Tuning of MT neurons depends on stimulus contrast in accord with canonical computation

Ambarish S. Pawar[1], Sergei Gepshtein[1], Sergey Savel'ev[2], Thomas D. Albright[1], [1]*Salk Institute for Biological Studies, La Jolla, CA, USA;* [2]*Loughborough University, UK*

SALK INSTITUTE FOR BIOLOGICAL STUDIES
Loughborough University

Background

One of the most important questions in neuroscience today concerns the mechanisms by which sensory systems acquire selectivity for sensory stimuli. This question has been addressed most extensively for the visual modality but many questions remain unresolved. What accounts, for example, for the limited range of visual sensitivities to luminance and chrominance, or to the spatial and temporal properties of an image?

Sensory neurons in cerebral cortex are characterized by their selectivity to stimulation. This selectivity was originally viewed as a stable property of individual neurons, later challenged by the evidence of surround modulation and adaptation. Here we use empirical and theoretical approaches to investigate how cortical selectivity to spatial frequency is influenced by stimulus luminance contrast.

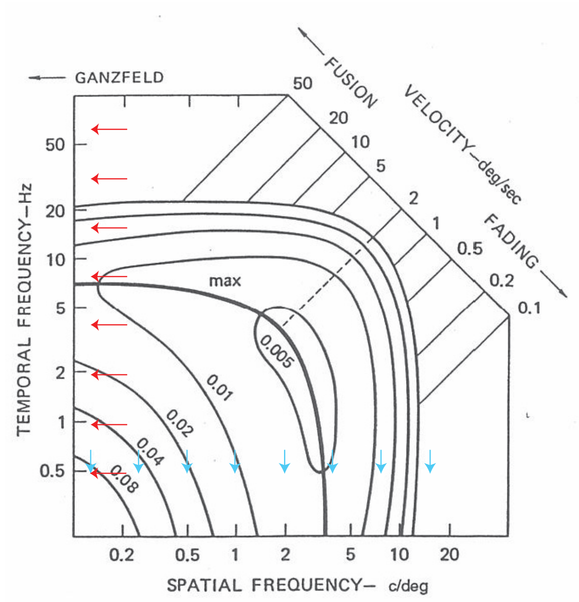
Our goal is a complete mechanistic account of spatial frequency selectivity in cortical neurons.

Methods

Neural responses were measured from single cells in the middle temporal area (MT) of the visual cortex of two alert fixating rhesus monkeys (Macaca mulatta).

For 130 cells, we obtained the receptive field center, preferred direction, spatial frequency (SF) and temporal frequency (TF) tuning of the neuron at 100% contrast.

Most neuronal receptive fields were within 6° of the fovea.



LEFT: Human contrast sensitivity for all visible SF and TF.

Neural responses measured at:

- 5 SF (0.015 to 16 cycles/degree).
- 1-3 TF (0.25 to 32 Hz).
- 5-7 contrasts levels (0.5-100%).

For the population of neurons, stimulus space covered the entire range of spatiotemporal frequencies. Tested SFs and TFs are marked by arrows.

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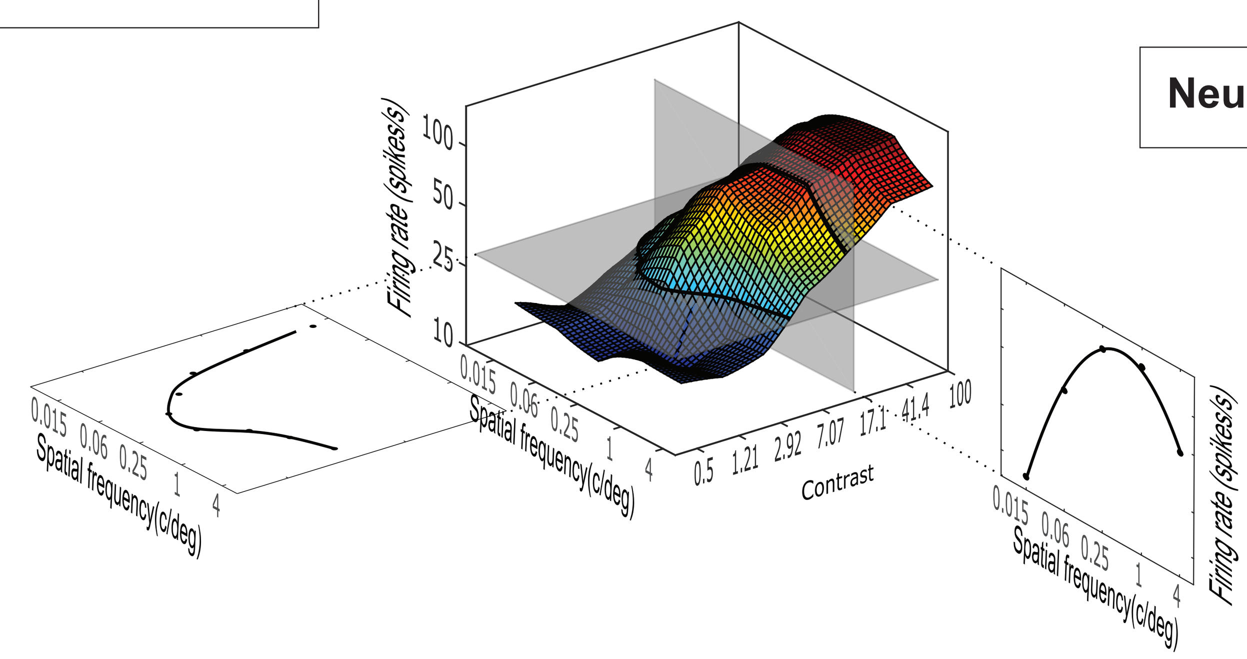
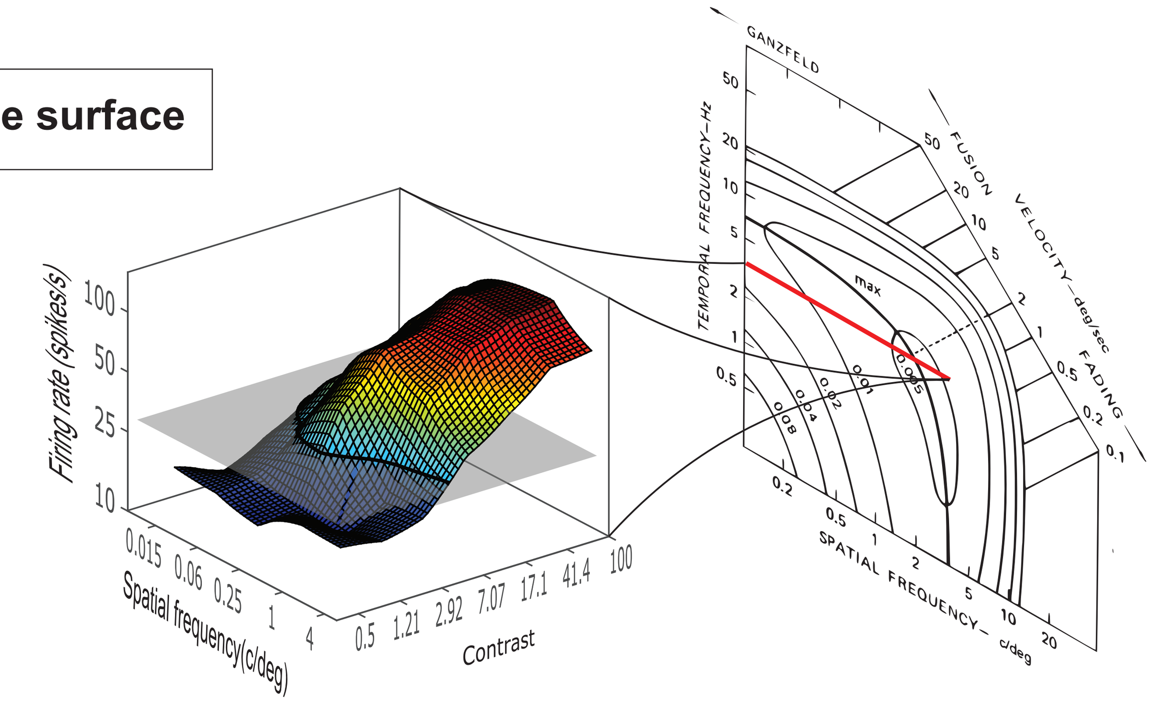
Results

Neuronal response surface



Neuronal response surface is a 3D plot of neuronal firing rate vs. spatial frequency and contrast.

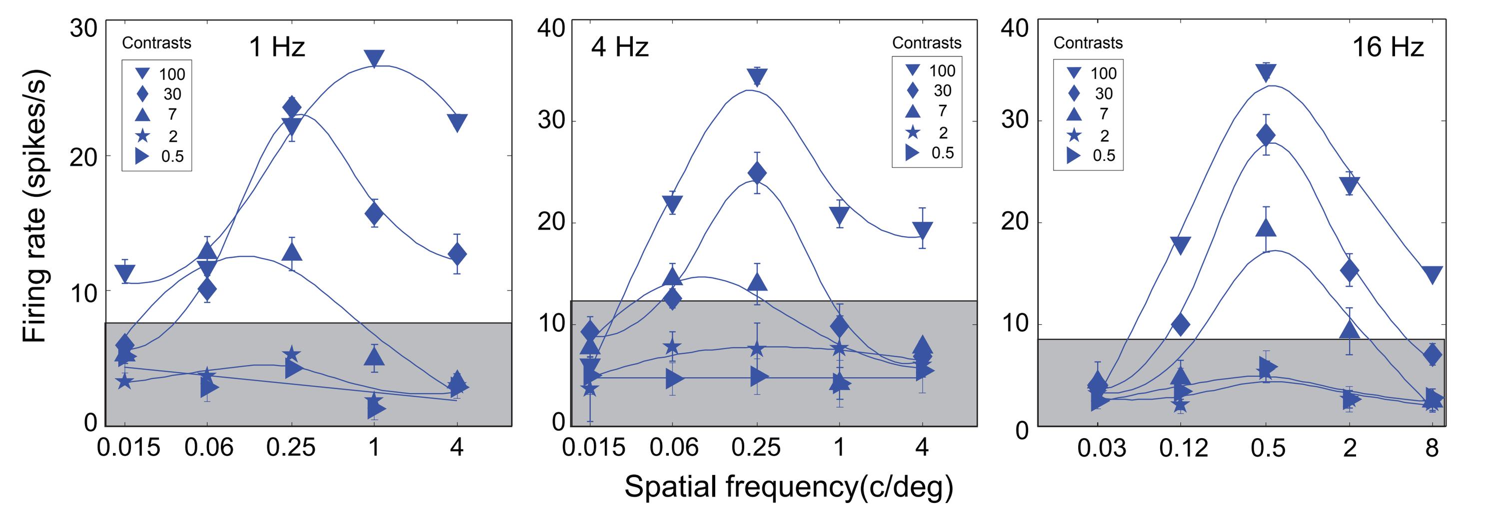
The vertical slice at RIGHT is a response function: firing rate at a single contrast (here 17.1%) across SF. The horizontal slice at LEFT is a contrast sensitivity function: stimulus contrast that elicited the threshold firing rate (resting rate ± 1 sd).



Neuronal response surface measured at a single TF. The TF corresponds to a horizontal slice on the contrast sensitivity function (red). The human contrast sensitivity function (RIGHT) is for representative purposes only.

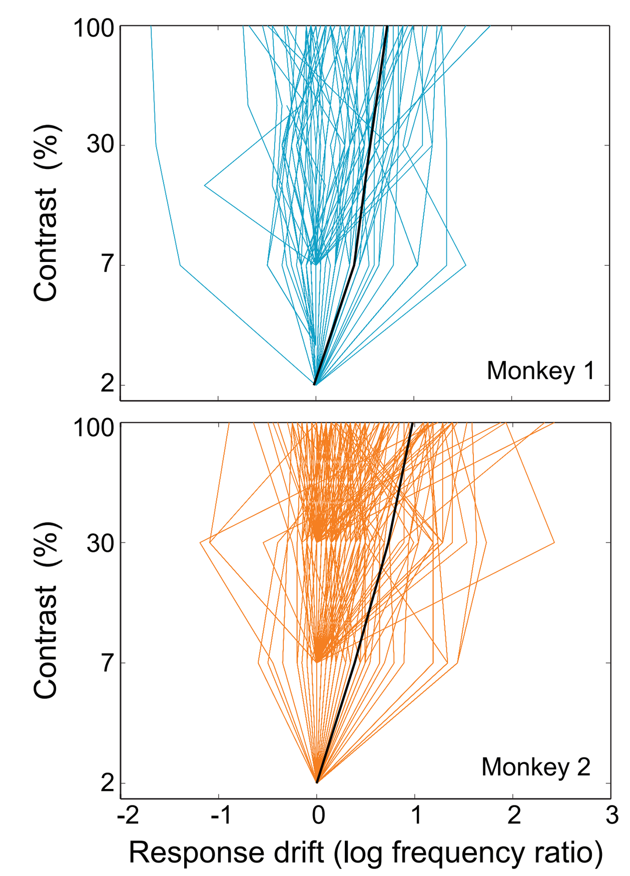
1-3 such surfaces were measured from each neuron.

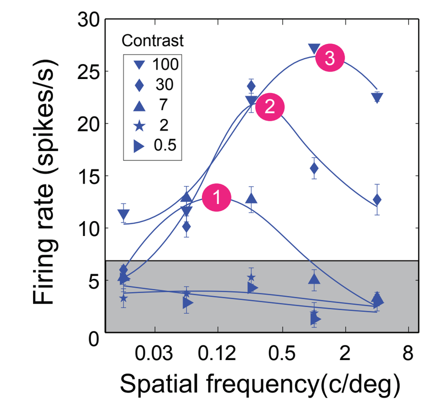
Spatial frequency tuning across contrasts



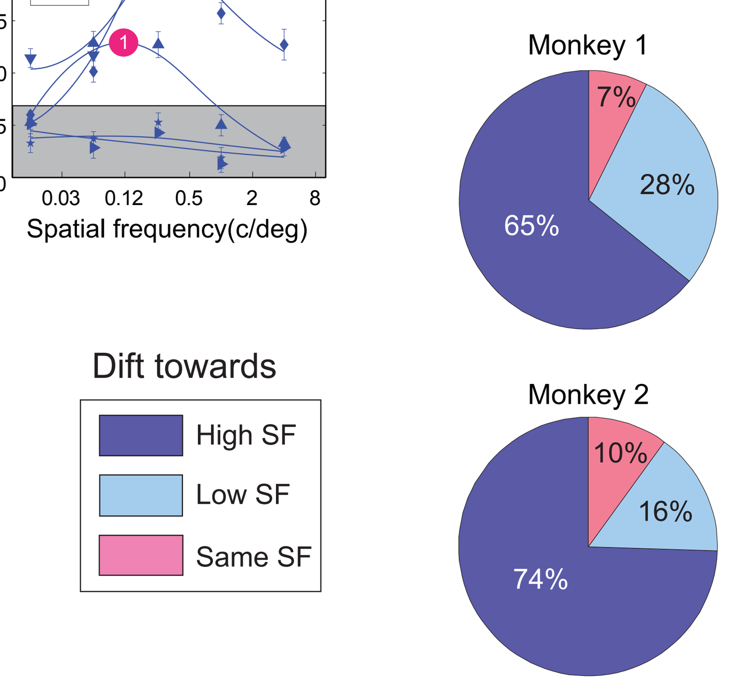
Five response functions derived from the neuronal response surface at 5-7 contrasts (see legend). These are examples of the patterns of behavior found in MT cells, as a function of stimulus contrast: strong drift of peak response toward high SF (LEFT), weak drift of peak response toward high SF (MIDDLE), no change in peak response (RIGHT). Each panel is data from a different neuron.

Below we summarize data for these and other patterns.





Percent of samples with different tuning dynamics



Response drift: Decimal log ratio of peak SF at high contrast to peak SF at low contrast.

The positive and negative values of drift indicate that peak SF respectively increased and decreased.

Pie charts: Most TF samples shift toward high SF (RIGHT).

Spatial frequency tuning depends on temporal frequency

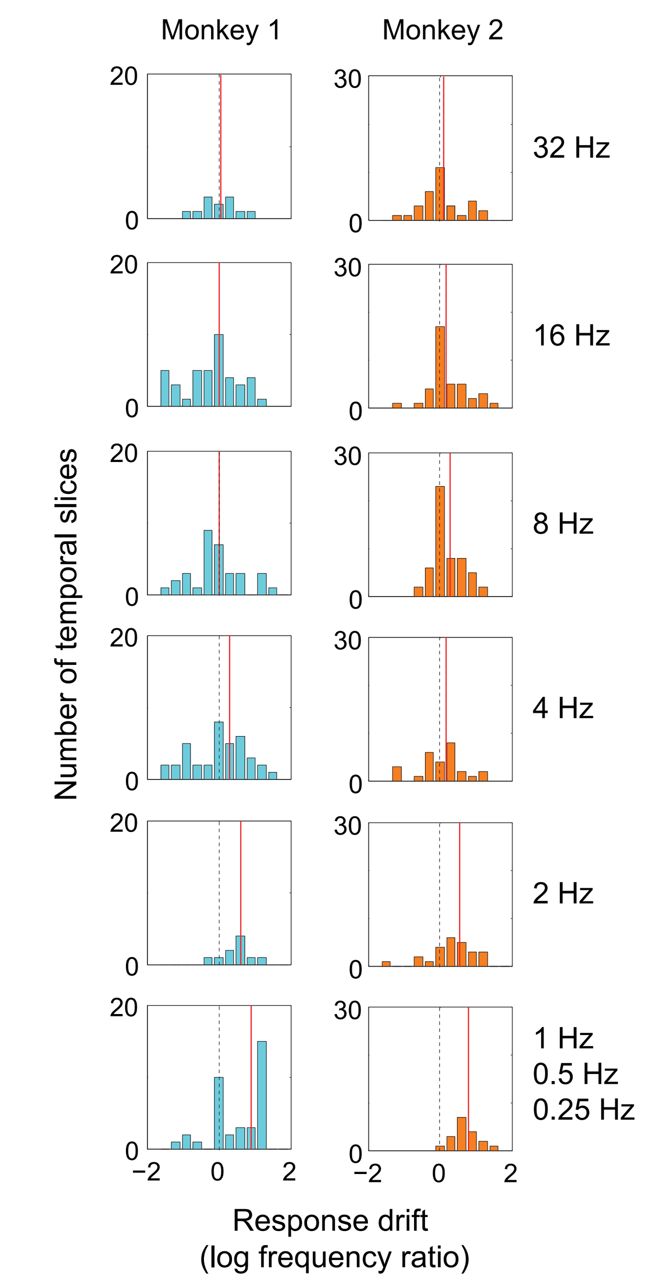
Histogram of peak SF changes at different temporal frequencies (TF).

Dotted vertical line: zero drift.

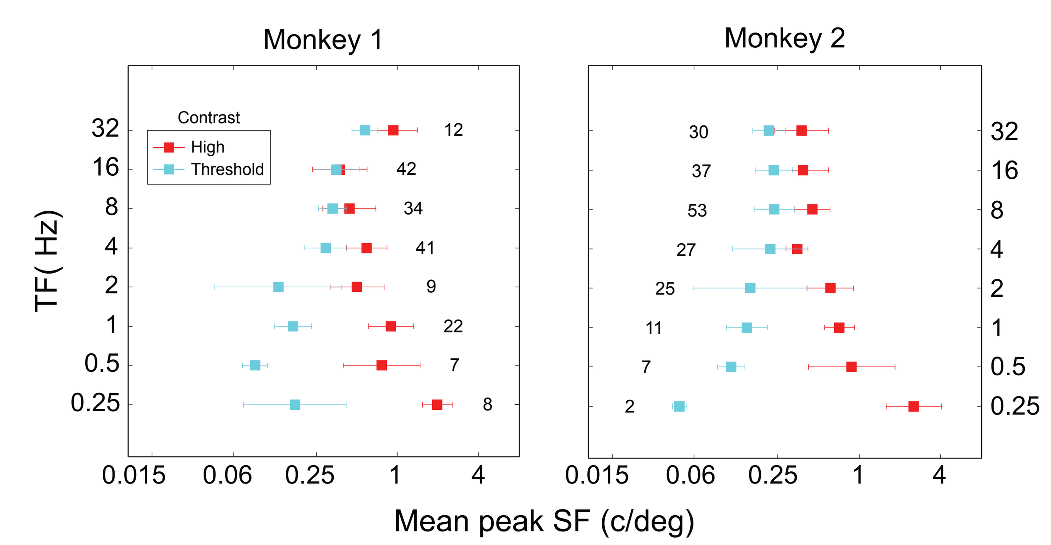
Red vertical line: median of the drift distribution.

As TF increases, the medians move to the left (indicated by the red lines getting closer to the dotted lines).

These data show that in both monkeys, response drifts are higher at low TFs and get progressively lower as TF increases.



Comparison of SF tuning at threshold (blue) and high (red) contrasts for two monkeys.

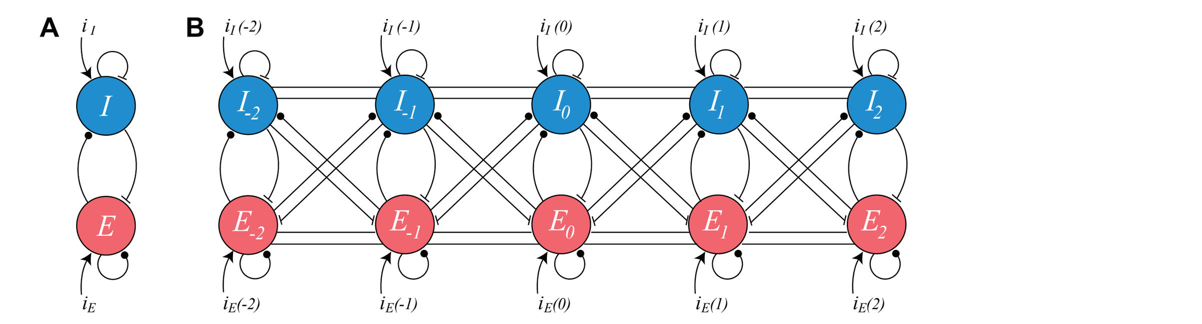


Each point above represents the mean and standard deviation of peak SF.

At threshold contrast, SF tuning increases with TF. And at high contrast, SF tuning decreases with TF.

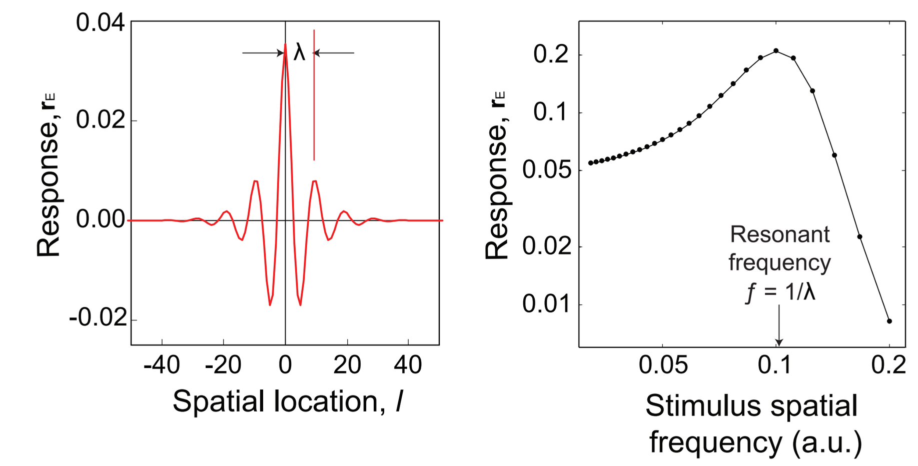
The numerals inside the panels indicate the number of samples at each TF.

Model



A canonical inhibition-stabilized motif (A) is repeated with nearest-nighbor coupling (B). Each node contains excitatory and inhibitory cells wth reciprocal and recurrent connections.

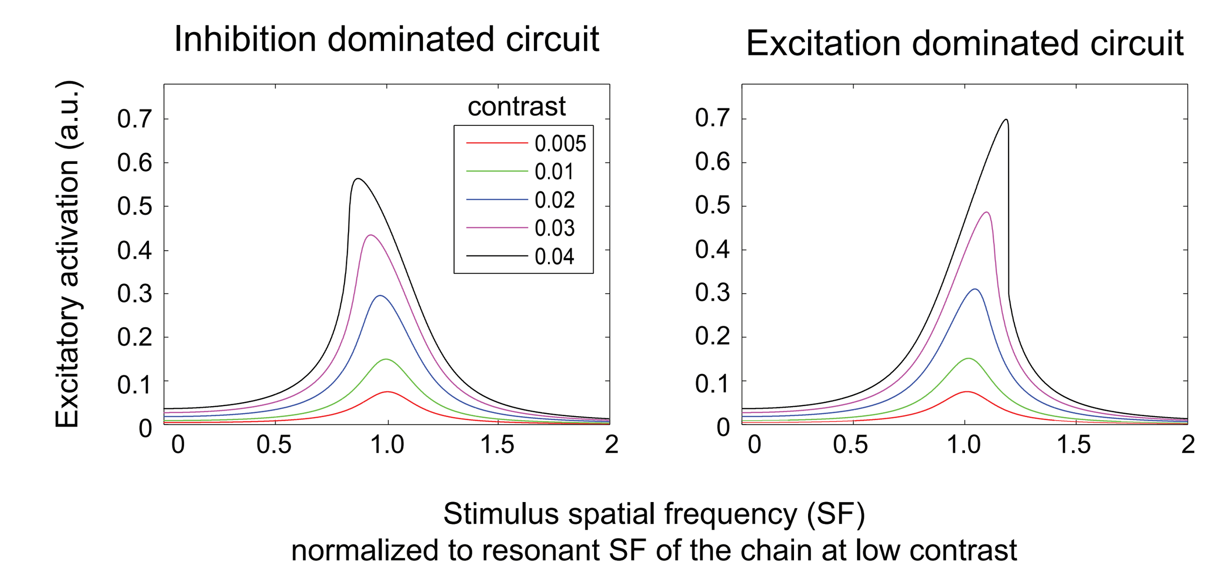
Simulation results



LEFT: Network response to a low-contrast stimulus applied to a single node of the chain. It generates a neural wave that has the shape of damped oscillation.

The periodic response reflects the magnitudes of weights that provide network stabilization.

The wavelength of oscillations generated by the chain is its resonant (intrinsic) wavelength. In the linear regime, properties of such spatial oscillations help to predict system response to complex stimuli. The waveform generated by a complex stimulus is predicted by linear interference of the waves generated on multiple nodes of the chain. The panel at right contains one example of such neural wave interference produced by a periodic stimulus (Gabor patch) at different spatial frequencies.



The curves above are solutions of the differential equations describing the model of the distributed inhibition-stabilized circuit. Each curve represents activation of one excitatory cell at one stimulus contrast, plotted as a function of stimulus spatial frequency.

Here, stimulus spatial frequency is normalized to the resonant spatial frequency of the network measured at the lowest tested contrast (red curves).

In general, increasing stimulus contrast reveals different magnitudes of the resonant spatial frequency: increasing resonant frequency in a system dominated by excitation; decreasing resonant frequency in a system dominated by inhibition.

Conclusions

Tuning of MT neurons shifts with contrast toward high spatial frequencies. The shift is smaller at high temporal frequencies.

A canonical model of distributed inhibition-stabilized circuit predicts such drift of frequency tuning. The model suggests that neuronal tuning depends on the balance of excitation and inhibition in the circuit.

These results offer a mechanistic account of the interaction between spatial frequency selectivity of cortical circuits and stimulus contrast.