Linear Models of Simplified Cells

This section *introduces* a model of a simplified cell.

The cell receives inputs $\mathbf{I} = (I_1, I_2, ..., I_N)$ from *dendrites* which are weighted by *synaptic strengths* $\mathbf{w} = (w_1, w_2, ..., w_N)$.

These are summed at the *soma* (cell body) to obtain:

$$\mathbf{w} \cdot \mathbf{I} = \sum_{i=1}^{N} w_i I_i$$

.

The cells outputs a response $f(\mathbf{w} \cdot \mathbf{I})$ along its *axon*, indicated by the firing rate of the neuron. $f(.)$ is a monotonic function, see next slide, but in this lecture we use a linear approximation:

$$S = \mathbf{w} \cdot \mathbf{I} = \sum_{i=1}^{N} w_i I_i.$$

The non-linear function $f(.)$

$f(.)$ is monotonic non-linear function, which takes value 0 if the input is small, then increases linearly in the *linear regime* until it saturates at a maximum value.

A typical choice of $f(.)$ is the sigmoid function $f(\mathbf{w} \cdot \mathbf{l}) = \sigma(\mathbf{w} \cdot \mathbf{l} - T)$, where T is a threshold and $\sigma(.)$ is a soft-threshold.

In this lecture, we ignore $f(.)$ and study the behavior of the model in the linear regime.

Cells in the retina and Lateral Geniculate Nucleus (LGN) are often modeled without the non-linear function $f(.)$, but adding instead a constant C to the output, to account for spontaneous firing of the cell, and yielding an output $\mathbf{w} \cdot \mathbf{l} + C$, see [190].
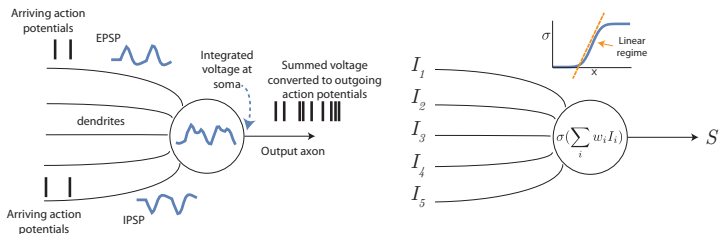
Linear Filter Figure

Figure 12: Left Panel: A neuron receives input – action potentials from other neurons – at its dendrites which generate excitatory and inhibitory postsynaptic potentials (EPSPs and IPSPs respectively) whose voltages are integrated at the soma and converted to outgoing action potentials. Right panel: a simplified model of a neuron. There are inputs $(I_1, ..., I_5)$ at the dendrites, with synaptic strengths $w_1, ..., w_5$, these are summed at the soma, $\sum_i w_i I_i$, and the output S is given by a sigmoid function $\sigma(\sum_i w_i I_i)$. The sigmoid function $\sigma()$ (top right) has a linear regime (brown line) and low- and high-thresholds.

This model $S = \mathbf{w} \cdot \mathbf{I}$ is linear in two respects.

Firstly it is linear in the input $\vec{I}$ so that if we double the input $\mathbf{I} \mapsto 2\mathbf{I}$, then the output doubles also $S \mapsto 2S$. Secondly, it is linear in the weights $\mathbf{w}$.

Most importantly, it obeys the *principle of superposition* so that if S^1, S^2 are the outputs to input $\mathbf{I}^1, \mathbf{I}^2$ respectively, then the output to input $\lambda_1 \mathbf{I}^1 + \lambda_2 \mathbf{I}^2$ is $\lambda_1 S_1 + \lambda_2 S_2$.

This result is important for characterizing the response of simple neural cells, since it implies that we can determine the output of the cell to any stimulus by observing its response to a limited set of input stimuli $\mathbf{I}$.

Note that this property still remains if we re-introduce the non-linear function $f(.)$, provided the function is known.

The retinotopic organization of the early visual system has two implications for these cells. *Firstly*, the weights of the cell depend on its retinotopic position $\vec{x} = (x_1, x_2)$ and the positions $\vec{y} = (y_1, y_2)$ of its dendrites.

We replace the input I_i by $I(\vec{y})$ and the weights w_i by $w(\vec{x} - \vec{y})$. The *receptive field* $w(\vec{x} - \vec{y})$ will typically be zero unless $|\vec{x} - \vec{y}|$ is small.

The neuron is modelled by:

$$S(\vec{x}) = \sum_{\vec{y}} w(\vec{x} - \vec{y}) I(\vec{y}) = \mathbf{w} * I.$$

Secondly, retinotopy implies that there are cells with similar properties (e.g., the same weights $\vec{w}$) arranged roughly evenly in spatial position (apart from the log-polar transformations [151]).

This can be thought of as having "copies" of the same cell at all positions in space. In terms of linear filter theory, see later this section, these sets of cells are *convolving* the image $\vec{I}$ by a filter $\vec{w}$.

Receptive Fields in Retina and LGN.

The receptive fields of the ganglion cells in the retina and cells in the Lateral Geniculate Nucleus (LGN) can be determined by measuring the firing rate of the neurons in terms of its response to different input stimuli $\vec{I}$ and estimating a model for the response, as discussed in the next section.

The experimental findings are that many simple cells have a characteristic receptive field called *center-surround*. But these findings are done using synthetic stimuli and their response may be more complex if they are studied using natural stimuli.

Photoreceptors have different properties, see [139].

On-center and Off-center receptive fields

There are two different types: on-center and off-center. The receptive field weights $w(\vec{x} - \vec{y})$ are radially symmetric and take the form of a Mexican hat or inverted Mexican hat, for on-center and off-center cells respectively [109]. These cell responses are usually thresholded, e.g., by the sigmoid function, so that they usually only give positive responses.

The weights $w(\vec{x} - \vec{y})$ can be approximated by the *Laplacian of a Gaussian* (LOG) or by its negative:

$$w_{LOG}(\vec{x}) = -\{\frac{\partial^2}{\partial x_1^2} + \frac{\partial^2}{\partial x_2^2}\} G(\vec{x} : \vec{0}, \sigma^2).$$

where $G(\vec{x} : \vec{0}, \sigma^2) = \frac{1}{2\pi\sigma} \exp\{-(x_1^2 + x_2^2)/(2\sigma^2)\}$.

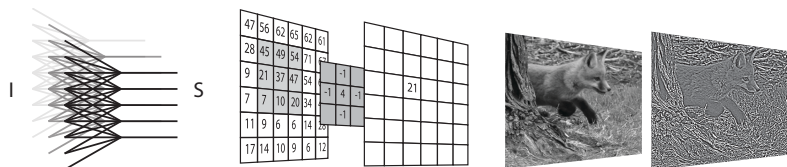# Illustration of Center-Surround Cells

Figure 13: This figure shows the input-output of a center surround cell (e.g., Laplacian of a Gaussian) in three different ways. First in terms of the inputs and outputs of neurons (left). Second in terms of the digitized input image, the filter, and the digitized output (center). The output at each pixel is given by the product of the filter to the appropriate intensity values in the input image, e.g.,
$4 \times 37 - 1 \times 49 - 1 \times 47 - 1 \times 10 - 1 \times 21 = 21$. Thirdly, in terms of the input and output images (right).

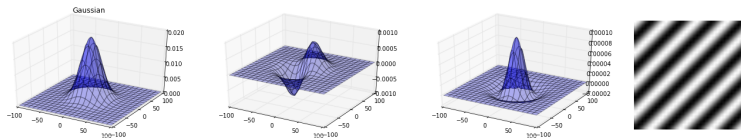# Figure of Gaussians and Derivatives of Gaussians

Figure 14: A Gaussian filter (far left). The first derivative of a Gaussian (left). The laplacian of a Gaussian or Mexican hat (right). A sinusoid (far right).

These cells have two important properties:

(I) They are radially symmetric in the sense that $w_{LOG}(.)$ is invariant to rotation, e.g. suppose we express position $\vec{x}$ in terms of radial components: $x_1 = r\cos\theta, x_2 = r\sin\theta$, then $w_{LOG}(r\cos\theta, r\sin\theta)$ is independent of θ. (II) The receptive field weights $w(.)$ sum up to zero. More precisely,

$$\sum_{\vec{x}} w_{LOG}(\vec{x}) = 0.$$

Note that center-surround cells are often modelled as the *differences of two Gaussians*: $w_{DOG}(\vec{x}) = A_1 G(\vec{x} : \vec{0}, \sigma_1^2) - A_2 G(\vec{x} : \vec{0}, \sigma_2^2)$, where σ_1, σ_2 take different values [190]. This gives a similar model, if $|\sigma_1 - \sigma_2|$ and $|A_1 - A_2|$ are small.

Purpose of Center Surround Cells: Dynamic Range

The purpose of these center-surround cells is believed to help deal with the large dynamic range of images.

Suppose we can express the image locally as $I(\vec{x}) = C(\vec{x}) + B$ where $C(\vec{x})$ is the *contrast*, which describes the local details of the image, and B is the *background*. Then filtering an image by a center-surround cell, whose receptive field sums to 0, removes the background term and preserves part of the contrast.

More precisely, using equation (57):

$$S(\vec{x}) = \sum_{\vec{y}} w_{LOG}(\vec{x} - \vec{y}) I(\vec{y}) = \sum_{\vec{y}} w_{LOG}(\vec{x} - \vec{y})(C(\vec{y}) + B)$$

$$= \sum_{\vec{y}} w_{LOG}(\vec{x} - \vec{y}) C(\vec{y}).$$

Encoding Information for Transmission

Receptive fields of this type can also help efficiently encode the information at the retina in order to transmit it efficiently to the visual cortex.

This can be studied using information theory and the statistics of natural images to predict properties of receptive fields and how they change in different environments [6].

This theory is beyond the scope of our chapter and we refer to the detailed exposition in [190].

Is the retina more complex?

These models of cells in both the retina and the LGN are well studied. Although many of their properties were estimated using synthetic input data it has been shown that in some cases the input image can be estimated from the response of cells in either the retina or the LGN using these types of models [175, 24, 19].

But other authors [47] argue that the retina is more complex and that, in particular, the neurons may act more as *feature detectors* instead of as spatial-temporal filters as described in this section.

In particular, [47] describes many finding suggesting that the retina is more complex that the linear filtering model described above. It is known, for example, that if the light levels go down then the receptive field size becomes larger [190].

A more realistic model models the output as

$$S(\vec{x}, t) = \sum_{\vec{y}, \tau} w(\vec{x} - \vec{y}, t - \tau) I(\vec{y}, \tau)$$

where $w(\vec{x} - \vec{y}, t - \tau)$ is a space-time filter.

There are two types of cells with different temporal properties:

(I) M-cells whose receptive fields are spatially large but temporally small (faster) and which project to the dorsal stream.

(II) P-cells whose receptive fields are spatially smaller but temporally larger (slower) and which project to the ventral stream.

We can also model the dependence of the cells on the wavelength of the input light by

$$S(\vec{x}) = \int d\lambda \, w(\vec{x} - \vec{y}) w_c(\lambda) I(\vec{x}, \lambda),$$

where λ denotes the wavelength and $w_c(\lambda)$ specifies the sensitivity of the cell to color, see [190].

Tuning of Receptive Fields to Sinusoids

To determine the receptive field of a neuron we study its response to a class of stimuli while varying the stimulus parameters (i.e. the perceptual dimensions). To find how well the neuron is *tuned* to particular stimulus parameters, see [64]. In this section, we analyze tuning when the stimuli are sinusoid gratings. We stimulate the receptive field of a neuron by a sinusoid grating

$$I(\vec{x}) = A\cos(\vec{\omega} \cdot \vec{x} + \rho) + I_0,$$

where A is the *amplitude*, ρ is the *phase*, $\vec{\omega}$ is the *frequency* and I_0 is the mean light level.

The frequency specifies the orientation of the stimulus, by the unit vector $\hat{\omega} = \vec{\omega}/|\vec{\omega}|$, and the period of the oscillation by $|\vec{\omega}|$. The phase ρ shifts the center of the sinusoid. To see this, re-express $A\cos(\vec{\omega} \cdot \vec{x} + \rho) = A\cos(\vec{\omega} \cdot (\vec{x} - \vec{x}_0))$, where $\vec{x}_0 = -\rho\vec{\omega}/|\vec{\omega}|^2$ is the shift in position. If $\rho = 0$ the center occurs at $\vec{x} = 0$.

The Response of a Center-Surround Cell to sinusoids

We assume that the neuron is a center-surround cell and its receptive field is a laplacian-of-a-gaussian $w_{LOG}(\vec{x})$.

The predicted response is:

$$\int d\vec{x} w_{LOG}(\vec{x}) A \cos(\vec{\omega} \cdot \vec{x} + \rho) = A(\cos \rho)(\vec{\omega} \cdot \vec{\omega}) \exp\{-(\sigma^2 \vec{\omega} \cdot \vec{\omega})/2\}.$$

We deduce three properties: (i) the response is biggest if the center of the sinusoid is aligned to the center of the cell, i.e. $\rho = 0$, falling to zero at $\rho = \pi/2$, (ii) the cell responds best to frequencies with $|\vec{\omega} \cdot \vec{\omega}| = 2\sigma^{-2}$ (by maximizing the response with respect to $|\vec{\omega}|$), and (iii) the cell is insensitive to the orientation of the stimuli.

We can characterize a neuron by measuring its firing rate when stimulated with sinusoids. We can use these properties to determine if it is center-surround or not. And if it is, to estimate its parameter σ^2.