

Specific Aims - *Deciphering the mechanisms of spatial vision and their perceptual consequences*

The goal of this project is to characterize spatial processing in the early visual system, and to relate it to the visual performance of trained observers. Neurons in visual cortex represent the spatial structure of the visual environment. These representations change systematically throughout the visual hierarchy because of a cascade of transformations which begin simply with the retinal image. In nature, the contrast and the complexity of spatial frequency content in images vary considerably. Specifically, we and others have shown that lowering the contrast (Sceniak et al, 2002) and broadening the frequency distribution of images reduces the preferred spatial frequency of visual neurons; others have shown that human observers overestimate the spatial frequency of sinusoidal gratings when image contrast is reduced (Georgeson, 1985). We propose to develop a mechanistic account of the way that contrast and frequency dispersion alter tuning, and to relate that account to perception.

Aim #1: Uncover the mechanisms of contrast dependent changes in spatial tuning

Neurons in primary visual cortex (V1) – unlike their inputs from lateral geniculate nucleus (LGN) – are often orientation selective and narrowly tuned for spatial frequency. It is unknown whether the contrast dependence of neuronal responses in V1 is inherited from the LGN, or whether intracortical computations like normalization and surround modulation are the driving force. By recording activity in the LGN and V1 to a common battery of stimuli - including the family of spectrally dispersed, superimposed gratings used in our prior experiments, a similar family of stimuli whose orientation content is dispersed (Goris et al, 2015), and stimuli designed to measure the strength of normalization and surround modulation - we will quantify the impact of each of these mechanisms on the overall tuning and tuning shifts we have observed in V1. Our hypothesis is that the shifts in tuning properties are both present in the thalamus and dependent on thalamic computation, but are enhanced by the normalization and surround modulation mechanisms present in the cortex.

Aim #2: Characterize and model the perception of spectrally diverse stimuli

The effect of contrast on perceived spatial frequency is known for single sinusoidal gratings but not for spectrally complex images. We will collect psychophysical data from humans in a task designed to determine the effect of changes in contrast and spectral complexity on perceptual biases and detection thresholds. In one experiment, subjects will have to judge the spatial frequency of a test stimulus relative to a reference stimulus as we adjust the variables of interest. In a related experiment, subjects will have to detect the presence or absence of a stimulus as we again adjust contrast and spectral complexity. Our physiological results - which showed increased tuning shifts with increasing spectral dispersion - suggest that the contrast dependent shifts in perceived spatial frequency for single gratings should be enhanced for the spectrally complex images. On the other hand, recent Bayesian frameworks for understanding perception under different levels of certainty suggest that the contrast dependent bias in spatial frequency perception should be reduced or even reversed with increased stimulus uncertainty. Contrast and spectral complexity give us two independent ways to manipulate uncertainty, and the experimental richness to carefully fit models of perceptual choice which incorporate our physiological findings as well as ideas in Bayesian frameworks for perception.

The expected outcomes of our work are an illumination of the finer details of cascaded computation and a broadening of our understanding of how the activity of sensory neurons drives behavior. Both of these outcomes hinge on our appreciation for the *cascaded* nature of sensory processing. The contrast dependent changes in spatial processing - a selectivity which is shaped throughout the visual hierarchy - provide a window onto mechanisms like surround modulation, normalization, and linear filtering. By relating this physiological phenomenon to behavior, we can gain novel insight into how sensory neural activity is used by downstream circuits to support perception.

APPROACH

Significance and Innovation

Perception is necessarily constrained by the fidelity with which sensory information is encoded by populations of relevant neurons, because perceptual choices rely on a readout of this population activity. An outstanding goal of systems neuroscience is to link neural activity to perception. The field has progressed by studying the influence of single neurons on behavioral choice (Britten et al, 1992) and by relating the way in which representations of stimuli by tuned populations of neurons and the subsequent decoding of these representations define perceptual capabilities (cf. Goris et al, 2013). The latter approach entails building populating coding models which often have a much simpler tuning structure than is found physiologically (cf. Ganguli and Simoncelli, 2014). What remains to be accomplished is the construction of a rich, physiologically grounded population coding model which links the more complex reality of sensory representation to the gamut of perceptual capabilities; furthermore, the ways in which the cortical computations of encoding (e.g. normalization, surround modulation) influence perception have yet to be described within these frameworks.

Through our previous electrophysiological recordings in macaque V1 - both with single unit and laminar electrodes - and our ongoing work to fit a functional model to these neural responses, we have a complete picture of how spatial frequency tuning is altered by changes in contrast and spectral dispersion. We can thus build a population coding model of perception whose encoding front-end captures the diversity of real population responses under these stimulus manipulations. Our second aim will characterize the perception of spatial frequency under the same manipulations. We can then test the predictions of our model against the psychophysically measured perceptual thresholds and biases. Finally, our first aim will uncover the mechanisms which shape spatial frequency tuning in the early visual hierarchy. With this knowledge in hand, we can relate those mechanisms to their shaping of tuning and their perceptual consequences as seen in the perceptual model.

Our project will close the existing gap in models which link neurons to behavior. A more realistic instantiation of neural populations will put the literature on mechanisms and properties of tuning in a position of greater relevance. Equipped with a common model linking the machinery of perception, scientists interested in understanding perception - physiologists and psychophysicists, experimentalists and theorists - will be able to more directly propose joint experiments and test common hypothesis. By forming the link first in a stimulus domain (spatial frequency) whose physiological underpinnings and psychophysical measurements are tractable, the field can then more quickly advance models which link other stimulus representations to their perception.

Aim #1: Uncover the mechanisms of contrast dependent changes in spatial tuning

Introduction: Unlike orientation tuning which emerges anew in primary visual cortex (Hubel and Wiesel, 1977), spatial selectivity first arises in the retina, is modified by the LGN, and is further sculpted by cortical mechanisms. Tuning in the LGN - in both magno- and parvocellular (M&P) neurons - is low-pass for spatial frequency (Derrington and Lennie, 1984) and can be modeled by a difference-of-gaussians model which posits opponent linear center and surround mechanisms (Enroth-Cugell and Robson, 1966). On the other hand, the distribution of spatial frequency bandwidth and preference in V1 neurons is more varied, and tuning is generally much sharper than in the LGN (De Valois, Albrecht, and Thorell, 1982). The exact influence of spatial tuning in the thalamus - as opposed to intracortical mechanisms - on the properties of V1 neurons is not well understood. Most importantly, there are observed changes in spatial size tuning with contrast in both thalamus (Nolt et al, 2004; Solomon et al, 2002) and primary visual cortex (Sceniak et al, 2002; Tailby et al, 2007). The goal of this aim is to decipher and model the exact mechanistic origins and computational principles underlying these observations.

Justification and feasibility:

Review of relevant literature. Spatial frequency tuning in macaque V1 is contrast dependent: single cell tuning curves measured at lower contrast have narrower octave bandwidths and lower preferred spatial frequencies (Sceniak et al, 2002). Physiologically, Sceniak et al (1999) suggest that contrast can alter spatial summation due to lateral excitatory connections which grow stronger at low contrast, thus enhancing spatial pooling and

increasing the effective receptive field size. This proposal nicely implies a functionally useful trade-off between spatial localization and overall visual sensitivity, but it does not address the possibility of a feed-forward, thalamic origin of contrast dependent spatial summation changes. In both cat (Nolt et al, 2004) and primate (Solomon et al, 2002), reduced contrast results in a larger radius of spatial summation, implicating a feedforward component to the observed cortical tuning. A concise, physiologically-inspired model developed by Tailby et al (2007) suggests that cortical neurons can inherit the contrast dependent size tuning of realistic thalamic input. A receptive field model fit to size tuning data in primate V1 (Cavanaugh et al, 2002a) suggests that the key computation is a change in relative contribution of cortical center and surround mechanisms with contrast.

In the thalamus, two distinct suppressive mechanisms exist - one which is linear and part of the classical receptive field, and another which imbues thalamic responses with non-linear properties like contrast saturation (Derrington and Lennie, 1984) and size tuning (Solomon et al, 2002). The two mechanisms have a similar spatial extent and are untuned for orientation, but the extra-classical suppressive field is more broadly tuned for spatial frequency and, unlike the linear surround, is sensitive to stimulus energy rather than intensity (Bonin et al, 2005). This extra-classical suppression likely arises via feedforward input from the retina and intrathalamic processing (Bonin et al, 2005; Solomon et al, 2002). Furthermore, extra-classical suppression has been shown to give rise to the contrast dependent size tuning observed in the thalamus (Solomon et al, 2002), attaching a mechanism to the thalamically observed and modeled contrast dependent size tuning. Surround suppression in cortex, on the other hand, is tuned for orientation and has spatial specificity in its action (Cavanaugh et al, 2002b).

Preliminary data. In our previous work, we characterized the contrast dependence of spatial frequency tuning in single cells in macaque V1 to mixtures of sinusoidal gratings with varied dispersion in spatial frequency content (*fig. 1, left*). We replicated the finding that the preferred spatial frequency as measured with single gratings is reduced as contrast is lowered. This contrast dependent shift, though, is reliably enhanced as spectral dispersion is increased (*fig. 1, right*). We believe that these stimuli offer a unique approach to probing the mechanisms which shape contrast dependent tuning in the early visual hierarchy. Preliminary efforts to fit a cascaded model of cortical computation (*fig. 2, left*) to the data are promising (*fig. 2, right*) and will hopefully clarify the contributions of linear filtering, surround suppression, and normalization in shaping tuning. As of yet, though, the model does not capture the contrast dependent changes in spatial frequency preference.

Research design: We will extend our existing characterization of spatial tuning by additionally recording neurons in LGN and by more carefully measuring the mechanisms at play in both LGN and V1. Our goal is to more carefully document changes in spatial tuning resulting from changes in contrast and spectral dispersion. Additionally, to relate these changes to specific computations and origins within the visual hierarchy, we will quantify the spatial extent, tuning properties, and relative strength of the mechanisms which shape spatial tuning. Finally, we will improve upon our existing model of cortical computation by incorporating our newly refined understanding of suppressive effects and the cascaded shaping of spatial tuning; by fitting this model to data, we can better understand the computations which support the processing of spatial information in the early visual system.

As in our preliminary experiments, we will extracellularly record the spiking activity of individual cells in anesthetized macaque monkeys with single unit electrodes while presenting carefully controlled stimuli on a CRT monitor. The setup and monitoring of these experiments will be consistent with our lab's typical protocol (e.g. Cavanaugh et al, 2002a). The precise laminar organization, monocularly, and functional properties of thalamic neurons will allow us to readily characterize recorded LGN cells as being magnocellular or parvocellular based on any number response properties (Wiesel and Hubel, 1958). We will determine the basic tuning properties of the cell using drifting gratings (cf. Solomon et al, 2002). We will measure the spatial extent of the linear receptive field and the suppressive surround, respectively, by determining the inner diameter at which responses to a contrast-modulated, uniform annulus or the diameter of a drifting grating plateau (Bonin et al, 2005). By quantifying the drop-off in response to the above stimuli as the size goes from optimal to too large, we can also quantify the strength of the linear and extra-classical suppressive effects (Alitto and Usrey, 2008). Most importantly, we will present the same spectrally dispersed stimuli used in our

preliminary experiments, again at different total contrasts and different levels of dispersion. Similar to a previous experiment in the lab (Goris et al, 2015), we will also present a family of stimuli with different dispersions of orientation content. The parameters of the dispersed stimulus families (e.g. temporal frequency, size) will be chosen to match each cell's optimal tuning parameters. We intend to repeat the extent and strength characterizations at different contrasts - at minimum, the two contrasts corresponding to those used with the spectrally dispersed stimuli.

Recordings in primary visual cortex will largely mirror those in the LGN. This is, of course, by design - we aim to directly compare the influences of contrast, spectral dispersion, and spatial extent on overall tuning and particular mechanisms in the two brain areas. One primary difference between the thalamic and cortical recordings will be our approach to characterizing the extent and properties of the center and surround mechanisms. After Cavanaugh et al (2002a), we will use drifting gratings presented as both annuli and as expanding disks to characterize the spatial extent of these mechanisms. The size at which response to the disk peaks is considered the extent of the regime where excitatory contributions dominate (grating response field, GRF). The size at which the response to the disk plateaus is the diameter of the surround. The overall extent of the classical receptive field is taken to be the maximum of GRF and the largest inner diameter of the annulus which still elicits a response above baseline. With these measurements in hand, we can then characterize the tuning properties of the surround by simultaneously presenting stimuli within the GRF and outside of the classical receptive field extent and varying their contrast, orientation, and spatial frequency (Cavanaugh et al, 2002b).

Analysis and model fitting. Each part of the large battery of experiments described above serves a meaningful purpose in our analysis and interpretation of the data. For each cell, we will have a relatively complete picture of its tuning for spatial frequency, orientation, contrast, as well as the extent and strength of the inhibitory mechanisms which further shape tuning. The determining of these measures from the recorded responses are relatively straightforward. For example, we can easily determine the preferred spatial frequency and octave bandwidth of each cell for each spectral dispersion and contrast combination by fitting a descriptive function to the responses. For our preliminary data, we used a simple function which is comprised of two half-Gaussians "stitched" together at the preferred spatial frequency. Similar suitable functions can be determined for each of our measurements so that we can get a fine-grained estimate of, for example, the orientation bandwidth for any particular cell. The measurements of extent and strength of the different mechanisms do not require any data fitting, though well-matched descriptive functions will make interpreting the results easier, particularly given the variable nature of neural response rates.

The most enlightening step in our analysis is to look for correlations between variables of interest. In particular, we are interested in understanding the relationship between surround mechanisms and the magnitude of contrast dependent shifts in spatial frequency tuning. In our preliminary analysis, we determined that the simple ratio of preferred spatial frequency at high to low contrast is reflective of contrast dependent shifts in tuning; the change in this ratio with dispersion, then, captures the dispersion dependence of the contrast shifts. These are simple metrics which can be readily correlated with, for example, the measured strength of suppression as measured in any particular cell. We will also investigate the relationship between the size of the surround mechanism and the strength of contrast dependent changes in tuning. We will be able to distinguish between de novo suppression in cortex from inherited suppressive effects by examining the response strength and tuning properties of suppressive mechanisms to the orientation mixtures. Cortical suppression is tuned for orientation, and thus there should be an appreciable difference in suppression as measured to orientation mixtures versus spatial frequency mixtures. No such difference should exist in the thalamus, where the suppressive field is untuned for orientation.

We already have a working model which we fit to the measured spiking activity of individual cells in V1 on a trial-by-trial basis. This model is written in the language python and within the tensorflow module. The model receives input in the form of the properties of the image components (e.g. the contrast or spatial frequency of each grating) and computes a linear filter response which is scaled by a contrast gain control and passed through a nonlinearity to obtain a firing rate. The optimization routine seeks to minimize an objective function which computes, for each trial, the negative log likelihood of the measured neural response given the model prediction. This model captures the overall shape of spatial frequency selectivity and changes in

response amplitude with manipulations in contrast and dispersion, but fails to replicate changes in spatial frequency preference with contrast. In earlier iterations of the model, we proposed a pre-cortical stage in which two input populations roughly mirroring the M and P pathways first filtered the stimulus with their own spatial frequency and contrast selectivities. We found that this model succeeded only with unrealistic tuning properties. By collecting thalamic responses to a rich stimulus set, we can implement a biologically plausible thalamic front-end to our model. This stage will be simpler than the cortical processing stage - we will need only a center-surround linear filtering and a suppressive field which instantiates the key computations which give rise to contrast gain in the thalamus (Bonin et al, 2015). The adjustments to our V1 stage will be quite simple - rather than the linear filter acting on the stimulus, it will act on the stimulus information as it is following LGN processing. The two stages together comprise a hierarchical model of spatial processing.

Expected outcomes: This methodical cataloguing of response properties in LGN and V1 should prove helpful in elucidating the mechanisms behind spatial frequency tuning in the early visual pathway. We hypothesize that responses in the LGN to orientation stimuli are not altered by orientation dispersion, since neither the receptive nor the suppressive fields are tuned for orientation. On the other hand, we expect that the relative strength of suppression will increase with spectral dispersion, since the suppressive field is more broadly tuned for spatial frequency than the classical receptive field and our stimuli span as much as three octaves. In V1, we expect the surround to be sensitive to both dispersions of orientation and spatial frequency. The surrounds of V1 neurons are tuned for orientation, so orientation dispersion should decrease the strength of the surround as compared to a stimulus containing only optimal orientations. We already know that spectral dispersion tends to increase contrast dependent shifts, but now we can associate that increase with a set of mechanisms. We expect that the observed shifts in tuning will originate in the thalamic suppressive surround and be further shaped both by normalization and by the independent cortical surround modulation. The cascaded model of spatial processing will allow us quantify these contributions and to directly observe the effects of manipulating any particular computation, e.g. reducing the strength of suppression in the LGN.

Potential pitfalls: The downside to such a thorough investigation of single cell response properties is the required recording time, which brings about the possibility of losing cell isolation. In our preliminary experiments, the spectrally dispersed stimuli alone required approximately 30 minutes of recording time. If we find that the necessary recording time is too long for most cells, we can economize our protocol. For example, our existing data on the interactions between spectral dispersion and contrast suggest that we can observe similar effects just by presenting stimuli of minimal and maximal dispersion. We might find that the metric of preferred spatial frequency is uninformative in the thalamus, given the broad tuning for spatial scale. In this case, we can rely on a measure which calculates, for example, the center of mass of the tuning curve. To permit comparison between LGN and V1 measures, we can repeat this calculation for cortical cells. Fitting models is difficult, particularly when there is more than one layer of computation. With our early successes fitting the cortical model, though, any difficulties should be easy to isolate as originating in the new thalamic stage of the model, and therefore problems should be tractable.

***Aim #2:** Characterize and model the perception of spectrally diverse stimuli*

Introduction: One model of perception posits that perception is an inferential processes which combines the expected statistical distribution of information in the natural environment - encapsulated by the prior - and the probability over sources of noisy sensory measurements. This Bayesian framework helps to make sense of the following result: if the contrast of a sinusoidal grating drifting at low temporal frequency is reduced, observers will perceive the drift speed as being slower than veridical (Thompson, 1982). Stocker and Simoncelli (2006) estimated the expected distribution of probable speeds for each subject and found that the prior peaked at low speeds and monotonically decreased with higher speeds. As stimulus uncertainty increased, for example by reducing stimulus contrast, then Bayes' rule predicts the posterior will be shifted towards the peak of the prior - this model prediction exactly aligns with Thompson (1982). Temporal frequency is not the only perceptual variable which is sensitive to changes in contrast. A reduction in the contrast or presentation time of a sinusoidal grating results in an increase in its perceived spatial frequency (Georgeson et al, 1985). Our

experiment will reconcile this result with a Bayesian model of perception and with our previous results on the changes of spatial frequency tuning which accompany modifications in contrast and spectral dispersion.

Justification and feasibility:

Review of relevant literature. A rich literature has developed to understand the perceptual capabilities - and flaws - of human observers in Bayesian terms. The core principle is that subjects perceive whichever stimulus is most likely given the measured sensory response; using Bayes' rule, this then becomes the product of the prior distribution over stimuli and the likelihood of the measured sensory response given a particular source stimulus. There is theoretical and physiological evidence that the response properties of neural populations - their response variability, the shape and distribution of tuning functions over a particular stimulus dimension - actually permit the computation of likelihoods (Ma et al, 2006; Jazayeri and Movshon, 2006). Models which more directly link neural population activity and perception through explicit encoding and decoding computations can explain a range of psychophysical results in detection and adaptation (Goris et al, 2013) and also suggest that humans are suboptimal in evaluating likelihood distributions (Putzeys et al, 2012). More recent work suggests that if the prior also influences the sensory representations found in a neural population, then the prior also shapes the likelihood distribution used in calculating the percept; this model implies a differential effect of sensory and stimulus noise (Wei and Stocker, 2015). This insight is grounded in the efficient coding hypothesis (Barlow, 1961) and models which directly link the distribution of information in the natural environment to populations of tuning curves (Ganguli and Simoncelli, 2014).

Contrast changes are not the only way of inducing bias in spatial frequency perception. Adding spectral noise to a sinusoidal grating can also influence a subject's percept: low-pass filtered noise results in subjects perceiving a stimulus as having a lower spatial frequency than is veridical; high-pass filtered noise does the opposite, and both biases are roughly 0.5 octaves (Putzeys et al, 2012). Thresholds in spatial frequency discrimination have proved comparatively stable to manipulations of orientation (Caelli et al, 1983) and contrast well within the threshold regime (Campbell et al, 1970) as measured thus far - thresholds are constant in spatial frequency octaves relative to the reference point regardless of orientation and contrast.

Preliminary data. No psychophysical data has been collected for this aim. We hope to build a physiologically realistic model which incorporates Bayesian ideas of perception. Towards this end, our existing and future body of measured neural responses to stimuli of varying contrast and spatial frequency content will provide a foundation for the sensory processing stage of the model. Specifically, our work-in-progress model of spatial frequency tuning in V1 will allow us to simulate a population of neurons whose tuning properties are diverse enough to tile the space of spatial frequency content and realistic enough to improve upon our understanding of the connection between neural tuning and perception.

Research design and analysis: Similar to previous work (Putzeys et al, 2012), our primary task for assessing spatial frequency bias will be a two-alternative, two-interval forced-choice task in which two brief stimulus presentations are presented successively. We can pilot the temporal structure of the task based on Putzeys and colleagues (2012) and adjust to fit the perceptual realities of our stimuli. One interval contains the reference stimulus whose spectral "fingerprint" (i.e. modal spatial frequency and distribution of spatial frequency content) and contrast are kept constant while the other interval contains a stimulus of variable spectral fingerprint and contrast. We will use method of constant stimuli and randomly interleave the different spectral dispersions, spatial frequency centers, and contrasts in blocks where those same properties are kept constant for the reference stimulus. The subjects must decide which interval contained the image of higher spatial frequency; crucially, this task requires them to compare both stimuli rather than make a judgement based on one stimuli alone. The biases reported by Georgeson (1985) are similar for all reference spatial frequencies, so our choice of reference spatial frequency is restricted only by our desire to compare to with the stimuli we used in our physiological experiments; thus we will choose some intermediate spatial frequency (say 3-5 cpd). As in our physiological work, the temporal frequencies of each component will be drawn from a gaussian distribution centered about some mean which we will choose to be near the peak of human sensitivity. To begin with, we can restrict the levels of spectral dispersion used for both the reference and test stimuli to the first, third, and fifth as described in aim 1 (fig. 1, left). We can measure the point of subject equality by determining at what test spatial frequency the subject was equally likely to choose either interval; this serves as

our measure of bias. A second experiment will give us an indication for the overall visibility of stimuli as we vary spectral dispersion. In this detection task, we will simply vary the contrast of a stimulus of fixed properties (e.g. spectral fingerprint and contrast) and subjects will report if they perceived the stimulus or not. Again, we will use the method of constant stimuli and can interleave different spectral dispersions. We can fit a suitable psychometric function (e.g. Weibull) to these responses and measure the contrast detection threshold for different spectral dispersions.

Using our own hard-won understanding of population tuning for spatial frequency in V1 and existing models of Bayesian perception (cf. Goris et al, 2013; Wei and Stocker, 2015) we can link the subtleties of our physiological results to the measured psychophysical biases and thresholds. In particular, we hope to test existing models against the results of both aims and our preliminary work; ideally we can incorporate a more realistic encoding stage than has been achieved.

Expected outcomes: Recent work has made explicit predictions about this experiment. By increasing spectral dispersion, we are increasing stimulus noise, not sensory noise like contrast manipulations bring about. Increases in stimulus noise broaden the likelihood function and therefore predict a return to prior-dominated perceptual biases (Wei and Stocker, 2015). Recall that the Georgeson result (1985) is actually in opposition to a framework in which only the peak or slope of the prior distribution drive bias, since natural images have a $1/f$ spectrum, peaking for lower spatial frequencies (Ganguli and Simoncelli, 2014). The recent framework of Wei and Stocker (2015) is quite convincing, and thus we believe that increased spectral dispersion will lessen if not reverse the contrast-induced bias towards higher perceived frequency at lower contrast. We also suspect that spectral dispersion will increase contrast detection thresholds, similar to Putzeys (2012), and that this increase will scale with dispersion. Finally, a population coding model of perception which has a series of explicit encoding computations will allow us to simulate the perceptual consequences of different computations and to relate our existing understanding of spatial frequency tuning to the measured perceptual results.

Potential pitfalls: Ensuring that our subjects are performing the task at threshold is of course crucial. It is perhaps advisable to begin the subjects on the simple zero-dispersion case (i.e. single gratings) where the task is more clear. Through instruction and monitoring of the subject's performance, we will have to ensure that the subjects are judging the spatial frequency of the dispersed stimuli on some averaging or holistic measure rather than simply the lowest or highest perceived component spatial frequency. If the measured contrast detection thresholds are substantially different across the dispersion levels, then we might need to consider equating perceived contrast rather than absolute contrast. This can be accounted for by the results of the second experiment.

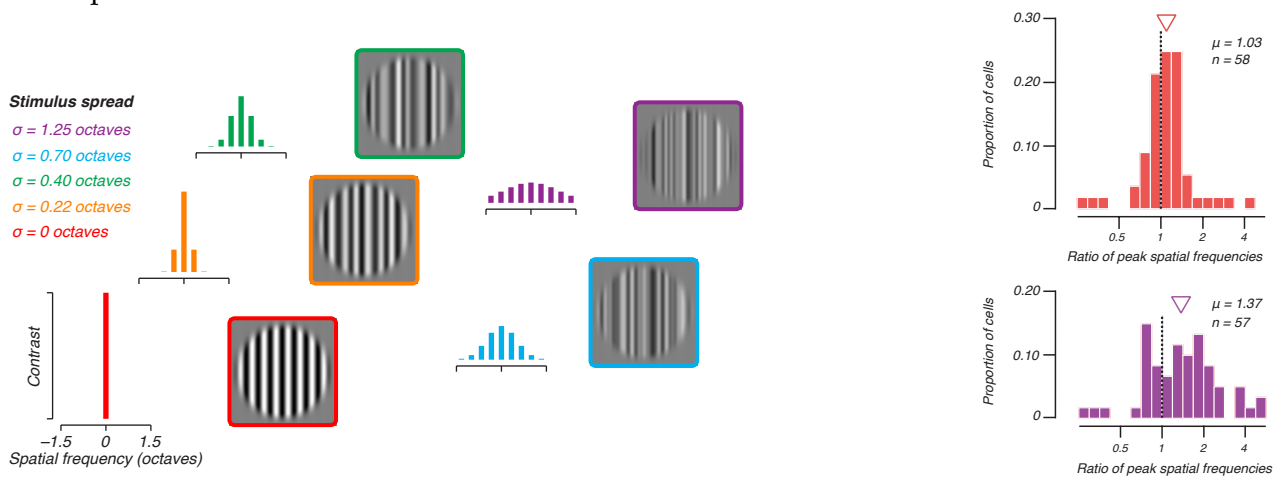


Figure 1. A (left): Each stimulus consisted of a windowed sum of incoherently drifting sinusoidal gratings, with spatial frequencies drawn from one of five unimodal distributions (colored histograms), centered around a variable primary frequency. An example movie frame is shown for each distribution. B (right): The ratio of peak spatial frequency measured at high contrast to that at low contrast for single gratings (top; red) and the most dispersed stimulus (bottom; purple).

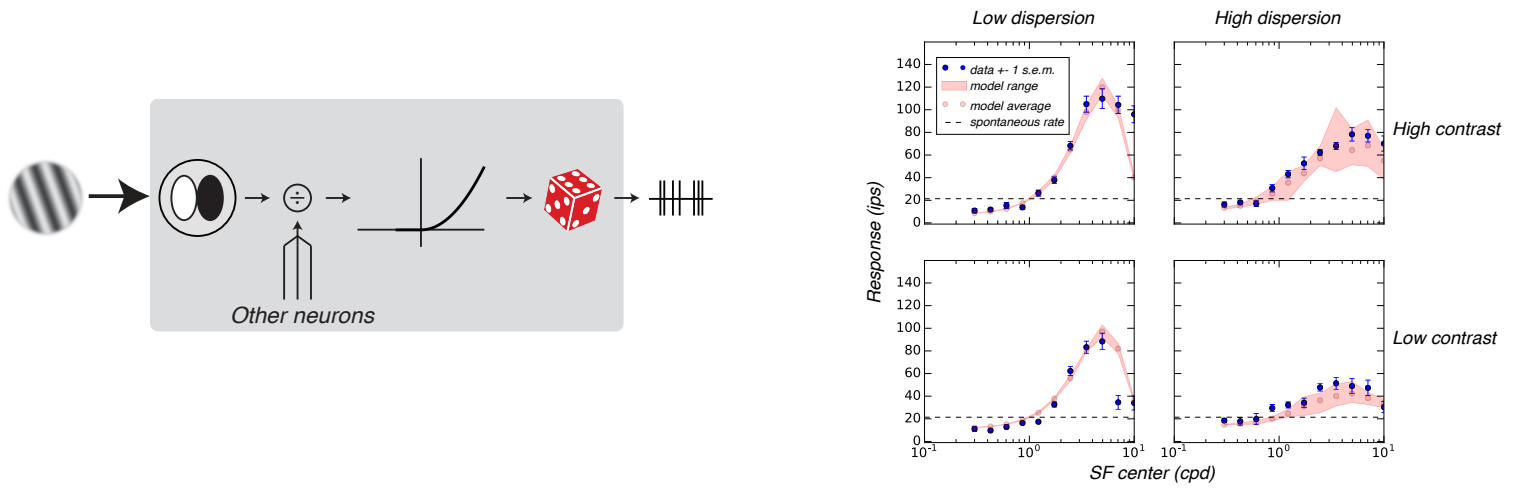


Figure 2. A (left): A schematic of our functional model as it stands now. A linear filter acts on the stimulus and that response is normalized by a pool of neurons which act as a gain control mechanism. A threshold non-linearity acts on this stimulus drive to serve as the rate of a Poisson spike generator. B (right): Example fits from one cell to four conditions - the lowest and highest dispersion at low and high contrast. This cell is a representative fit capturing the ability of the model to match a range of response properties that we have measured in V1.