Tuned inhibition accounts for adaptation-induced tuning shifts in macaque V1 and V2

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Introduction and Motivation

The visual system utilizes inputs from the recent past to adjust its representations of the sensory world. This ubiquitous property of sensory systems - adaptation - influences neural response characteristics including gain, stimulus preference, and degree of selectivity. To identify the adaptation-induced alterations in tuning properties, we measured and modeled the effects of adaptation on excitatory and inhibitory neurons in V1 and V2 of the primate visual cortex.

Methods

We performed multi-tetrode single-unit recordings to measure neural responses to drifting sinusoidal gratings before and after 0.4 sec and 40 sec adaptation to preferred and non-preferred stimuli.

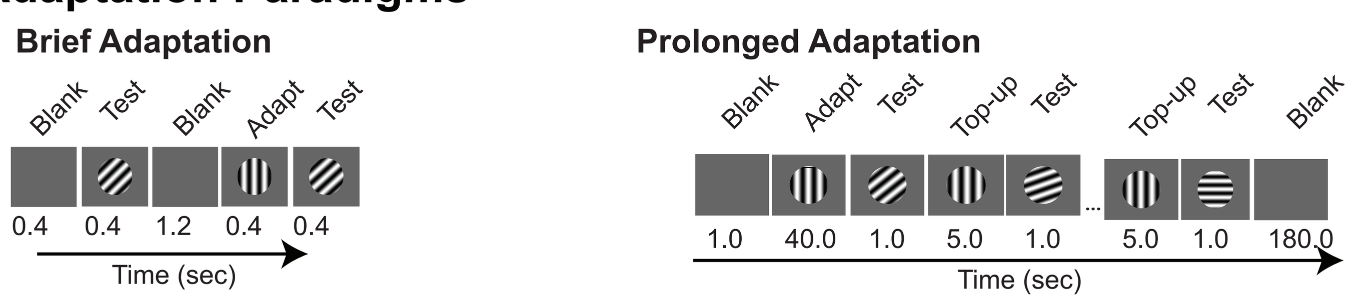
Physiological methods

Macaque V1 and V2
Anesthesia: sufentanil and propofol
Neuromuscular blockade: rocuronium

Recordings

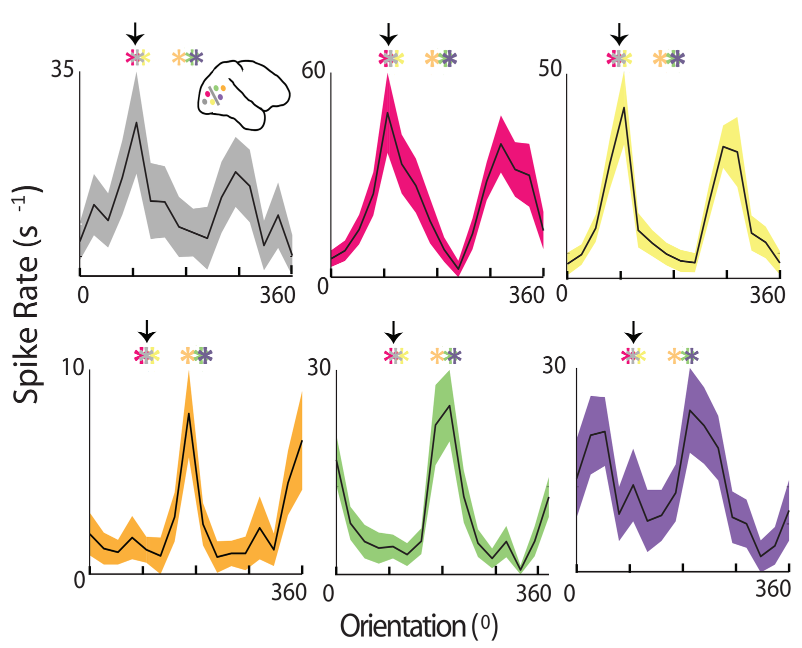
6-tetrode array, each independently movable
Spike sorting (KlustaKwik and Klusters)
Lesions and histology - post experiment

Adaptation Paradigms



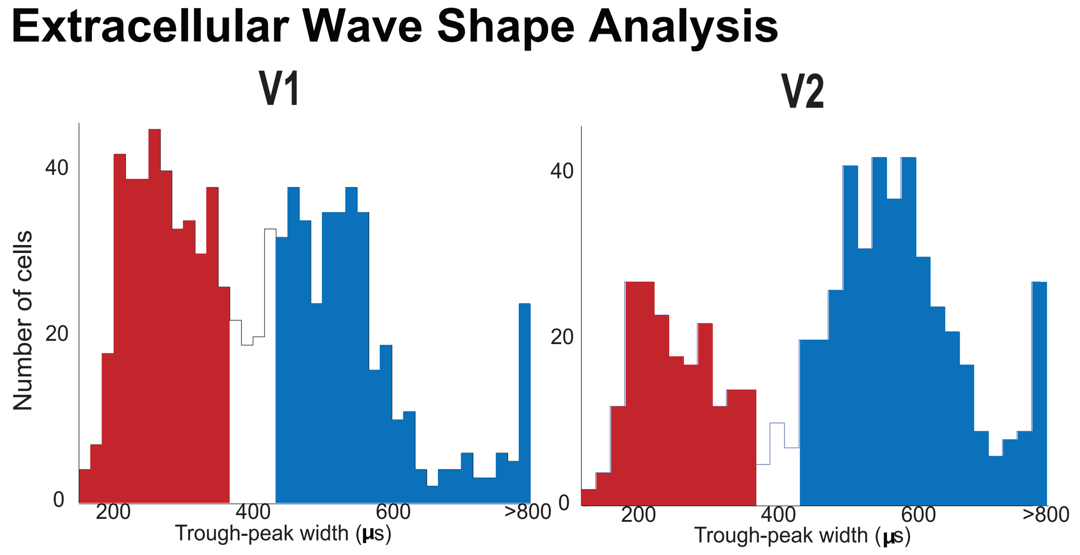
For each recording site, two adaptation experiments are performed: brief adaptation (0.4 sec) and prolonged adaptation (40 sec). These paradigms are known to demonstrate adaptation-induced effects in V1 (Patterson et al, 2013).

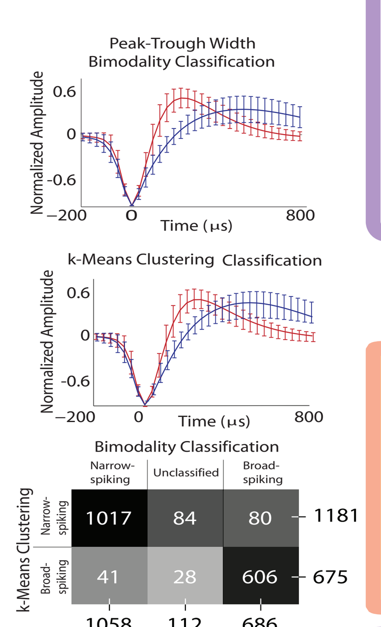
Selection of Adaptation Parameters



Based on the tuning of the multiunit activity measured at 6 tetrodes, the adapting orientations are chosen. In this example, neural activity at 3 of 6 tetrodes have peaks within 22.5 deg of a common direction. Here 90 deg (arrow) is chosen to be the adapting orientation - it targets 3 of 6 tetrodes (grey, magenta, yellow) at the preferred orientation and the rest at a non-preferred orientation. Stimuli are presented at the spatial frequency that is optimal for at least one tetrode.

Extracellular Wave Shape Analysis





Based on the bimodality in the distribution of trough to peak widths in the lab database ($p < 0.01$ by the Hartigan dip test), we classified extracellular waveforms as narrow-spiking (<405μs) putative inhibitory interneurons and broad-spiking (>430μs) putative excitatory neurons (consistent with Mitchell et al., 2007). Neurons within 10% of the notch were labeled unclassified and not used in further analyses.

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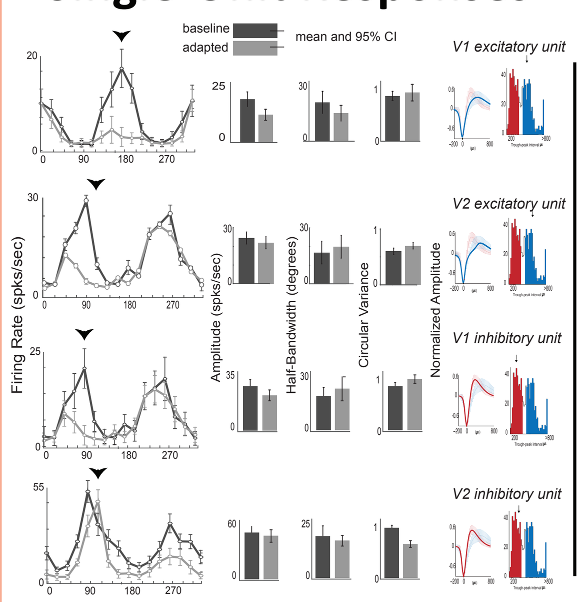
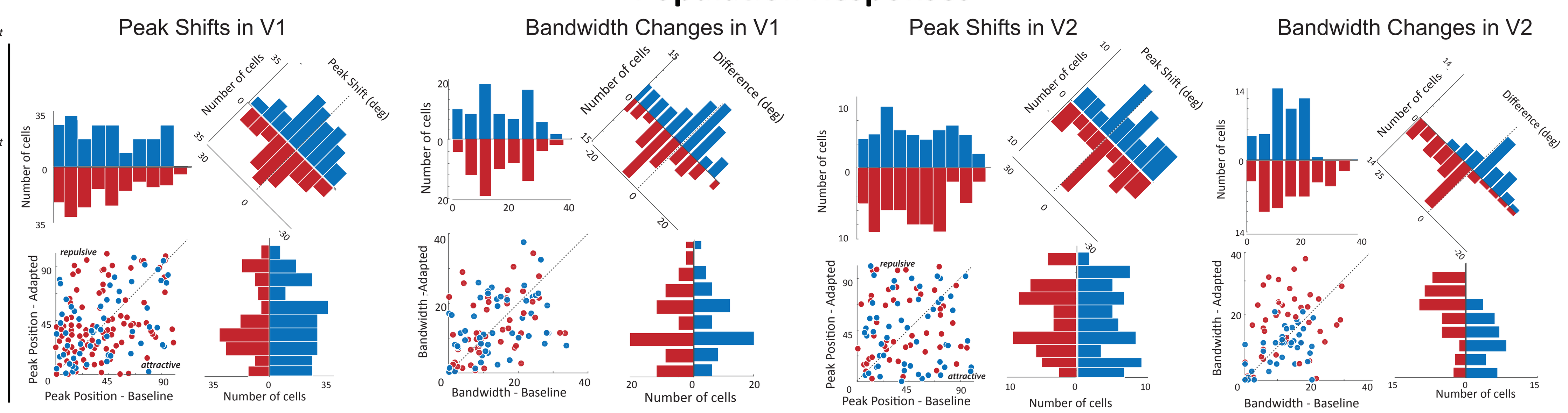
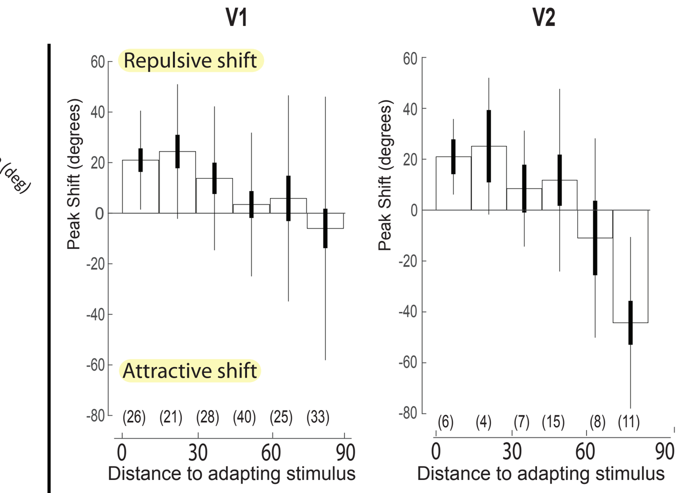
Single-Unit Responses

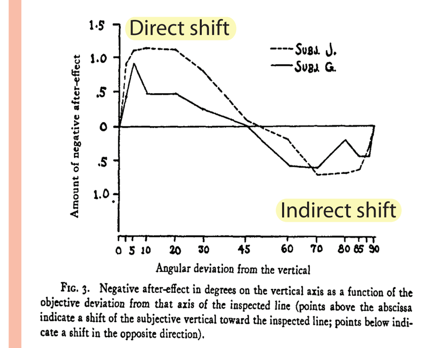


Population Responses



Relationship to Perception



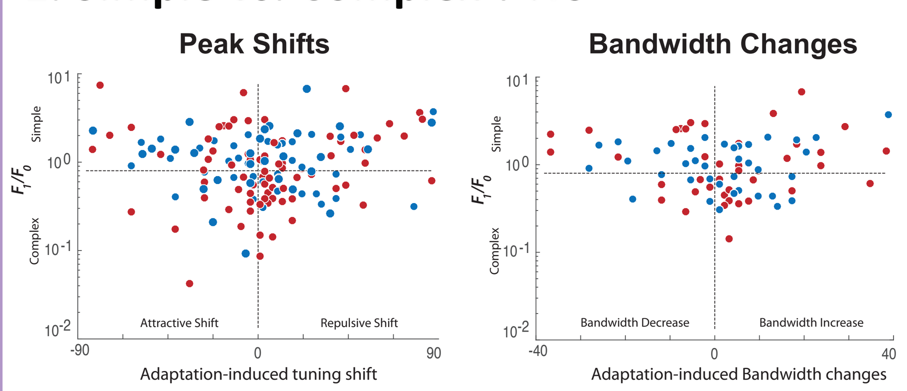


(Gibson, J. J., & Radner, M. (1937). Adaptation, after-effect and contrast in the perception of tilted lines. I. Quantitative studies. Journal of Experimental Psychology, 20(5), 453.)

Repulsive tuning shifts dominate when the adapting stimulus is <45 deg and attractive shifts dominate when the adapter is 70-90 deg away. These effects likely correspond to the "direct" and "indirect effect" previously reported in psychophysical studies to orthogonal adapters.

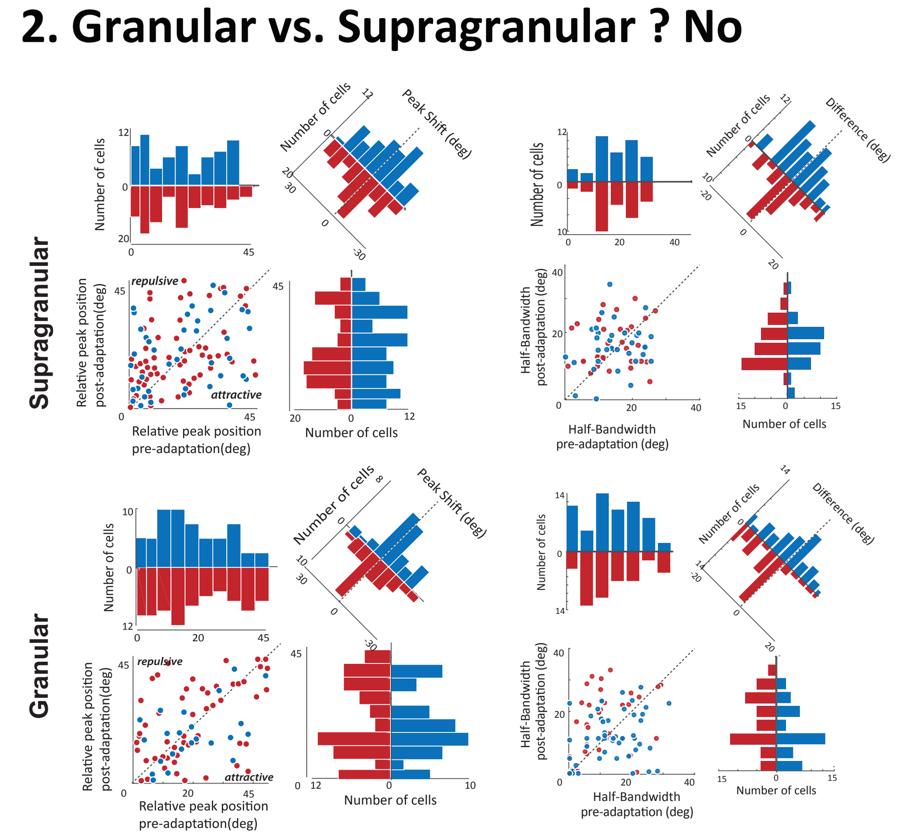
What accounts for the diversity of adaptation effects in V1?

1. Simple vs. Complex ? No



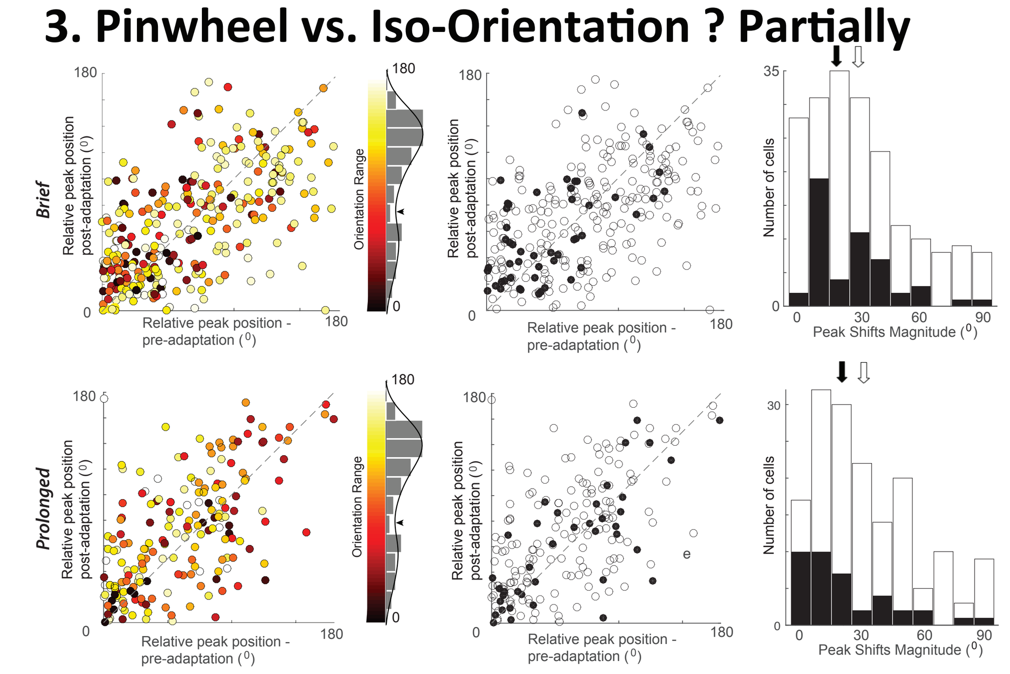
- The simple/complex distinction did not appear to account for the diversity of adaptation-induced tuning shifts and bandwidth changes.

2. Granular vs. Supragranular ? No



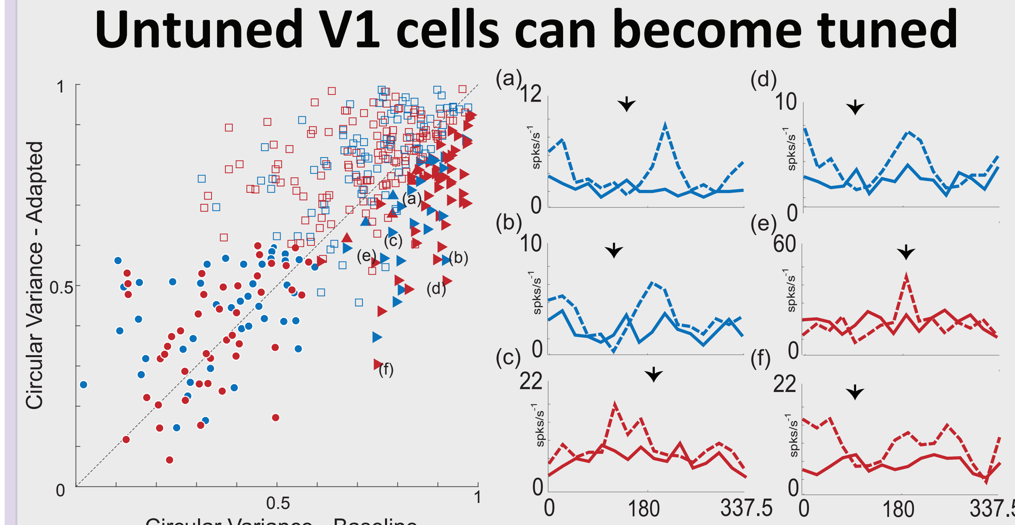
- The laminar position did not account for the diversity of adaptation effects to the orientation tuning. However there was a suggestion that, in layer 4, adaptation predominantly increases tuning bandwidth of I cells, and not E cells.

3. Pinwheel vs. Iso-Orientation ? Partially



- Cells in putative pinwheel centers (median : open arrow) revealed larger tuning shifts than cells in putative iso-orientation domains (median - filled arrow) (Wilcoxon rank sum $p<0.05$).

Untuned V1 cells can become tuned



- About 19% of untuned cells became tuned after adaptation. These cells (indicated by triangles) had a circular variance that were not significantly different from randomness under baseline conditions but showed significant tuning after adaptation. This phenomenon was present in both excitatory (blue) and inhibitory (red) cells.

Summary and Conclusions

- At the individual neuronal level, brief and prolonged adaptation induced a striking diversity of adaptation-induced effects in both excitatory and inhibitory celltypes in V1 and V2 in the form of gain changes, bandwidth changes, selectivity changes, and tuning shifts.
- At the population level, repulsive shifts predominated when the adapting stimuli are within 45 degrees of the preferred orientation, and attractive tuning shifts pre dominated when the adapters are 75-90 degrees away, with larger effects in V2, than in V1. This likely corresponds to the "direct" and "indirect" aftereffects observed in the classical psychophysical study of Gibson and Radner (1937).

- Diversity of adaptation-induced effects did not appear to be related to the excitatory vs inhibitory division, or to the simple vs complex distinction, or to the laminar location.
- Location on the orientation map appeared to contribute to the nature of adaptation-induced tuning shifts: cells in pinwheel centers demonstrated larger tuning shifts than in those located in iso-orientation domains.
- Adaptation induced tuning in a subset of V1 neurons that were untuned under baseline conditions.

- Only models with pre-synaptic adaptation and tuned inhibtion could account for the attractive shifts that are widespread in the data.
- Parameters within the physiological range accounted for the diversity of adaptation-induced tuning effects.

Models

Common to all Models

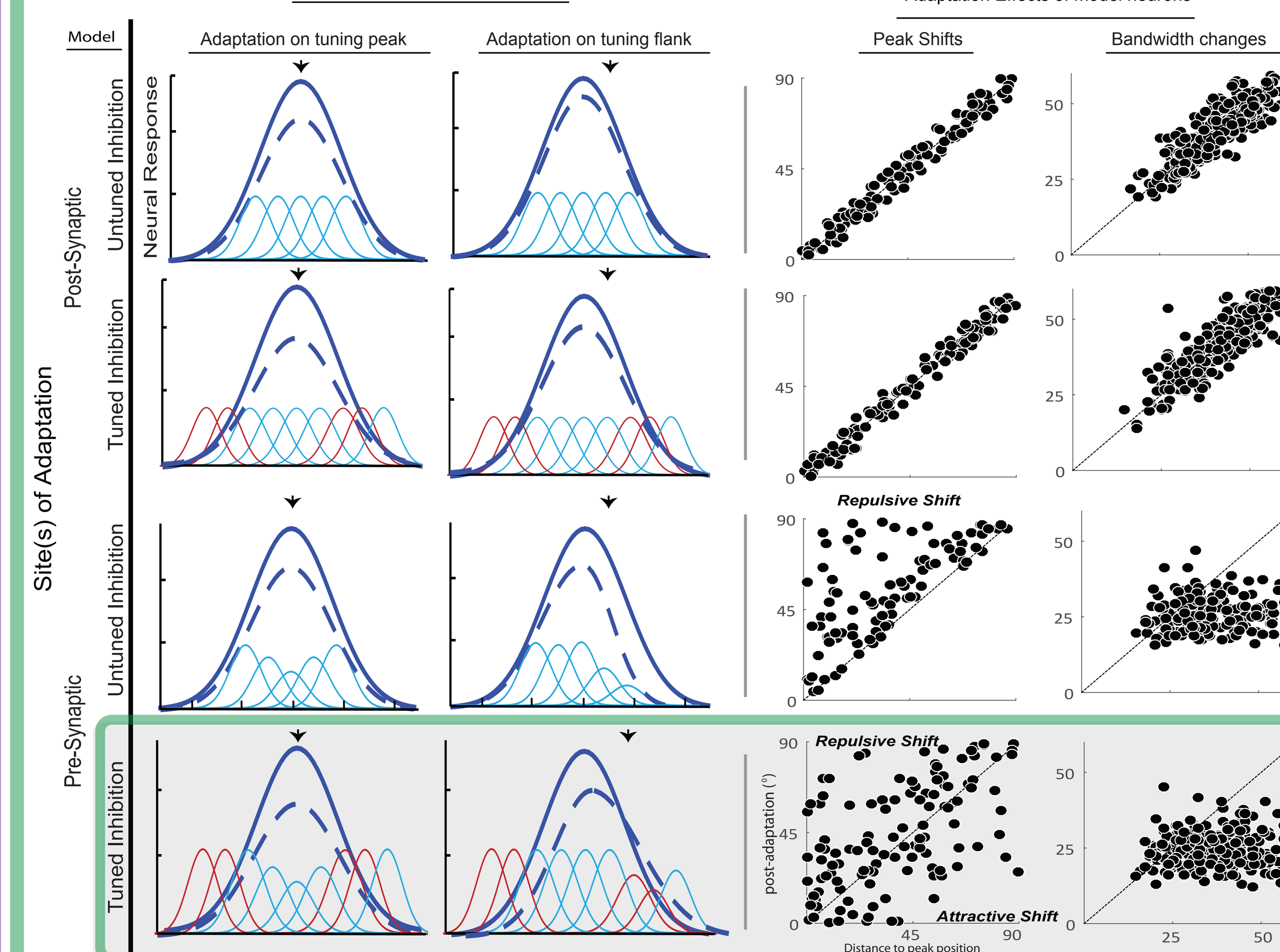
- Feedforward architecture
- Tuning fucntion parameters drawn from our neural data
- Output neuron activity modeled as Poisson spike trains
- 80% excitatory neurons 20% inhibitory neurons
- Input neuron orientation tuning modeled with von Mises functions

Distinguishing features of Models

- Tuned vs. Untuned inhibition
- Post-synaptic vs. Pre-synaptic adaptation

Adaptation Rules

- Post-synaptic adaptation influences connection strengths inputs by a common factor, determined by post-synaptic neuron
- Pre-synaptic adaptation influences connection strengths proportionally to the pre-synaptic unadapted response



Input Neuron (von Mises function)

$$R_{input}(\varphi_{stim}, j) = B_j + M_j e^{\beta_j \cos(2(\varphi_{stim} - \mu_j)) - 1)}$$

Connectivity

$$P_E(j,k) = \frac{1}{K} e^{-(\mu_j - \mu_k)^2/2\sigma^2} \quad \textit{excitatory}$$

$$P_{I_{tuned}}(j,k) = \frac{1}{K}\left(e^{-(\mu_j-(\mu_k-\sigma/2))^2/2\sigma^2} + e^{-(\mu_j-(\mu_k+\sigma/2))^2/2\sigma^2}\right) \quad \textit{tuned inhibitory}$$

$$P_{I_{untuned}}(j,k) = constant \quad \textit{untuned inhibitory}$$

Adaptation Factor

$$f(\varphi_{adapt}, j) = 1 - \alpha\left(\frac{R(\varphi_{adapt}, j) - R_{min}(j)}{R_{max}(j) - R_{min}(j)}\right)$$

$$R_{min}(j) = \min_{\varphi}(R(\varphi_{stim}, j))$$

$$R_{max}(j) = \max_{\varphi}(R(\varphi_{stim}, j))$$

Output Neuron

$$R_{output}(\varphi_{stim}, k) = \sum_{j \in input} C(j,k) A(j,k) R_{input}(\varphi_{stim}, j)$$

$C(j,k) = 1$ *with probability* $P(j,k)$ *and* 0 *otherwise*

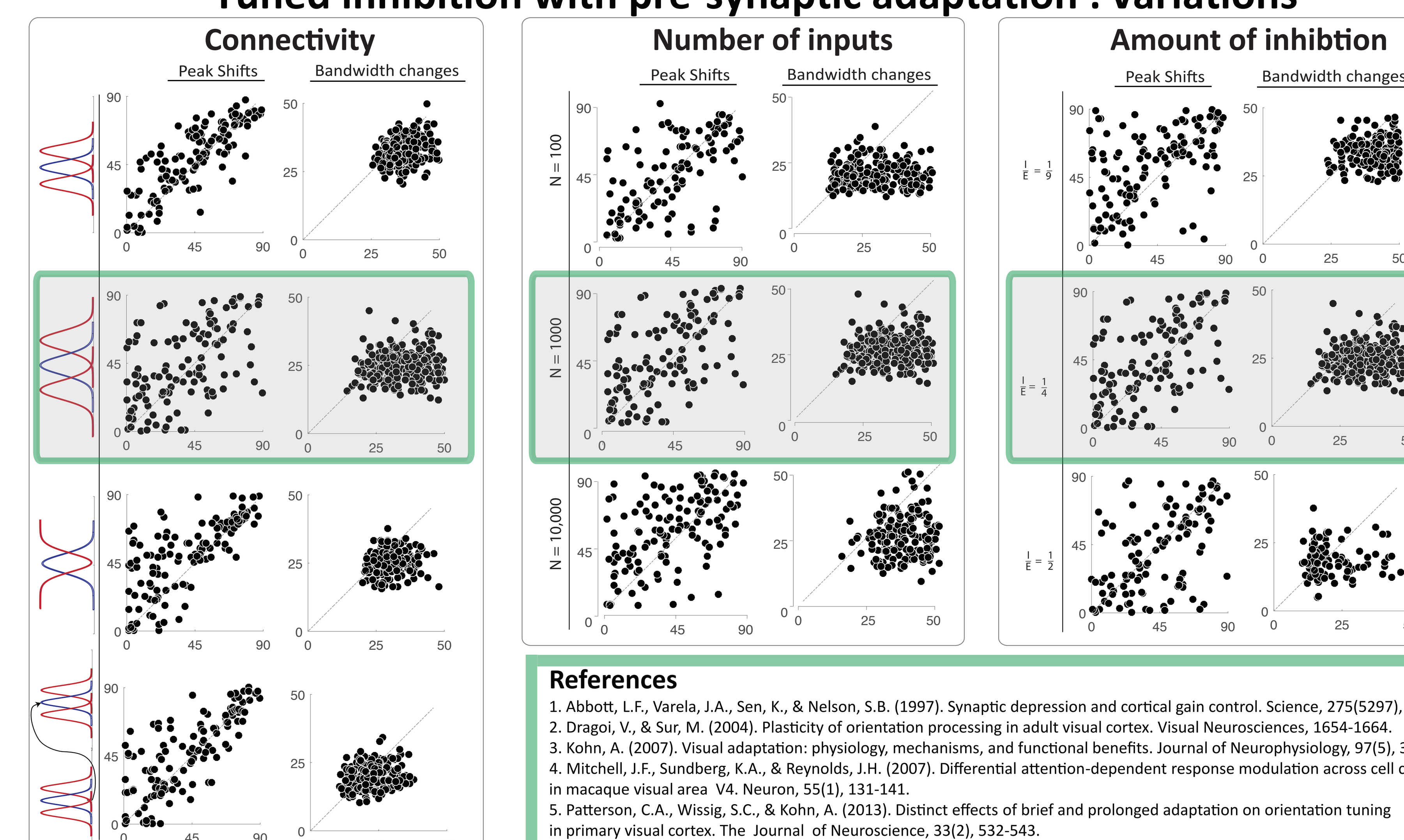
$A(j,k) = 1$ *before adaptation*

$A(j,k) = f(\varphi_{adapt}, j)$ *for pre-synaptic adaptation*

$A(j,k) = f(\varphi_{adapt}, k)$ *for pre-synaptic adaptation*

	Symbol	Mean	25th percentile	50th percentile	75th percentile
Excitatory Input Neurons					
Half-Bandwidth (deg)	n/a	26.3	20.5	24.5	50.2
Concentration	β_j	1.9	2.6	2.4	0.5
Amplitude (s^{-1})	M_j	11.5	6.2	8.2	29.2
Baseline Firing Rate (s^{-1})	B_j	9.5	3.2	9.5	12.2
Inhibitory Input Neurons					
Half-Bandwidth (deg)	n/a	32.3	18.6	35.5	60.2
Concentration	β_j	1.1	2.8	0.8	0.2
Amplitude (s^{-1})	M_j	12.2	8.4	14.2	35.8
Baseline Firing Rate (s^{-1})	B_j	12.4	7.6	8.5	12.5

Tuned inhibition with pre-synaptic adaptation : variations



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