Simple Cell Receptive Fields in V1.

The receptive field properties of *simple cells* in V1 were studied by Hubel and Wiesel [65][66] who showed that many cells were *tuned* to the orientation of edges and size of bars of light.

They also showed that these cells were spatially organized with hypercolumns and retinotopic organization. Further electrophysiological studies by Roner and Pollen [133] and Jones and Palmer [70] showed that the receptive field properties of these cells could be approximately modelled by *Gabor filters* [25] which are the product of Gaussians and sinusoids. Derivative of Gaussian filters give an alternative model [181].

It was also reported that the receptive fields occur in quadrature pairs [133] so that neighboring cells are ninety degrees out of phase (e.g., a cosine Gabor is paired with a sine Gabor).

Gabor Filters

Gabor functions are the product of a Gaussian
$G(\vec{x}; \vec{0}, \Sigma) = \frac{1}{2\pi|\Sigma|} \exp\{-(1/2)\vec{x}^T \Sigma^{-1} \vec{x}\}$

with covariance Σ times a sinusoid:
$\exp\{i\vec{\omega} \cdot \vec{x}\} = \cos \vec{\omega} \cdot \vec{x} + i \sin \vec{\omega} \cdot \vec{x}$.
This gives two basic types of Gabors: (i) cosine-Gabors

$$G_{\cos}(\vec{x}) = G(\vec{x}; \vec{0}, \Sigma) \cos \vec{\omega} \cdot \vec{x}$$

and (ii) sine-Gabors

$$G_{sin}(\vec{x}) = G(\vec{x}; \vec{0}, \Sigma) \sin \vec{\omega} \cdot \vec{x}.$$

These form a *quadrature pair*, because sin(.) and cos(.) are ninety degrees out of phase.

Properties of Gabor Filters

Gabor filters give a good trade-off between *localization* in position and in frequency.

The Gaussian has good localization in position, in the sense that its response is very small if $|\vec{x}| > 2\sigma$. The sinusoid has perfect localization in frequency (due to the orthogonality of sinusoids) but is unable to localize in position (because a sinusoid does not tend to zero for large $\vec{x}$).

Gabor derived the Gabor function by optimizing a criterion that balanced optimality in frequency with optimality in position [25].
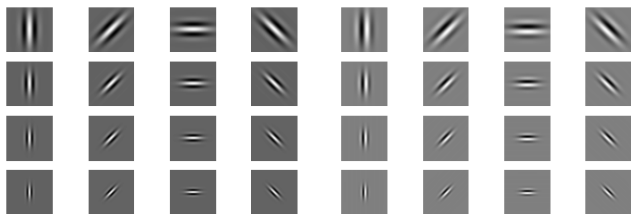
Illustration of Gabor Filters

Figure 15: A family of Gabor receptive fields. The panels show cosine-Gabors (left panel) and sine-Gabors (right panel) at different orientations (rows) and different scales (columns). Observe that the cosine-Gabors have biggest responses at their centers (because $\cos 0 = 1$) while the sine-Gabors have small responses there (because $\sin 0 = 0$).

The response of Gabor filters

Figure 16: A Gabor functions aligned to the vertical axis (left). The image of a zebra (center). The response of the vertical Gabor filter on the zebra image (right).

Modelling V1 neurons with Gabor filters

It was argued [94] that many simple cells in V1 could be modeled by a family of Gabor filters with specific relationships between the parameters of the gaussian and the sinusoid, Σ and $\vec{\omega}$. The orientations of the Gaussian and the sinusoid are aligned and the aspect ratio between the major and minor axes of the Gaussian is 4.

In more detail, express the frequency of the sinusoid by $\vec{\omega} = \omega(\cos\theta, \sin\theta)$, where θ is its orientation and ω is the frequency. Then the covariance Σ of the gaussian is proportional to

$(1/4)(\cos\theta, \sin\theta)(\cos\theta, \sin\theta)^T + (-\sin\theta, \cos\theta)(-\sin\theta, \cos\theta)^T$ (T denotes vector transform).

The sinusoid $\exp(i\vec{x} \cdot \vec{\omega})$ has its "propagating direction" along the shorter axis of the Gaussian, so the gaussian smooths more in the direction perpendicular to the propagating direction, by a factor of $1/2 = \sqrt{1/4}$.

A Family of Gabor Filters

This family is specified by:

$$\psi(\vec{x}; \omega, \theta, K) = \frac{\omega^2}{4\pi K^2}$$

$$\times \exp\{-(\omega^2/8K^2)\{4(\vec{x} \cdot (\cos\theta, \sin\theta))^2 + (\vec{x} \cdot (-\sin\theta, \cos\theta))^2\}$$

$$\times \exp\{i\omega\vec{x} \cdot (\cos\theta, \sin\theta)\} \exp\{(K^2/2)\}\}.$$

The variance is proportional to K^2. This is normalized so that $\int d\vec{x}\{\psi(\vec{x}; \omega, \theta, K)\}^2 = 1$. $K \approx \pi$ for a frequency bandwidth of one octave, $K \approx 2.5$ for a frequency bandwidth of 1.5 octaves ("octaves" are the log ratio of the frequency – see [190]).
This family can also be scaled to give a form:

$$\psi_a(\vec{x}; \omega, \theta, K) = \frac{1}{a}\psi_a(\vec{x}/a; \omega, \theta, K)$$

We study the tuning of Gabor cells by stimulating them with a family of stimuli of form $A\cos(\vec{\omega} \cdot \vec{x} + \rho)$ and varying $\vec{\omega}$ and ρ .

We define $\omega_x = \vec{\omega} \cdot (\cos\theta, \sin\theta)$ and $\omega_y = \vec{\omega} \cdot (-\sin\theta, \cos\theta)$ to be the projections of the input sinusoid in the favored direction of the cell (i.e. $\vec{\omega}$) and in the orthogonal direction (i.e. $\omega_y = 0$ if the input sinusoid aligns perfectly with the orientation of the cell).

The responses of the cosine-Gabor G_{cos} and the sine-Gabor G_{sin} are given by:

$$\frac{A}{2}\cos\rho\exp\{-2K^2\omega_y^2/\omega^2\}$$

$$\times\{\exp\{-(K^2/2\omega^2)(\omega+\omega_x)^2\}+\exp\{-(K^2/2\omega^2)(\omega-\omega_x)^2\}\}\exp\{K^2/2\}$$

$$\frac{A}{2}\sin\rho\exp\{-2K^2\omega_y^2/\omega^2\}$$

$$\times\{\exp\{-(K^2/2\omega^2)(\omega+\omega_x)^2\}-\exp\{-(K^2/2\omega^2)(\omega-\omega_x)^2\}\}\exp\{K^2/2\}.$$

The cosine-Gabor cell is tuned to $\rho = 0$ and the tuning falls off as $\cos\rho$. The cell also favors sinusoid stimuli which are aligned to it (i.e. $\omega_y = 0$), and whose frequency $\omega_x = \pm\omega$.

The sine-Gabor prefers stimuli with $\rho = \pi/2$ and has similar tuning to the frequency with $\omega_y = 0$ and $\omega_x = \pm\omega$.

Complex cells are sensitive to orientation but they are less sensitive than simple cells to the spatial position of the stimuli. This illustrates the standard theory of the ventral stream where visual processing proceeds up this stream using receptive fields, similar to simple and complex cells, which are increasingly tuned to more complex structures and are less sensitive to the precise positions of the stimuli.

From this perspective, complex cells are the second stage after simple cells, forming a simple-complex cell module which gets repeated up the hierarchy.

Complex Cells energy model

We describe here the *energy model* where the complex cell receives input from two simple cells which are ninety degrees out of phase (i.e. cosine-Gabors and sine-Gabors). This is partly motivated by quadrature cells [70] and because, see the following slide, these cells are less sensitive than simple cells to the specific position of the stimuli.

More precisely, the energy model of a complex cell gives response:

$$S(\vec{x}) = \{\psi_{\sin} * I(\vec{x})\}^2 + \{\psi_{\cos} * I(\vec{x})\}^2$$

where $*$ indicates convolution..

Tuning of Complex Cells

We study the tuning of complex cells by measuring their response to sinusoid stimuli The findings show that these cells are, like simple cells, also tuned to orientation, frequency, and phase. But their tuning, particularly to phase, is less precise. Hence complex cells are less sensitive to the precise position of the stimuli. The response is given by:

$$\frac{A^2}{4} \exp\{K^2\} \exp\{-4K^2\omega_y^2/\omega^2\}$$

$$\{\exp\{-(K^2/\omega^2)(\omega + \omega_x)^2\} + \exp\{-(K^2/\omega^2)(\omega - \omega_x)^2\}$$

$$+2\cos 2\rho \exp\{-(K^2/\omega^2)(\omega + \omega_x)^2\} \exp\{-(K^2/\omega^2)(\omega - \omega_x)^2\}\}.$$

Observe that the dependence on the phase ρ is much small (the dominant term in the second line is independent of ρ).
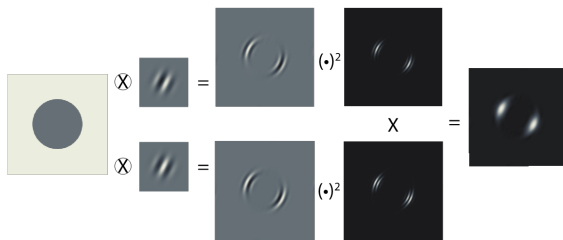
Illustration of Complex Cells

Figure 17: A complex cell can be modelled as a quadrature pair of Gabor filters. The stimulus is a grey circle on a white background (far left). A quadrature pair of Gabor filters is applied to the stimulus giving the largest responses when the orientation of the Gabors matches the orientation of the edge of the circle. The responses of the Gabors are squared and then summed to yield the final output (far right).

Complex Cells: Complications

There are other models where complex cells are built from simple cells in alternative ways, but where the complex cells retain their basic property of being tuned to orientation and frequency but being less sensitive to the position of the stimuli.

But some researchers question whether complex cells receive input from single cells arguing that the computations could be done by non-linear neurons which exploit the complexity of the dendridic tree [115].

Other researchers argue [113] that there is no sharp dichotomy between simple and complex cells but instead there is an continuum of cells with variable sensitivity to position.