

LINEAR AND NONLINEAR ORIENTATION DYNAMICS OF RECEPTIVE FIELDS IN THE PRIMARY VISUAL CORTEX OF THE CAT

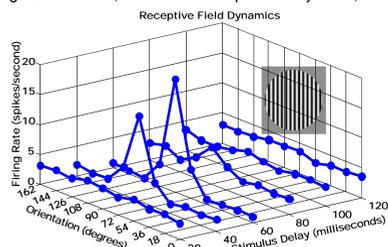
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BACKGROUND

RECEPTIVE FIELD DYNAMICS

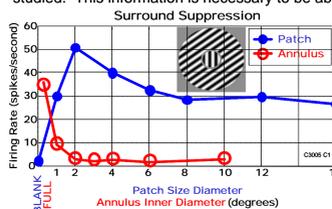
Investigation of visual receptive fields is crucial for explaining the role neurons play in visual perception. In the primary visual cortex, neuronal receptive fields possess a unique preference for stimulus orientation, responding maximally to lines tilted at precise angles. Moreover, this neuronal response is dynamic, peaking around 40 to 60 milliseconds after stimulus presentation, and occasionally demonstrating shifts or inversions of orientation preference (Ringach et al., 1997).



PRINCIPLE OF LINEARITY

If neuronal responses behave linearly then the response to any pair of lines could be predicted by adding the responses to each line separately.

Given that neurons are fundamentally nonlinear — a direct result of the action potential (or spike) threshold — such linear behavior would seem unlikely. However, nonlinear orientation-dependent dynamics have not been extensively studied. This information is necessary to be able to understand completely the mechanisms by which visual neurons process information, and is vital for the creation of accurate models of neurons in the primary visual cortex.



A substantial body of research in the field of visual neurophysiology (for recent review see Fitzpatrick, 2000) has shown that neurons integrate visual information not only from the classical receptive field (a.k.a., the center), but also from the non-classical receptive field (a.k.a., the surround). As shown above, stimulation of the non-classical receptive field alone — grating annuli with inner diameter ≈ 2 degrees for the receptive field of this neuron — does not induce the neuron to spike. In contrast, simultaneous stimulation of the classical and non-classical receptive field — grating patches with diameter > 2 degrees — produces a suppressive effect on the mean spike rate.

SURROUND SUPPRESSION

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OBJECTIVES

Our primary goal in this research is to characterize the nonlinear response properties of neurons in the primary visual cortex of the cat, with the aim of providing a more detailed framework under which accurate models of visual neurons may be constructed. To this end, we have investigated the myriad possible nonlinearities inherent in visual receptive fields, and have begun to establish the requirements necessary for rigorous models of visual perception.

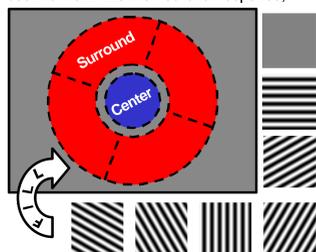
CHARACTERIZATION OF INTRINSIC DYNAMICS

The characterization of the intrinsic nonlinearities in the visual system is a computationally challenging task. The reason for the difficulty lies in the complex nature of nonlinear dynamics, and our inability to conform to the theoretical requirement that complete characterization of a complex system requires an infinite stimulus set. This theoretical impasse notwithstanding, we have developed a new method for characterizing receptive field nonlinearities which employs non-binary m -sequences. The primary benefit of using non-binary m -sequences is the ability to randomly explore a significant portion of the possible stimulus space in the most mathematically efficient manner possible. Furthermore, m -sequences — in contrast to other "random" stimulus paradigms — are nearly perfectly "well-balanced", thereby simplifying nonlinear analysis.

METHODS

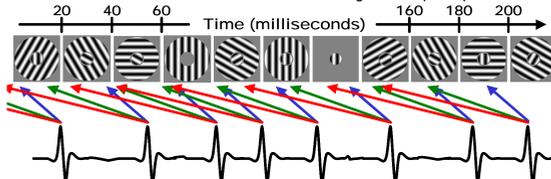
THE STIMULUS: Layout and Timing

We use traditional stimuli optimized for each neuron — namely, grating patches and annuli — as shown in the previous inset figure to determine the size and extent of the classical and non-classical receptive field. The size of the classical receptive field is chosen to maximize the neuronal response, while the size and extent of the non-classical receptive field is chosen such that stimulation of the non-classical region(s) alone does not influence the mean firing rate. Every 20 milliseconds each region is filled independently with an image token drawn randomly from a set of tokens at several orientations, plus a "blank" gray token (as shown to the right). This stimulus, tailored to each neuron, is then presented 4 or more times while recording extracellular action potentials from a neuron located in the primary visual cortex of a cat.



ANALYSIS: "Reverse" Correlation

Calculation of the linear portion of the neuronal response (the first-order kernel) involves correlating the occurrence of spikes with the type of token that preceded each spike (i.e., in reverse time). This is done for several post-stimulus (pre-spike) delays, within a narrow, physiologically-relevant window. Below is a cartoon depiction of this reverse correlation at 20, 40, and 60 milliseconds post-stimulus. The 4+ independent trial estimates of these first-order kernels are transformed to familiar units: firing rate in spikes per second.

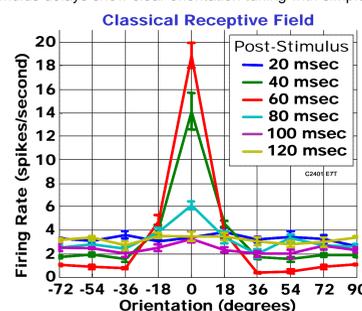


The calculation of the nonlinear, second-order kernels is conceptually the same as for the first-order kernels, but reveals the response to pairs of tokens at two different delays (e.g., 40 and 60 msec) or the interaction between pairs of tokens in two different regions of the receptive field (e.g., the classical and non-classical receptive field).

RESULTS: KEY DYNAMICS

FIRST-ORDER KERNELS

Responses to tokens in the classical receptive field at several post-stimulus delays show clear orientation tuning with simple dynamics

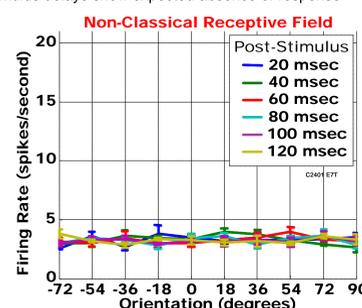


Note: the preferred orientation of all neurons is set to zero.

RESULTS: KEY DYNAMICS

FIRST-ORDER KERNELS

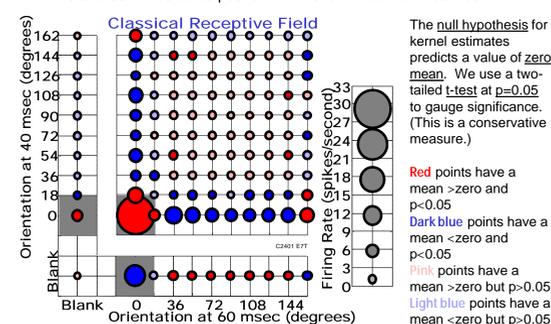
Responses to tokens in the non-classical receptive field at several post-stimulus delays show expected absence of response



RESULTS: KEY DYNAMICS

SECOND-ORDER KERNELS

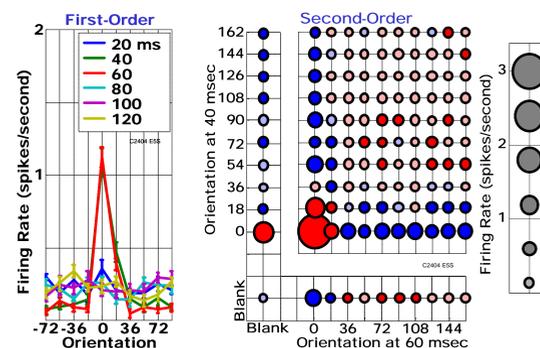
Responses to pairs of tokens in the classical receptive field at delays of 40 and 60 milliseconds post-stimulus show three nonlinearities



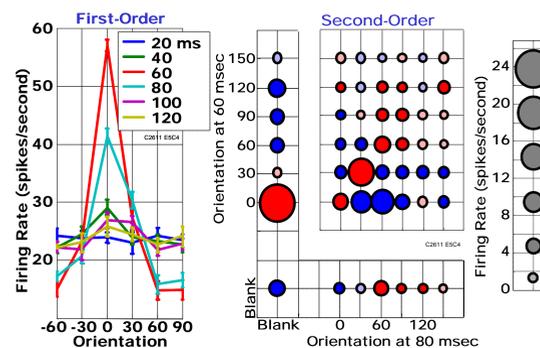
The null hypothesis for kernel estimates predicts a value of zero mean. We use a two-tailed t -test at $p=0.05$ to gauge significance. (This is a conservative measure.)

Red points have a mean > 0 and $p < 0.05$
Dark blue points have a mean < 0 and $p < 0.05$
Pink points have a mean > 0 but $p > 0.05$
Light blue points have a mean < 0 but $p > 0.05$

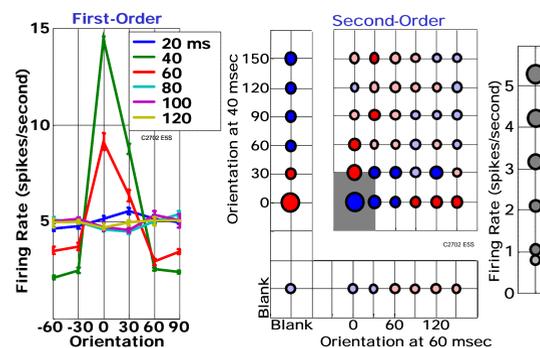
RESULTS: LOW SPIKE RATE



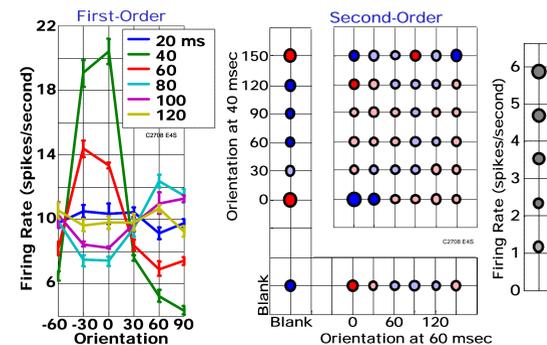
RESULTS: SLOW DYNAMICS



RESULTS: AN OPPOSITE



RESULTS: INSEPARABILITY



POPULATION SUMMARY

FIRST-ORDER RESPONSES

- 54% (50/92) of cells show well-defined orientation tuning profiles (first-order kernels) in the classical receptive field
- Absence of first-order response in the non-classical receptive field confirms proper placement of receptive field regions
- Peak first-order response (e.g., 40 msec) predicts the delay-to-peak in nonlinear response (e.g., strongest at 40/60 msec delay)

SECOND-ORDER RESPONSES

- 56% (28/50) of cells show orientation-specific nonlinear responses to pairs of tokens presented in the classical receptive field
- Facilitation or suppression for preferred/preferred token presentation
- Asymmetry involving facilitation for blank/preferred and suppression for preferred/blank token presentation
- Asymmetry is present regardless of preferred/preferred response
- No significant nonlinearities between the classical and non-classical receptive fields even in cells exhibiting traditional surround suppression (the non-classical receptive field may be unable to "see" such fast stimulus changes)

CONCLUSIONS

IMPLICATIONS FOR MODELS

- Static Nonlinearity
 - Accelerating (e.g., threshold) nonlinearity is sufficient to explain preferred/preferred facilitation
 - Saturating nonlinearity is sufficient to explain preferred/preferred suppression
 - Static nonlinearity model cannot explain the asymmetry between blank/preferred facilitation and preferred/blank suppression, precisely because this feature is present regardless of whether the preferred/preferred response favors facilitation or suppression
- Contrast Gain Control
 - Increased sensitivity to changes from low to high contrast is sufficient to explain preferred/preferred suppression
 - Orientation-dependent contrast gain control mechanism is stipulated by the asymmetry between blank/preferred facilitation and preferred/blank suppression

FUTURE DIRECTIONS

ALTERNATE SETS OF TOKENS

- We are currently carrying out experiments using different sets of tokens in order to more fully explore receptive field dynamics
 - A set of gratings at several spatial frequencies, optimized for orientation and randomized in spatial phase
 - A set of gratings at several spatial phases, optimized for orientation and spatial frequency
 - A set of low-contrast gratings at several orientations, optimized for spatial frequency and randomized in spatial phase

NON-CLASSICAL RECEPTIVE FIELD

- We have begun to explore classical/non-classical receptive field dynamics using slower "visible" stimulus changes in the non-classical receptive field in hopes of deciphering nonlinear interactions between the classical and non-classical receptive field

PHASE-DEPENDENT ANALYSIS

- We intend to re-analyze our data in a manner which pays attention to the precise phase of tokens (which is by default randomized) to extract the influence of apparent motion phenomena resulting from phase precession