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# On texture, form, and fixational eye movements

## Tatyana O Sharpee

Recent studies show that small movements of the eye that occur during fixation are controlled in the brain by similar neural mechanisms as large eye movements. Information theory has been successful in explaining many properties of large eye movements. Could it also help us understand the smaller eye movements that are much more difficult to study experimentally? Here I describe new predictions for how small amplitude fixational eye movements should be modulated by visual context in order to improve visual perception. In particular, the amplitude of fixational eye movements is predicted to differ when localizing edges defined by changes in texture or luminance.

### Address

Computational Neurobiology Laboratory, Salk Institute for Biological Studies, La Jolla, CA 92037, United States

Corresponding author: Sharpee, ([sharpee@snl.salk.edu](mailto:sharpee@snl.salk.edu))

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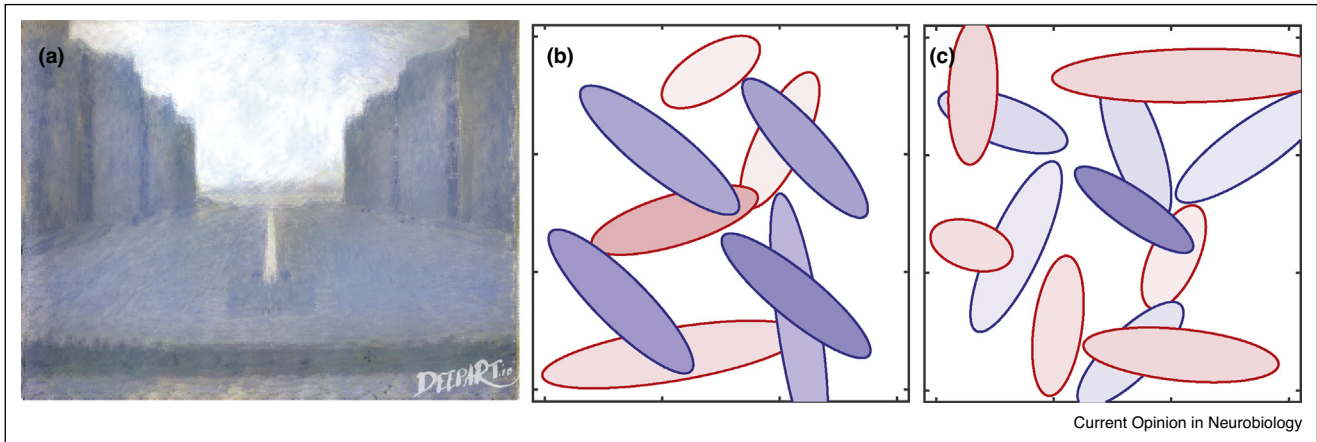
Impressionist paintings serve to illustrate the point that visual forms can be defined by changes in textures as well as by changes in brightness [1<sup>\*\*</sup>,2–5] (see [Figure 1](#) for an example). Recent studies have invigorated the debate in visual neuroscience as to whether form or texture are the primary drivers for visual perception [6,7<sup>\*\*</sup>,8]. For example, often shapes defined by textures are perceived more readily than those based on outlines [8]. However, textures themselves are determined by conjunctions of local shape elements, such as the predominance of signals at some orientation or conjunctions of edges [9]. Furthermore, cartoons illustrate that we can perceive shapes based on their outlines alone, without any textural information. Thus, both mechanisms work in parallel to allow for visual perception. In the primary visual cortex (V1), neural responses are tuned to specific combinations of angles at specific positions. Presumably this explains why V1 neurons are better at discriminating individual samples with a shared texture than different texture types

from each other [7<sup>\*\*</sup>]. This situation changes in the secondary visual cortex (V2) where neurons trade the ability to distinguish individual samples for their ability to distinguish between different texture types [6,7<sup>\*\*</sup>]. This review will first discuss recent results on the neural mechanisms for detecting edges defined in changes in luminance or texture. Then, we will discuss how differences in neural mechanisms translate into different predictions for optimal eye movements based on information theory.

### Neural mechanisms for detecting edges defined by textures

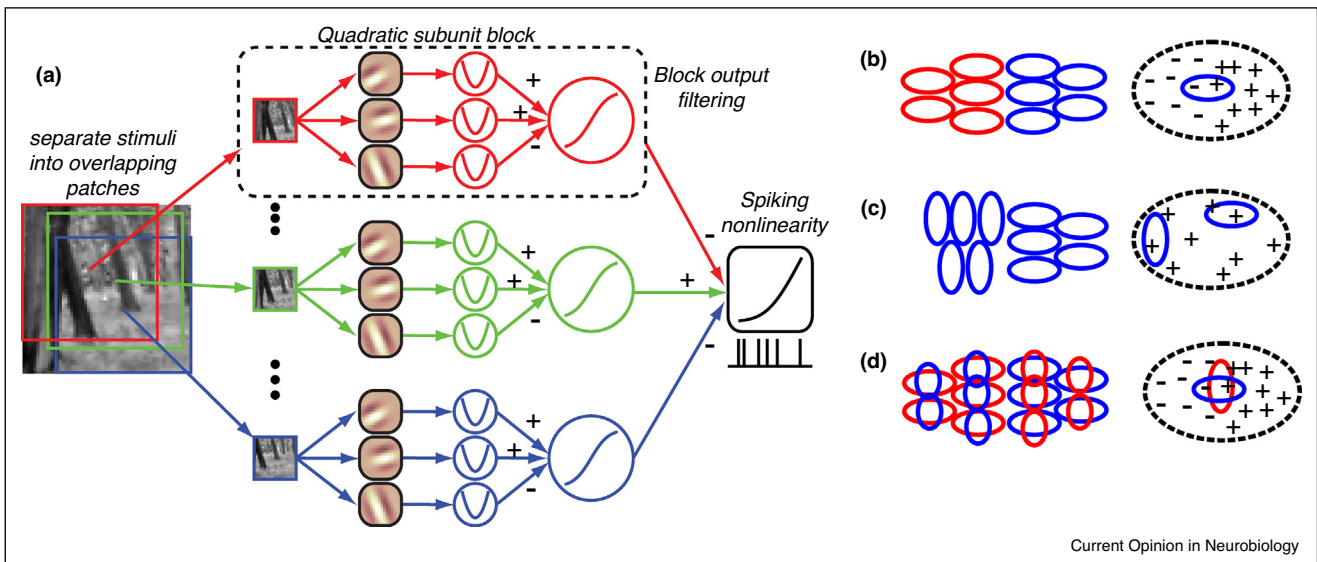
Because textures are defined as patterns with position-invariant statistical properties [10], the responses of neurons tuned to textures are often analyzed using multi-stage models that combine position-invariance with selective tuning to conjunctions of edges of different angles [1<sup>\*\*</sup>,2–5,11,12] ([Figure 2](#)). Analyses of V2 responses to natural stimuli using such models have yielded three organizing principles for their feature-selectivity [11]. First, the responses of V2 neurons are based on conjunctions of multiple edges at nearby positions. The selectivity to this preferred pattern is strengthened through the cross-orientation suppression where excitatory edge patterns are paired with suppressive edges of approximately orthogonal orientation [11]. Second, there is position invariance in at least two different space scales: at the level of individual edges that locally form the so-called quadrature pairs [13,14], and with respect to position invariance of the whole relevant pattern. This latter type of more global position invariance is the one that would be the most relevant for mediating texture selectivity. Importantly, some V2 neurons used biphasic pooling masks that can be used to detect edges defined by changes in textural characteristics across the boundary. The pooling masks of V2 neurons are computationally equivalent to the receptive fields of V1 neurons applied to luminance gratings (see [Figure 3](#) for an example). These three properties — cross-orientation suppression, local position invariance through quadrature pairing, and combinations of biphasic/monophasic pooling masks were observed for each of the sub-populations of V2 neurons that were previously identified based on the diversity of their preferred orientation patterns and temporal characteristics [11,15–18]. Thus, V2 neurons have the abilities to signal the presence of different types of textures and to detect edges defined by changes in texture, using similar computational principles that have been applied to V1 responses to decode position of luminance-defined edges.

Figure 1



(a) Example image with boundaries defined by either changes in luminance or textures. (b) A set of relevant edge features for an example V2 neuron. Data from [18] re-analyzed using the three-stage position-invariant model [11] (see also Figure 2). This neuron ‘e0043’ was identified as belonging to the sub-population with relatively homogeneous feature selectivity across space. Blue and red denote excitatory and suppressive features, respectively; opacity is proportional to the weight with which this feature affects the neural spike probability. (c) Example V2 neuron (‘e109’) from the sub-population with heterogeneous tuning across space.

Figure 2



(a) A three-stage model for characterizing responses of neurons selective to textures. The model incorporates selectivity for multiple excitatory and suppressive components at each position. This operation is repeated across space (red, green, and blue channels). Within each channel, the stimulus patch is projected onto a set of relevant features (same for all patches and shown here as heat maps) to which we refer as first-order features. The output of a projection onto a given feature is passed through a quadratic function (with a potentially non-zero linear term) [1\*\*]. These outputs are summed and passed through a compressive nonlinearity. This part of the model is designed to describe heterogeneous center-surround interactions, because the number of features and their spatial arrangement is not pre-specified and includes both excitatory and suppressive features (marked with + and – near the arrows in the schematic of the block). The output of each quadratic block within each patch is summed, with weights that could be either positive or negative, and the result passed through a soft threshold function to yield a prediction for the firing rate. The block output filtering allows one to connect with filter-rectify-filter (FRF) models [1\*\*,3,4,41–44]. (b) Left: Prototypical arrangement of features in the FRF model. Each ellipse denotes a Gabor feature, excitatory (blue) and suppressive (red). Right: equivalent representation in the composite model with a single first-stage filter (blue contour) and a broader block-output filter (dashed line) that includes both positive (+) and negative (–) weights. (c) Left: Arrangement of features that can model selectivity to a texture boundary or selectivity to pairs of orientation in the presence of position invariance. Right: Equivalent representation in the composite model with two first-stage filters (blue contours) and an approximately uniform block output filter (denoted by the dashed line). (d) Left: Generalization of a FRF model from B that includes cross-orientation suppression between features. The equivalent representation in terms of the composite model has two first stage filters (excitatory in blue and suppressive in red) followed by a biphasic block output filter (dashed line).

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