# Theory and physiology of spatial frequency tuning in cortical area MT

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## Background

One of the key questions in neuroscience concerns the mechanisms by which sensory systems acquire selectivity for sensory stimuli. This question has been addressed most extensively for the visual modality but even there the question remains 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?

As mentioned, sensory neurons in cerebral cortex are characterized by their selectivity to spatiotemporal frequency of 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 spatiotemporal frequency is influenced by stimulus luminance contrast.

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

## Conclusions

Tuning of neurons in cortical area MT shifts with contrast, more often toward high spatial frequencies. The shift is significantly reduced at high temporal frequencies.

A distributed model of canonical inhibition-stabilized circuit predicts such behavior 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 frequency selectivity and stimulus contrast in cortical circuits.

## References


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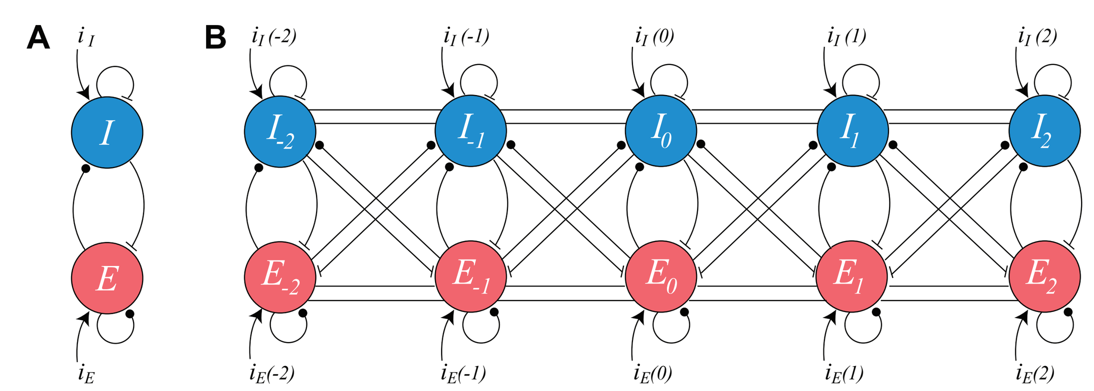
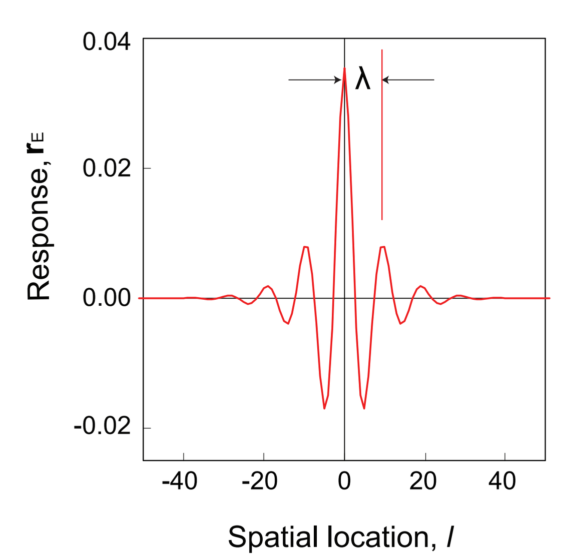
## Model

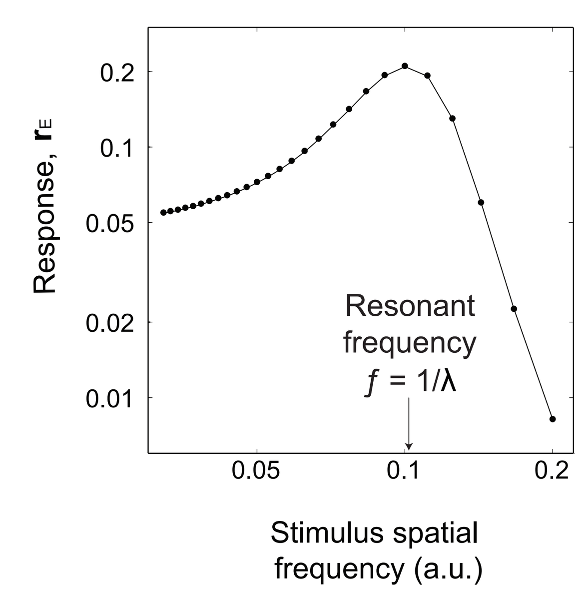


A canonical inhibition-stabilized motif (A) is repeated with nearest-nighbor coupling (B). Each node contains excitatory and inhibitory cells wth reciprocal and recurrent connections.

### Circuit response to point stimulus



### Circuit response to Gabor stimulus

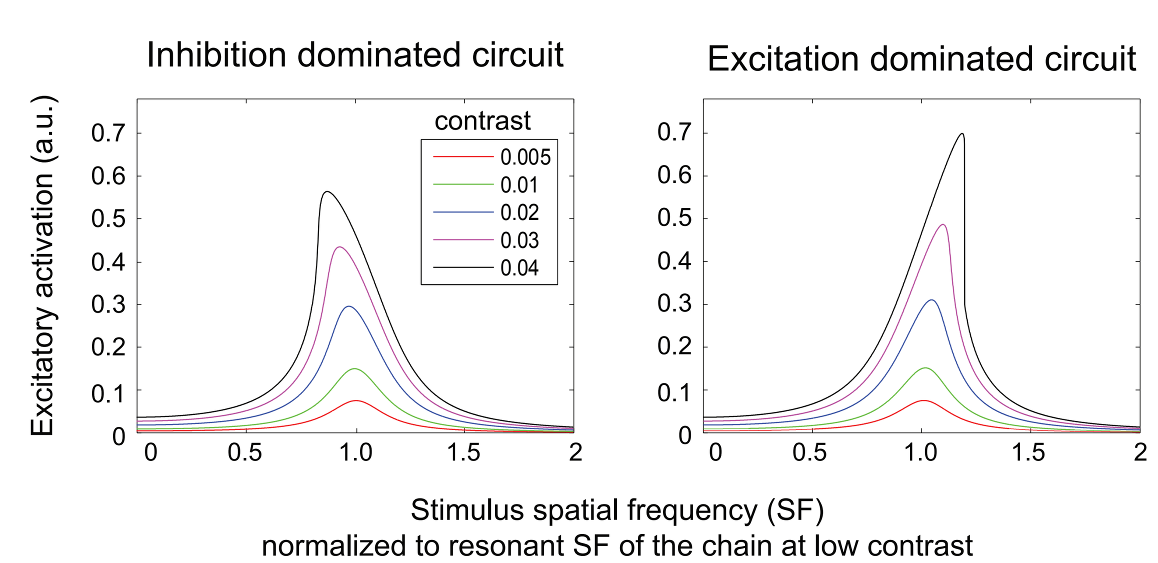


LEFT: Network response to a low-contrast stimulus applied to a single node of the chain. It generates a neural wave that has the shape of damped oscillation.

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.

RIGHT: One example of such neural wave interference produced by a periodic stimulus (Gabor patch) at different spatial frequencies.

### Circuit response to Gabor stimulus of increasing contrast



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.

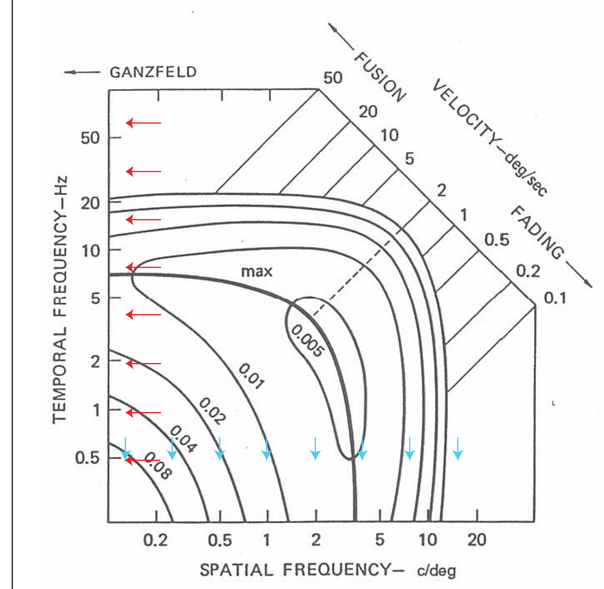
## Experiments

### 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 139 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.



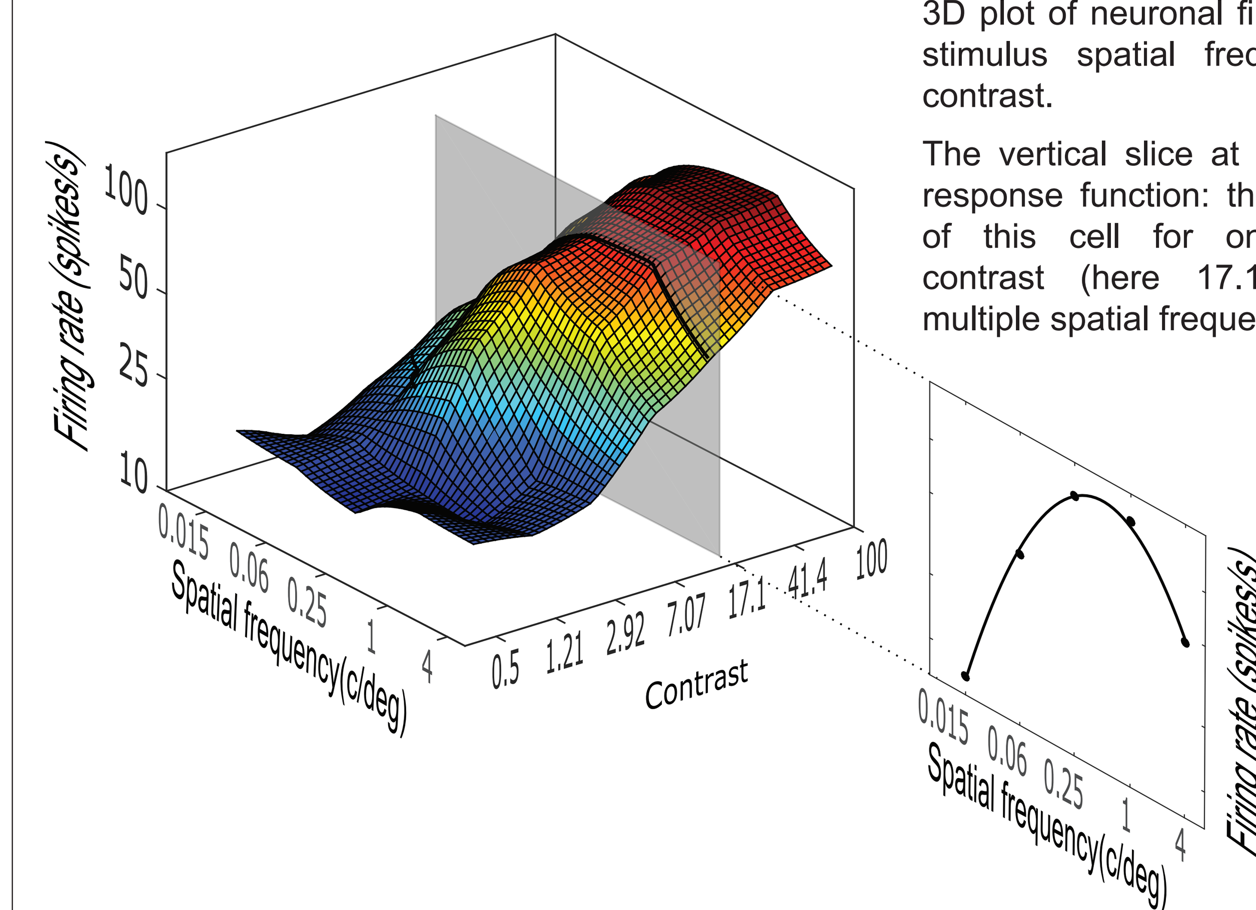
Human contrast sensitivity for all visible SF and TF derived by Kelly (1979).

Neural responses measured at:

- 5 SFs (0.015 to 16 cycles/degree).
- 1-3 TFs (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. The tested SFs and TFs are marked by blue and red arrows.

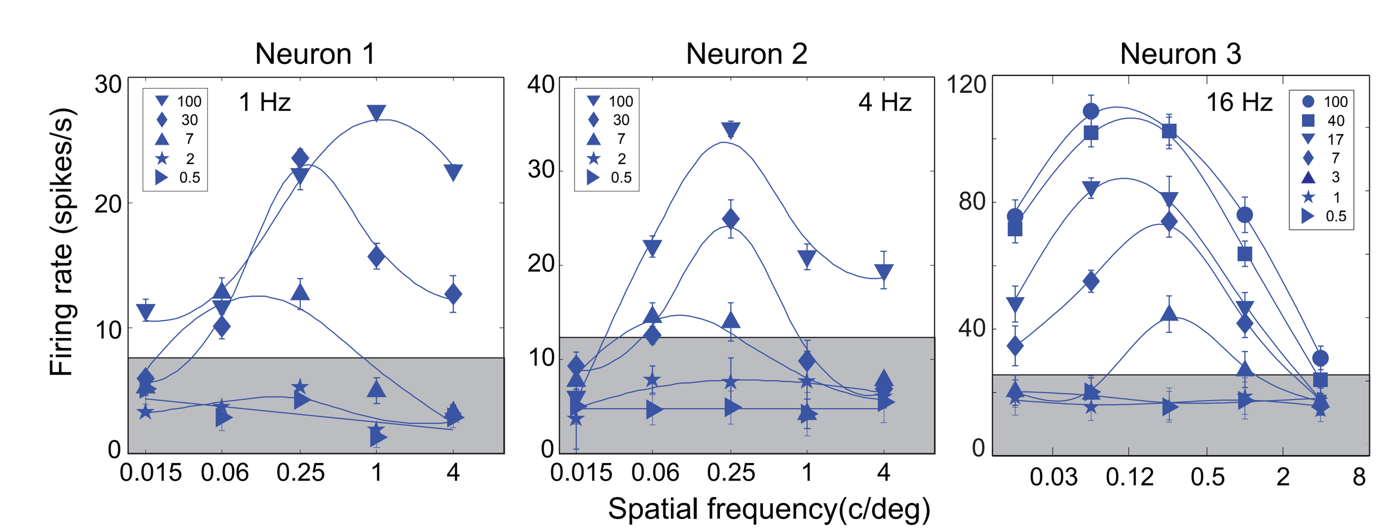
### Neuronal response surface



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

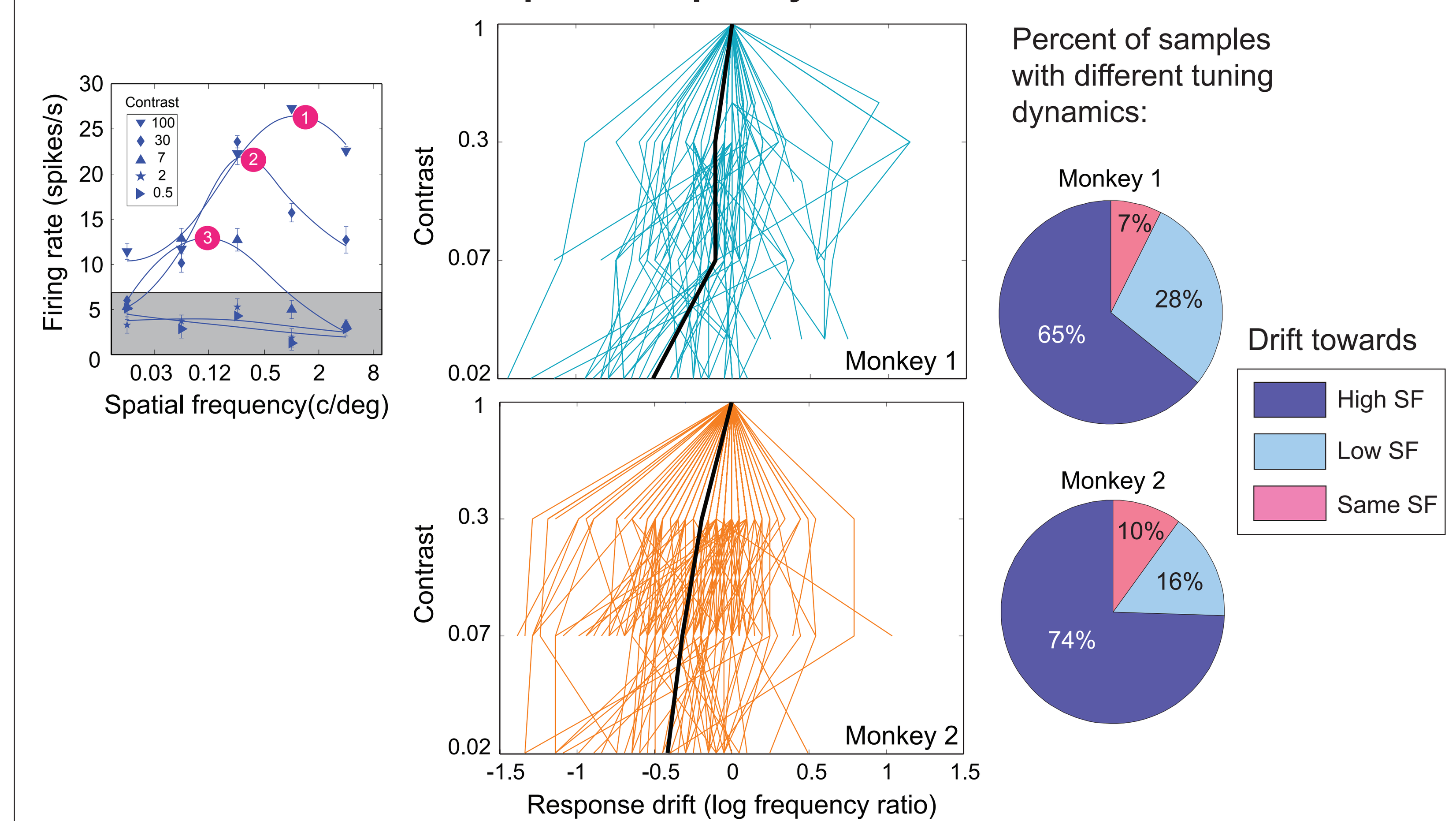
The vertical slice at RIGHT is a response function: the firing rate of this cell for one stimulus contrast (here 17.1%) across multiple spatial frequencies.

### Spatial frequency tuning across contrasts



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), strong drift of peak response toward low SF (RIGHT). Each panel contains data from a different neuron, measured at different TFs (as marked).

### Drift of spatial frequency across contrast

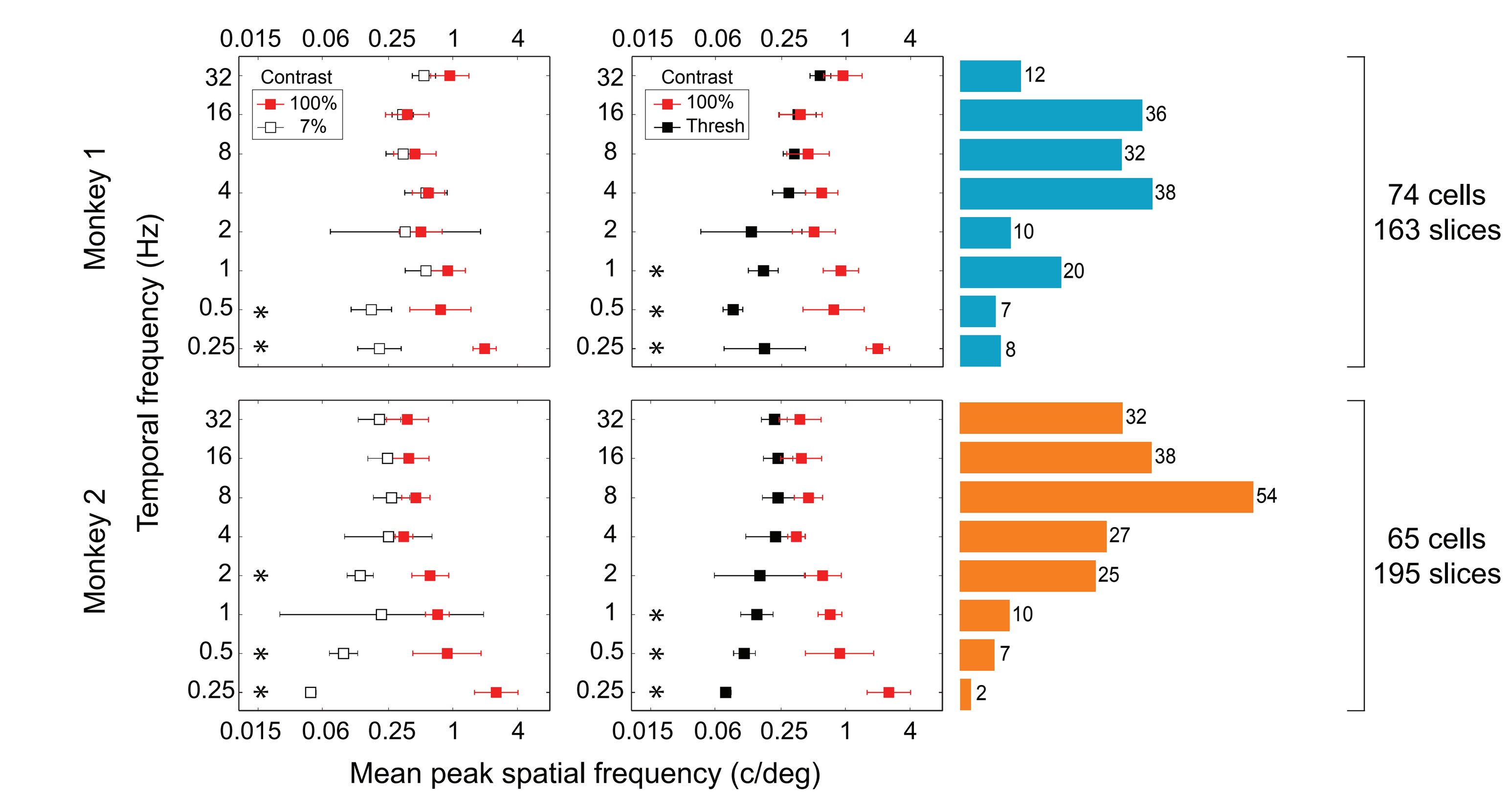


Response drift: Decimal log ratio of peak SF at low contrasts to peak SF at the highest contrast.

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

Pie charts at RIGHT: Most samples shift toward high SF.

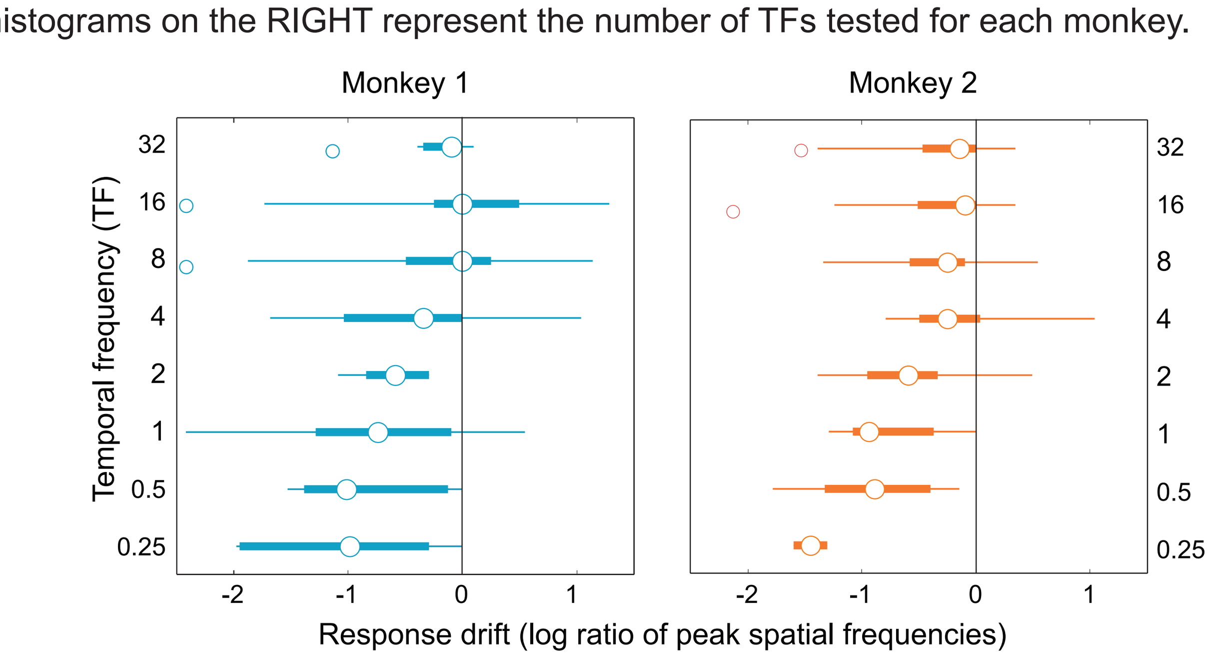
### Spatial frequency tuning depends on temporal frequency



Data points and error bars above represent the means and standard deviations of peak SF.

At low contrasts: 7% (open black squares) and threshold contrast (filled black squares), SF tuning increases with TF. At high contrast (red squares), SF tuning decreases with TF.

The histograms on the RIGHT represent the number of TFs tested for each monkey.



The boxplots above summarize the shift of peak response for all temporal frequencies in both monkeys.