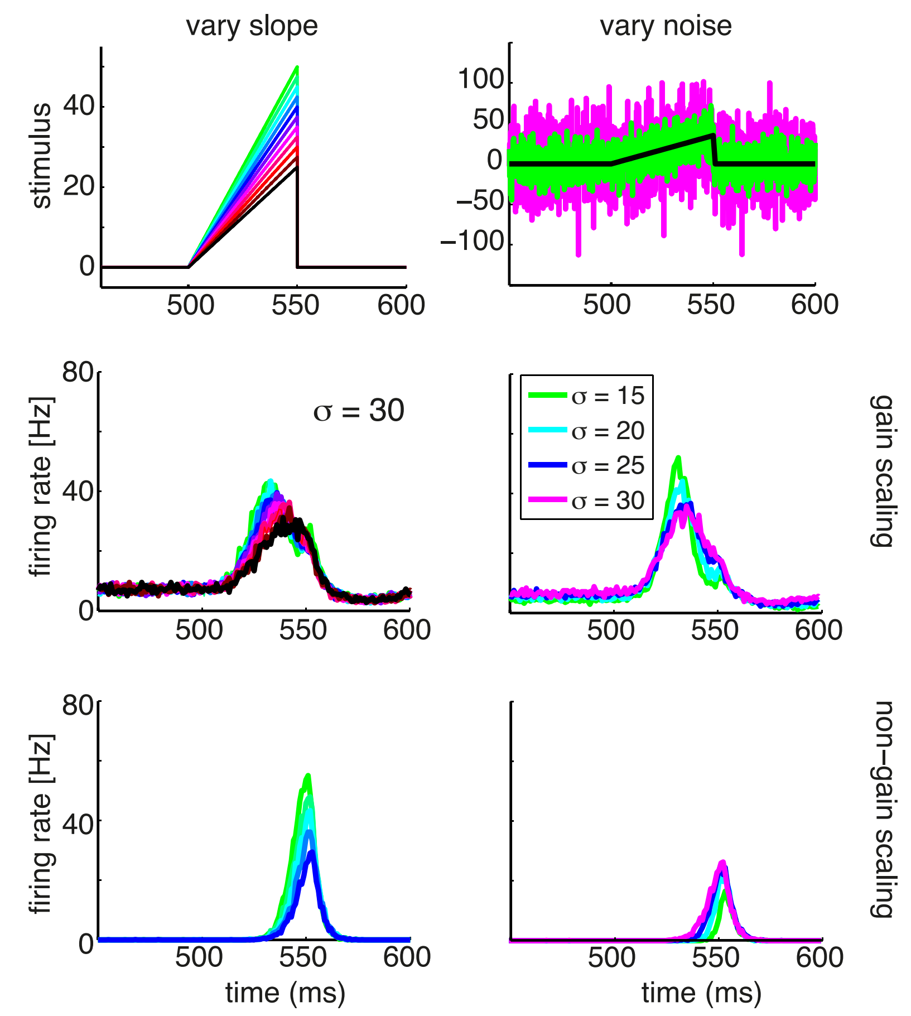
This input resembles synaptic noise generated in the pacemaker circuit just before it initiates a wave.

The lack of gain scaling in pacemaker neurons causes them to be relatively insensitive to the background synaptic noise.

Their responses are highly synchronous and driven by the ramp.

Thus, without gain scaling, different neurons are driven primarily by the large slowly-varying mean change.

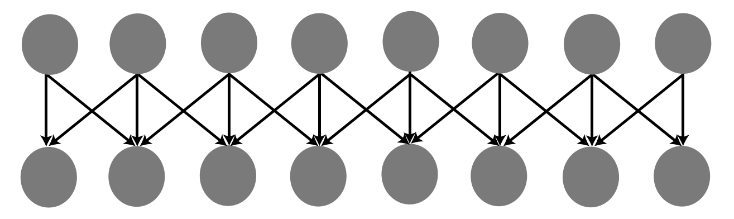
Due to their sensitivity to the fine-scale fluctuations in the stimulus, gain scaling neurons encode the ramp continuously.



Therefore, we study two modes of signal propagation in a feedforward network:

(1) propagation of pulse-like large amplitude events as during cortical waves, and

(2) propagation of slowly-varying mean inputs after the disappearance of cortical waves.



We consider networks consisting of L layers connected with feedforward connections to model wave initiation, propagation and degradation in developing cortex.

Neurons in layer 1 receive a slowly-varying stimulus and independent fast fluctuations.

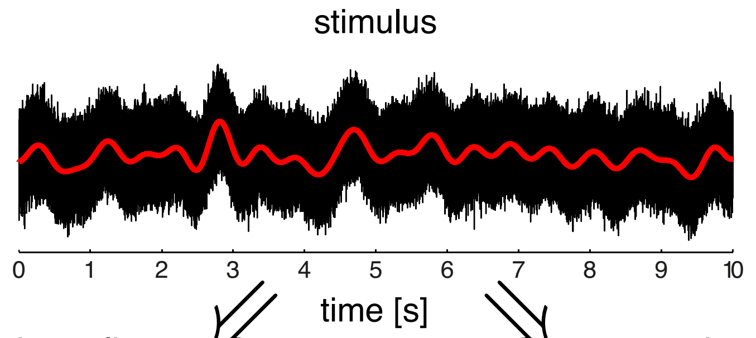
Neurons in layers >1 receive synaptic input from neurons in the previous layer from a neighbrhood of size N and also independent fast fluctuations.

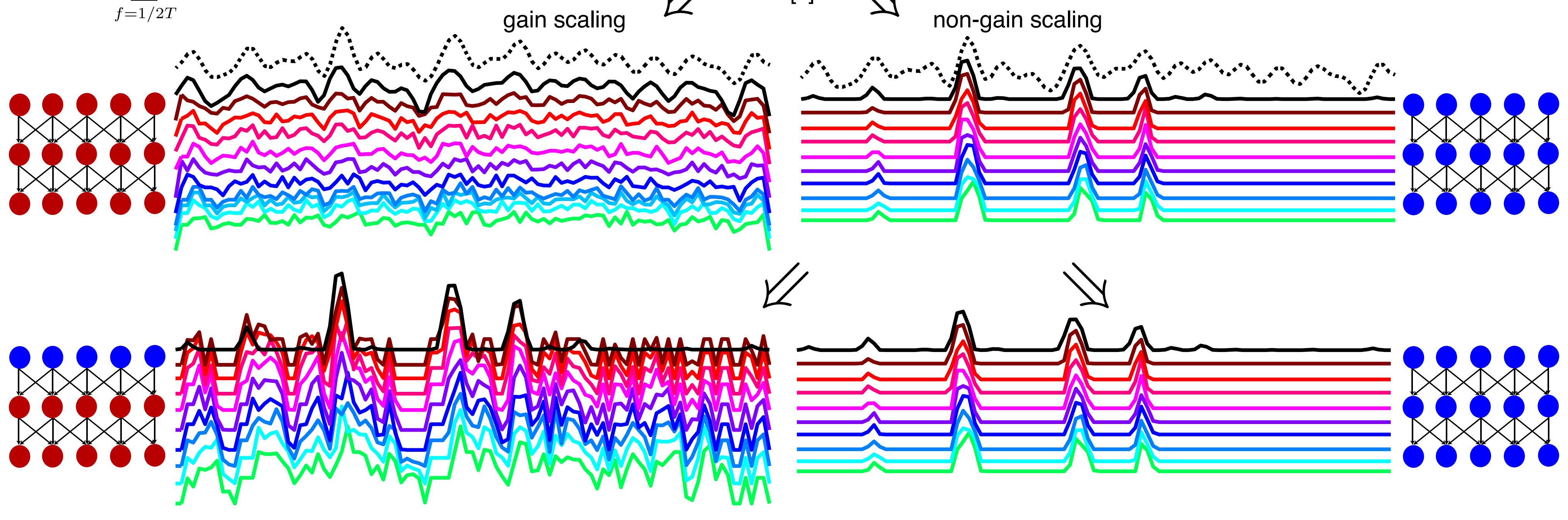
High fidelity responses to slowly-varying stimuli

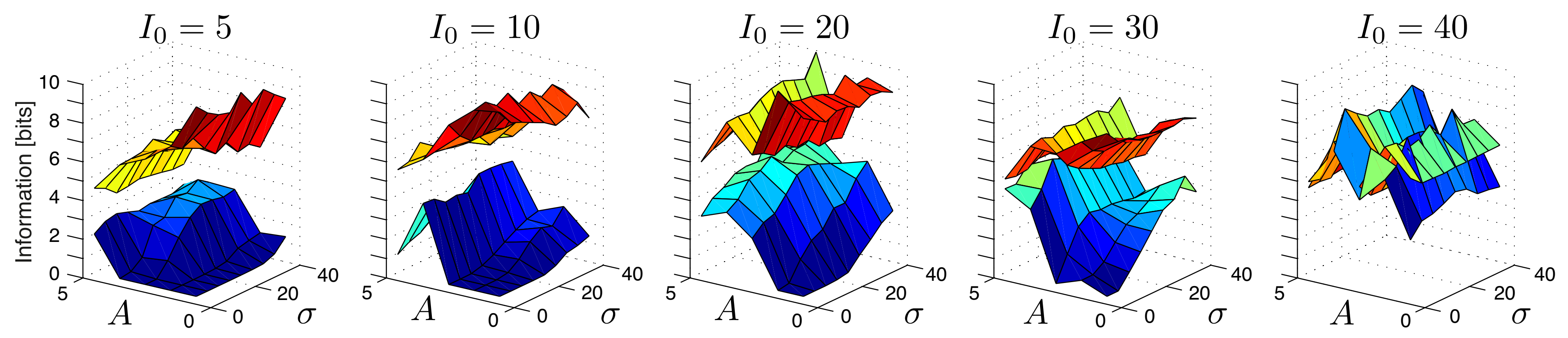
We describe a slowly-varying stimulus with a mean offset, slow fluctuations (red) and fast fluctuations (black)

$$\text{stimulus} = \underbrace{I_0}_{\text{mean offset}} + \underbrace{A\,g(t)}_{\text{slow fluctuations}} + \underbrace{\sigma\,\xi(t)}_{\text{fast fluctuations}}$$

$$g(t) = \sum_{f=1/2T}^{1\text{Hz}} \cos(2\pi f t + \varphi_f),\ \xi(t) \sim N(0,1)$$







Averaged peristimulus time histograms with different realizations of the fast fluctuations provide an estimate of the stimulus:

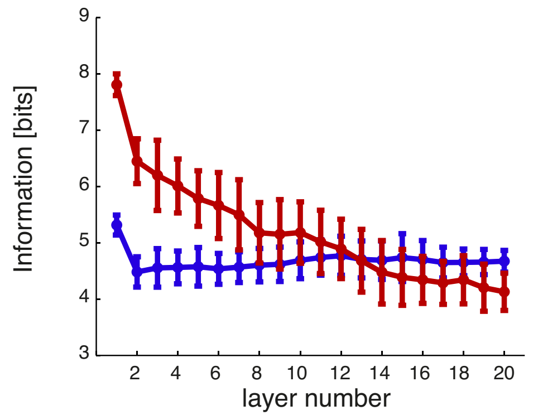
$$S_{\text{est}}(t) = \overline{R}(t) = \sum_i R_i(t - i\,\tau_{\text{EPSP}})$$

Noise: $N(t) = S(t) - S_{\text{est}}(t)$

Signal-to-noise ratio: $\text{SNR} = \frac{\text{Power } S_{\text{est}}(t)}{\text{Power } N(t)}$

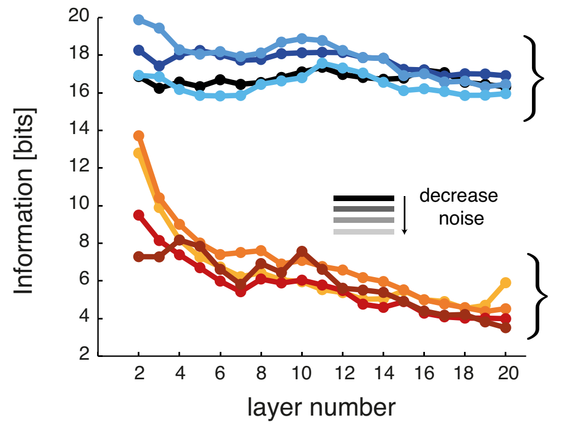
Lower bound of information transmitted between stimulus and response:

$$I(S,R) \leq I(S_{\text{est}},R) = \int_0^{1\text{Hz}} \log_2(1 + \text{SNR})\mathrm{d}t$$



Information about the signal is better preserved by gain-scaling networks.

This information degrades across layers.



Non-gain scaling neurons preseve wave-like timuli as they propagate through the network without losing information from one layer onto the next.

Gain scaling neurons degrade wave-like stimuli as they propagate through the network while monotonically losing information from one layer onto the next.

- Information rate is higher for gain scaling neurons (upper surface) than for non-gain scaling neurons (lower surface) for a wide range of stimulus offsets, amplitudes and noise levels.
- In gain scaling neurons, information rate increases with the amplitude of the slowly-varying stimulus and the fast fluctuations; the opposite is true for non-gain scaling neurons.

Conclusions

We observed two modes of signal propagation depending on the types of neurons in the feedforward network:

- Non-scaling networks showed synchronous response to inputs of large amplitude. This response can reliably propagate across many layers approximating wave propagation in developing cortex.
- Scaling networks degrade wave-like stimuli across layers and could be responsible for wave disappearance in cortex. However, as a population they can accurately track a slowly-varying input which cortical neurons may require as sensory inputs replace spontaneous waves.

Similar response modes have been observed in feedforward networks of integrate-and-fire neurons where the difference was due to the difference between rest and threshold voltage (van Rossum et al. 2002). This voltage difference is also modulated by the change in conductance ratio R.

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