

Revised 17 January 2022 19:10

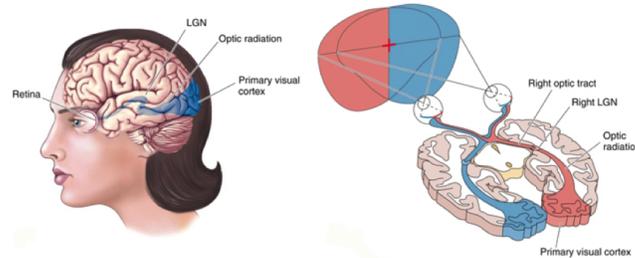
## 5 Stimulus-Invariant Tuning by Neurons

We continue in our quest to connect recurrent networks with biological neurobiological phenomena. One central issue is that of invariant tuning by sensory, albeit high order sensory, neurons, as well as by high-order heading cells to chart the direction of locomotion. Invariant tuning refers to the seemingly stable response of neurons to incomplete stimuli, stimuli whose persistence fluctuates or whose intensity varies, or stimuli that must be decoded in the presence of multiple distractors. Just as a Hopfield network uses attractor dynamics through recurrence to complete missing information, recurrence in general can be used to complete the missing information in coding a sensory feature or stabilize the description of a feature in the face of distractors. We will start with a few examples through a review of the literature, then construct a simple model that is motivated by the data.

### 5.0.1 Invariant tuning to orientation in mammalian primary vision

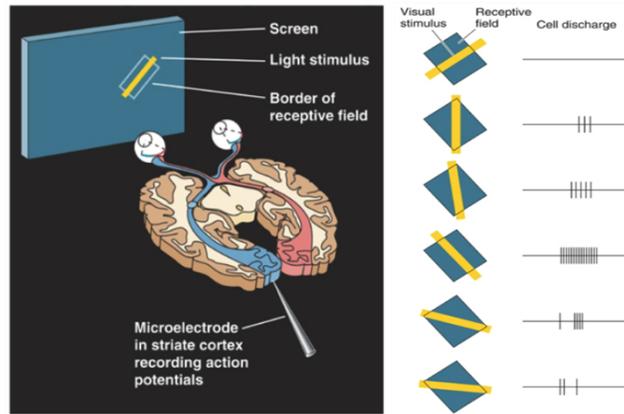
A classic case is that of the response of neurons in primary visual (V1) cortex to oriented bars, gratings, and/or edges that sweep across the visual field. We start with a quick overview of vision from image formation in the retina to responses in V1 cortex (Figure 1).

Figure 1: The gross layout of the visual stream in mammals, from the photoreceptors in the retina to primary visual cortex. From the textbook of Bear, Connors and Paradiso, 2007



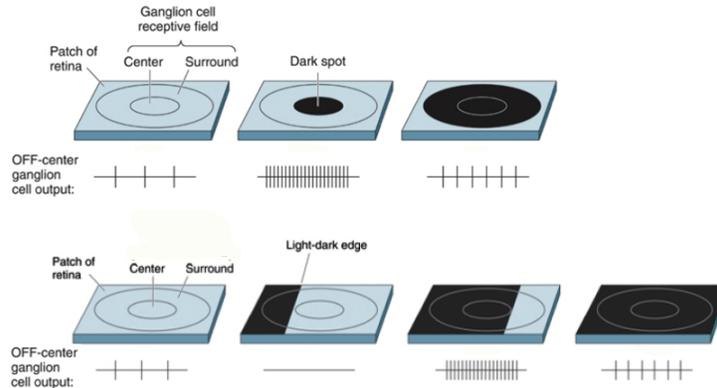
Different cells respond to different orientations of the edge, which are most simply described in terms of a peak spike rate, a baseline rate, and a width of the angular modulation of the rate (Figure 2). This composite information defines the tuning curve.

Figure 2: The phenomenology of orientation specificity in V1 cortex. From the textbook of Bear, Connors and Paradiso, 2007



Orientation specificity is believed to originate from the geometry of the input. Center-surround cells in the retina and thalamus respond like a Laplacian in all directions (Figure 5.0.1). This symmetry is inconsistent with orientation coding. The inputs of many center-surround cells appear to have their inputs "line up" as they synapse on cortical neurons (Figure 4). This break in symmetry leads to orientation specificity for a moving bar or edge or grating.

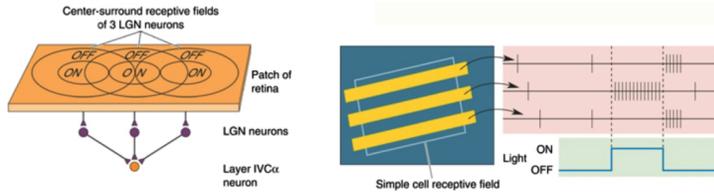
Figure 3: Many output cells from the retina, i.e., retinal ganglion cells, have a center-surround receptive field; Center OFF here. From the textbook of Bear, Connors and Paradiso, 2007



The details of the orientation preference can occur solely from feedforward connections or from a mix of feedforward and recurrent connections. The data indicates that the kernel of orientation results from the input but that the width of the tuning curve results from cortical interactions.

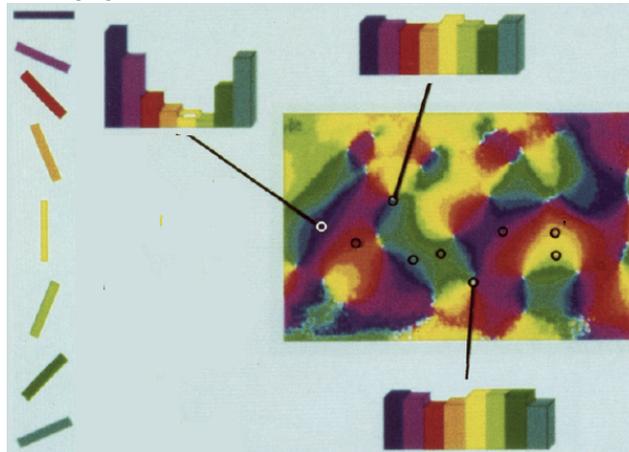
By the way, in large brains, e.g., monkey, many neighboring cells have a similar preference for different orientations and thus

Figure 4: Cortex synthesizes orientation preference from center-surround receptive fields. From the textbook of Bear, Connors and Paradiso, 2007



form a map across the brain. Since space is mapped onto the cortical mantle, the attempt to map the three dimensions of space and orientation onto the two dimensional cortical mantle leads to fissures in the map (Figure 5.0.1). This does not occur in small brains. While a well known feature, we will ignore it in our presentation as it does not impact the circuitry of forming the orientation specificity of individual neurons.

Figure 5: Overlap of orientation preference for neurons at three different locations obtained with IOS imaging of all of V1 cortex. From Bonhoeffer and Grinvald, 1993



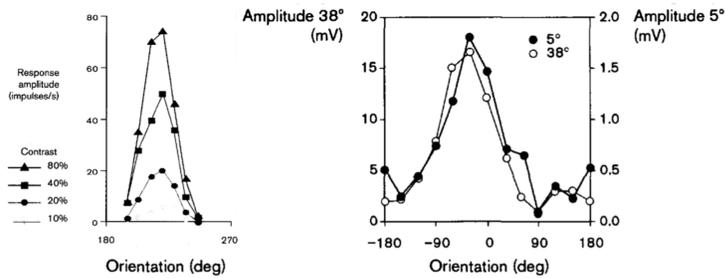
Individual neurons that respond to the orientation of a stimulus also respond to the contrast of the scene; at modest to high light levels the contrast and not the absolute intensity determines the average spike rate so long as the modulation is not too slow nor too fast. They may also respond to other features like the spatial frequency of a patterned input. Three (or more) conundrums arise:

**Contrast invariant tuning:** The width of the tuning curve is independent of contrast (Figure 6). This appears to be inconsistent with feed-forward models, in which a fixed threshold would cause the width to increase with increasing contrast. This is referred to as the "iceberg" effect.

**Size invariant tuning:** The width of the tuning curve is largely independent of the aspect ratio of the oriented bar. For small bars, this is inconsistent with a geometrically-based feed forward model, i.e., the Hubel-Wiesel model. More generally, it points to an invariance in the representation of a feature in the stimulus.

**Spatial frequency invariant tuning:** The width of the tuning curve is largely independent of the rate of spatial repetition of a grating, like the pickets in a fence.

Figure 6: Invariance of the width of the orientation preference to contrast, from Sclar and Freeman 1962, and invariance to spatial frequency, from Ferster, Sooyoung and Wheat 1996



A recurrent network with input tuned to orientation can use feedback connections to surmount these challenges. The stable states of the network are representations of features, i.e., preferred orientations of edges in the visual field. In fact, removing lateral interactions in cortex leads to a loss of tuning, supporting the notion of feedback for some if not all tuning properties of cortical neurons.

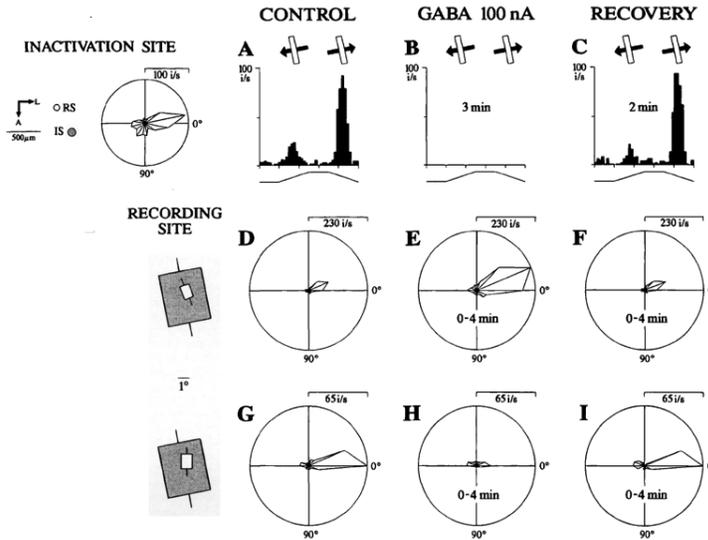
### 5.0.2 Invariant tuning to the spatial extent of touch

Invariance can refer to a signal that depends on the central location of a stimulus but not the spatial extent. This is seen for the case of vibrissa touch (Figure 8). The extent of the response in a neuron in primary vibrissa somatosensory (vS1) cortex that is sensitive to touch of the vibrissae is largely insensitive to the number of vibrissae that are activated.

### 5.0.3 Invariant tuning of neurons toward a heading

Neurons that are tuning to a particular heading have been long known, and more recently neurons that change their activity relative to the orientation of an animal toward or away from a landmark have been characterized (Figures 9 and 10). A special feature of these

Figure 7: Cortical interactions, as opposed to solely feedforward features, define the tuning width. From Crook, Kisvarday and Eysel



neurons is their immunity to distractors. As in the above case, a recurrent network with input tuned to heading can use feedback connections to surmount the challenge of distractors and incomplete input information. The stable states of the network are a manifold of preferred headings relative to a landmark in the sensory field.

One example is found in the head direction cells in anterior-dorsal (ADn) thalamus.

A second example, and one that is particularly dramatic, is found in the ellipsoid body of the central complex of the fly (Figures 11, 12, and 13).

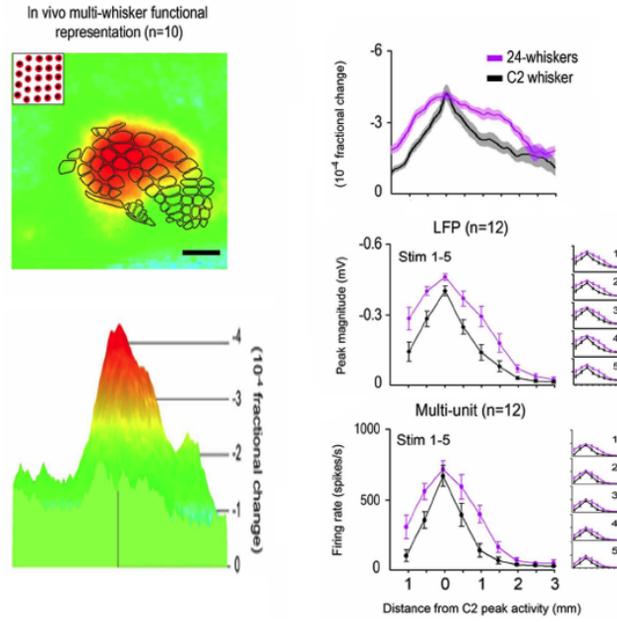
## 5.1 A rate model for neuronal firing

The notion of a tuning curve, with a smoothly varying rate of spiking, appears inconsistent with modeling using binary neurons with ON and OFF states. So we are going to add one level of complexity and work in terms of neurons that have a region where the where the neurons can fire that is a monotonic function of the input. A simple function is

$$S_i = \tanh [G(\mu_i - \theta)] \quad (5.1)$$

where  $G$  is the gain, and  $\tanh(x)$  becomes a step function when  $G \rightarrow \infty$ . Of course, the notion of  $\theta$  as a threshold is replaced by one of midpoint. The idea of rate is that we are still averaging over many spikes, but now we are counting spikes per unit time as opposed to just labeling the output ON or OFF. The other change we will make, which in this case simplifies some maths in addition

Figure 8: Invariance of the amplitude of the vibrissa touch response. Composite data. From Chen-Bee, Zhou, Jacobs, Lim and Frostig. 2012



to allowing a direct comparison with data, is to consider the rate between as a continuous variable that changes between 0 and 1 (Figure ??) Two common examples are

$$\begin{aligned}
 r_i &= \frac{2S_i + 1}{2} \\
 &= \frac{1}{e^{-G(\mu_i - \theta)} + 1}
 \end{aligned}
 \tag{5.2}$$

where the slope in the linear regions is just

$$\frac{dr_i}{d\mu_i} = G r_i (1 - r_i).
 \tag{5.3}$$

Another useful function is the piecewise-linear function

$$\begin{aligned}
 [r_i]_+ &= 0 && \text{for } \mu_i < \theta \\
 &= G(\mu_i - \theta) && \text{for } \mu_i > \theta
 \end{aligned}
 \tag{5.4}$$

The final point before we start is to note that the approach we follow is that of the "ring model". There are many substantiations (Figure 15) - we follow the one includes global inhibition and "cosine" tuning.

Figure 9: Bumps of activity in the heading direction system in rodent thalamus/ From Peyache, Lacroix, Petersen and Buzsaki 2015

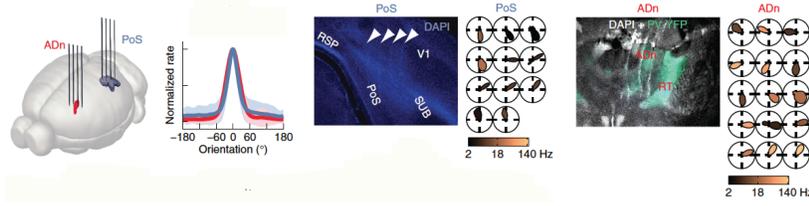


Figure 10: Bumps of activity in the heading direction system in rodent thalamus. From Peyache, Lacroix, Petersen and Buzsaki 2015

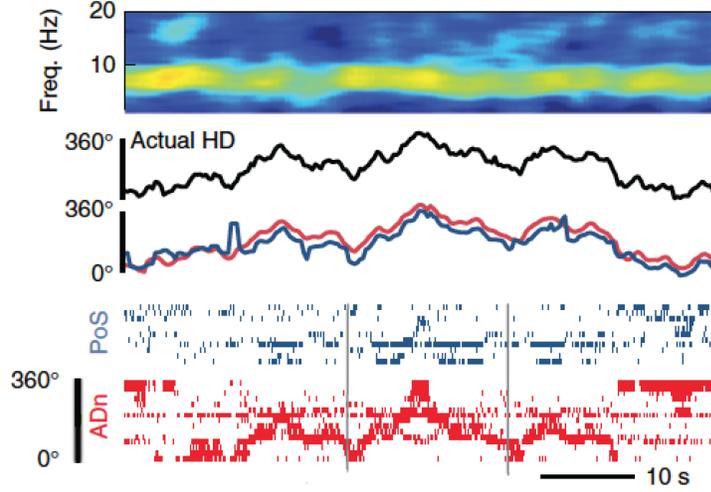


Figure 11: Bumps of activity in the landmark heading system in the fly ellipsoid body of the central complex thalamus. From Seelig and Jayaraman 2015

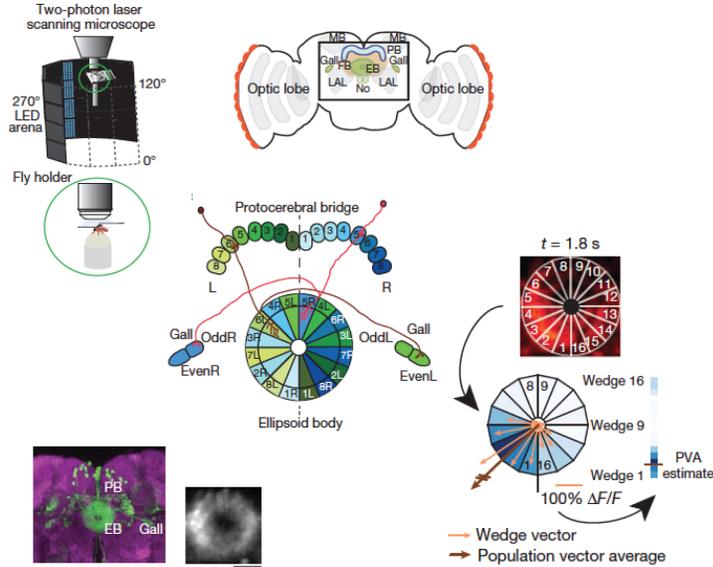


Figure 12: Bumps of activity in the landmark heading system in the fly ellipsoid body of the central complex thalamus. From Seelig and Jayaraman 2015

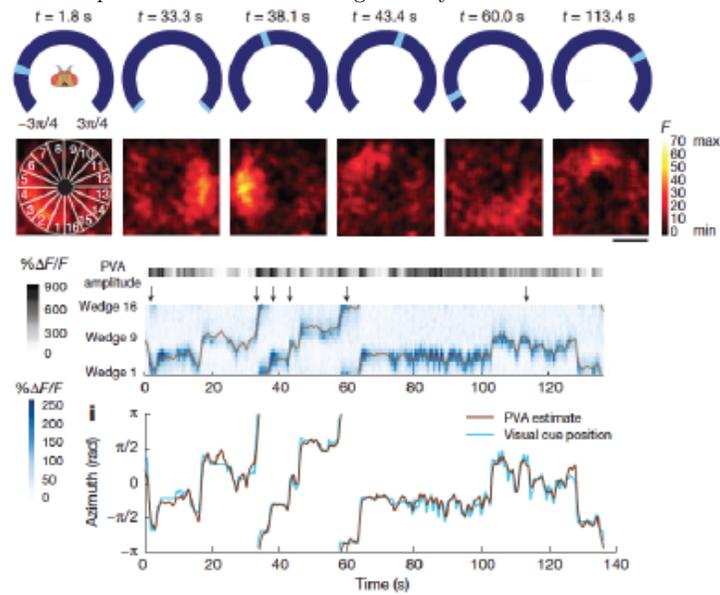


Figure 13: Bumps of activity in the landmark heading system in the fly ellipsoid body of the central complex thalamus in the presence of interfering stimuli. From Seelig and Jayaraman 2015

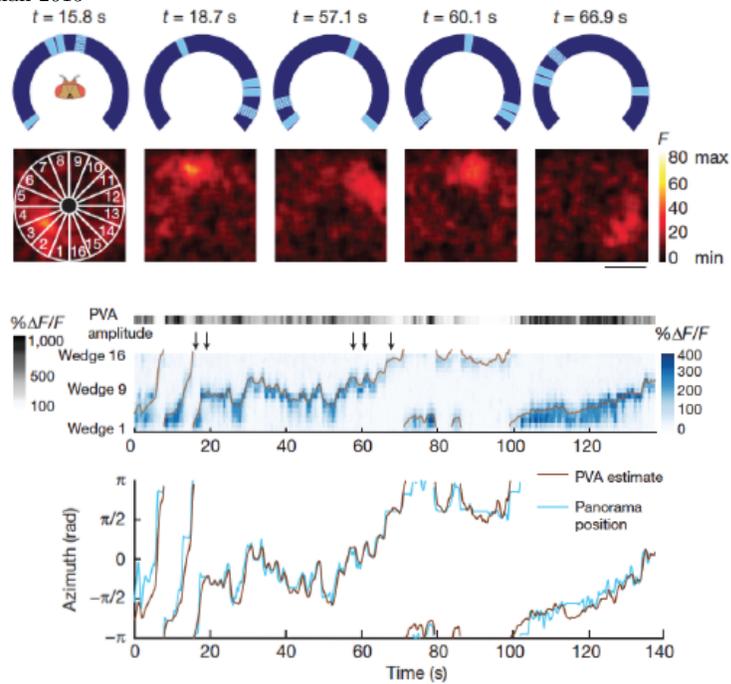


Figure 14: Neuronal f-I curves compared to the piece-wise linear function. BW is the Buzsaki-Wang model and QIF is the quadratic integrate and fire model. Adapted from Fourcaud-Trocme, Hansel, van Vreeswijk and Nicolas Brunel, 2003.

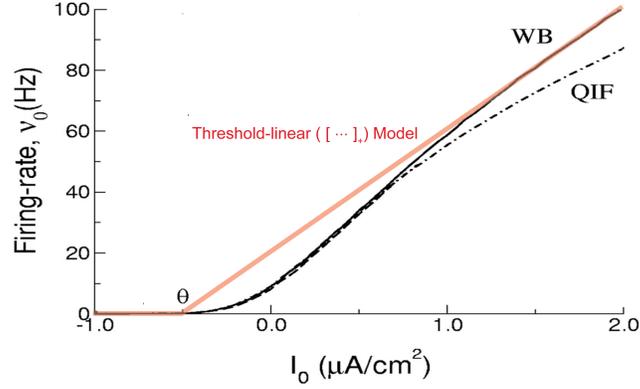


Figure 15: The global model (presented here) and models with local interactions (better suited for the fly) both lead to a moving bump

