Neural Computation
Practical 5: Simple and Complex cells in visual cortex

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# Part I
# Spatial properties of receptive fields in visual cortex

## 1 Aims

- Understand the properties of Gabor filters and the responses to sinusoidal grating stimuli
- Explore the properties of simple and complex cells in the visual cortex
- Understand the notions of spatial frequency, phase, and orientation tuning

## 2 Theoretical Background

The Gabor function[1] is a linear filter often used to approximate the spatial receptive field (**RF**) of simple cells in the primary visual cortex. It has been shown that the elementary components extracted using Independent Component Analysis (ICA) on natural images look a lot like Gabor filters or simple cell RFs[2]. On the other hand, models based on Gabor-like filters are far from accounting for the total variance observed in experimental data[3].

Mathematically, a Gabor filter is the result of multiplying a two-dimensional Gaussian function with a sinusoidal function. To get an intuition for this, think of looking at a sinusoidal function through a 2D-Gaussian-shaped window. What you would expect to see would resemble Figure 1.

The Gabor function is given by:

$D_s(x,y) = \frac{1}{2\pi\sigma_x\sigma_y} exp(-\frac{x^2}{2\sigma_x^2} - \frac{y^2}{2\sigma_y^2}) cos(kx - \varphi)$ [4]

Although this looks complicated, don't be discouraged. The first part of the equation simply defines the 2D-Gaussian function[5], which is characterized by $\sigma_x$ and $\sigma_y$, the extent of the function in the $x$ and $y$ directions, respectively. The second part is determined by the parameters $k$, the preferred spatial frequency of the filter[6], and $\varphi$, the preferred spatial phase of the filter[7].

[1] Named after the Hungarian Nobel laureate, Dennis Gabor.
[2] Check (*Bell and Sejnowski, Vision Res, 1997)* and (*van Hateren and Ruderman, Proc Biol Sci, 1998).*
[3] For two recent examples, you can check *(Stringer et al, bioRxiv, 2018)* and *(Cossell et al, Nature, 2015).*
[4] This is for a vertically oriented Gabor function only, as the one shown in Figure 1.
[5] which is just a product of two 1D-Gaussian functions in the $x$ and $y$ directions.
[6] (how *wide or narrow* the bands in the signal/stimulus need to be to optimally excite the filter/cell)
[7] *where* the ON/OFF regions are located.

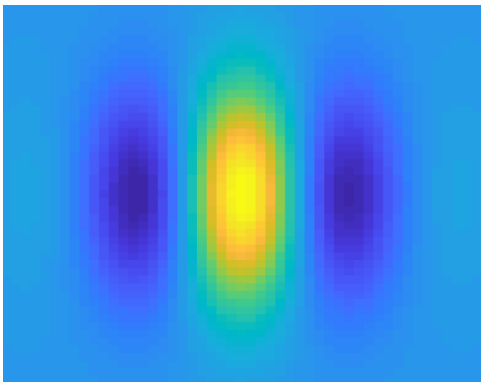

Figure 1: A 2D Gabor filter. The central yellow area would be the region of positive response, whereas the blue areas laterally would give negative responses.

During experimental recordings of visual neuron responses, the stimuli used are usually moving sinusoidal gratings (so they vary both in space, in terms of light intensity, and time, in that they are moving). This is given by:

$$s(x, y, t) = Acos(Kxcos\Theta + Kysin\Theta - \Phi)cos(\omega t)$$

where $A$ is the contrast amplitude, $K$ is the spatial frequency of the grating (how wide the bands are), $\Theta$ is its orientation, $\Phi$ is the spatial phase, and $\omega$ is the temporal frequency (how quickly the gratings are moving). Here, we will deal with the simple case of a static grating stimulus. You can imagine that we take $\omega = 0$, so that the time-dependent component of the equation drops out. This, for a specific value of $K$ and a $\Theta = 0$, would look like Figure 2.

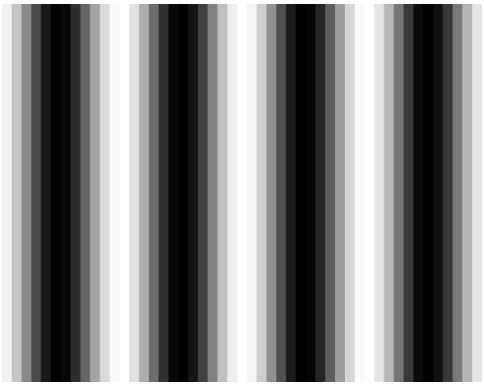

Figure 2: Sinusoidal grating.

To understand the response of a cell with a Gabor-like RF to a sinusoidal grating, you can think of the cell as *filtering* the input with its Gabor function. Another way to put this would be to say that the cell is performing a *convolution* of the input grating with its RF. And yet another way to think of it would be as the cell looking in the input for a *pattern* similar to its RF structure. The more similar the input to the RF, the higher the response, and vice versa. Based on the RF in Figure 1 and the grating in Figure 2, the response would look something like Figure 3[8].

[8]Please look at the images and convince yourselves that the response makes sense.

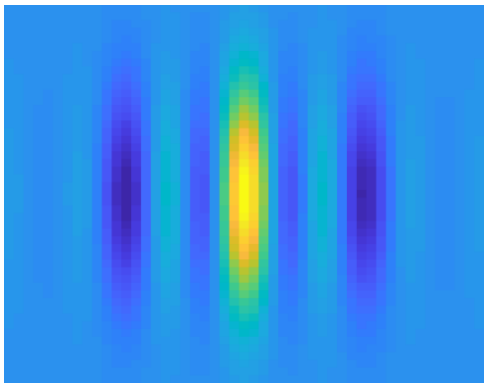

Figure 3: Response of Gabor-like RF to sinusoidal grating.

The linear spatial response is given by:

$L_s = \int D_s(x, y)s(x, y)dxdy$

which is essentially the form of the spatial convolution.
For additional information you can refer to Chapter 2 of Theoretical Neuroscience by Dayan and Abbott.

## 3 Modeling a simple cell's RF and a grating stimulus

Your first task is to numerically model a 2D Gabor function and a sinusoidal grating stimulus, based on the equations given above, in MATLAB. To start with you can simulate the stimulus with orientation $\Theta = 0$, $\Phi = 0$ and $A = 50$. For the RF kernel, you can use $\sigma_x = \sigma_y = 1°$, $\varphi = 0$, and $1/k = 0.5°$.
Hints:

- Useful functions (look up how they work in MATLAB's documentation or online): *surf, meshgrid*
- You can write your own functions. This can be done if you create a new document in MATLAB and then define your function with the general syntax:

  *function* ***outputs*** $=$ ***function_name(inputs)***
  **input-dependent commands to execute**
  **compute and return outputs**

- It would helpful to compute the RF and the stimulus in separate functions, so as to prevent confusion.
- To check whether you're on the correct path, compare what you get to the figures shown above.

## 4 Response of the cell to the stimulus

Now, compute the response of the cell to the stimulus. Does it look like you would expect?

## 5 Exploring the properties of the spatial RF

- Now, change the spatial frequency, $K$, of the grating stimulus. Plot the response, $L_s$, over a range of different spatial frequency values. What is the preferred spatial frequency of the cell? Discuss your observations with your neighbour. Which parameter of the RF do you think exerts the most influence on the resulting plot?[9]

[9] i.e. at which value the peak of the curve is observed

- Then, plot $L_s$ as a function of the spatial phase of the stimulus, $\Phi$, taking $1/K = 0.5°$ as constant. What is the preferred spatial phase of the cell?
- (Optional) Do the same for the parameter $\Theta$, the orientation of the stimulus. You will get the orientation tuning curve of the cell.

## 6 Modeling complex cells

Consider a complex cell with the spatial part of its response given by $L_1^2 + L_2^2$, where $L_1$ and $L_2$ are linear responses determined by the equation for $L_s$. Let $\sigma_x = \sigma_y = 1°$ and $1/k = 0.5°$ for both RFs; $\varphi = 0$ for $L_1$ and $\varphi = -\pi/2$ for $L_2$; stimulus orientation is $\Theta = 0$ again, but set $A = 5$.

- Compute the spatial frequency selectivity of the cell as in Section 5, taking $\Phi = 0$.
- Compute the spatial phase selectivity of the cell, taking $1/K = 0.5°$.

Discuss your observations. How are the responses of the complex cell different from the ones of the simple cell?

## 7 (Optional)

Consider changing the orientation of the cell's RF. How do its responses change then? Always check that the tuning curves make intuitive sense.

## 8 (Optional)

Consider complex cells with more complex RF structure. How would you model those? (Combine with Section 7)

# Part II
# Temporal properties of receptive fields

(Continuing from previous lab)

Until now, we have only considered spatial responses of simple and complex cells to presentation of static (non-moving) gratings. In reality, however, neurons don't respond in this highly simplified fashion.

## 9 Temporal RFs

The effect of a given stimulus on the probability of spike generation is not constant but depends on its timing. The shape of this dependency can be seen in Figure 4 and it is given by:

$$D_t(\tau) = aexp(-\alpha\tau)(\frac{(\alpha\tau)^5}{5!} - \frac{(\alpha\tau)^7}{7!})$$

where $\alpha$ is a constant that determines *how quickly* the temporal structure evolves, and $\tau$ is the "reverse" time, meaning the time *before* the spike occurs. This biphasic pattern is not the only one possible, and monophasic or triphasic response structures are also seen and can be modelled by simplifying or adding to the above function, respectively.

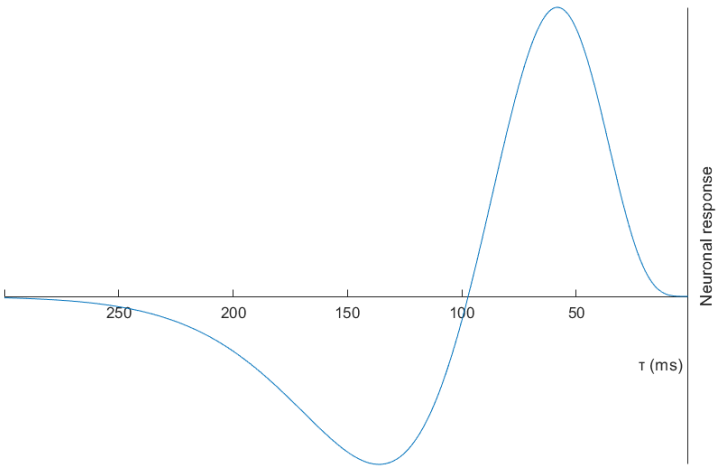


Figure 4: Temporal structure of a receptive field

- First model this structure of the temporal receptive field of the cell. You can take $\alpha = 1/15ms$, but feel free to explore what the effects of changing this parameter are.
- Next, look at the spatio-temporal receptive field of the simple cell, by combining its spatial Gabor-type RF with its temporal RF. How would you expect the RF to look like? Visualize the RF and compare with your expectations.[10]
- The linear temporal response of the cell will be given by $L_t(t) = \int_0^\infty D_t(\tau)cos(\omega(t-\tau))d\tau$. Compute this response for your cell, with angular frequency $\omega = 6\pi/s$.

# 10 Moving gratings

Cells in primary visual cortex (V1) respond most strongly to moving gratings, not to static images. The linear response estimate to a moving grating can be computed as just the product of the linear spatial and the temporal responses we saw above:

$L(t) = L_s L_t(t)$[11]

Now, compute the response to a moving grating with $s(x, y, t) = cos(Kx - \omega t)$. For $D_s$ and $D_t$ you can use the same parameters we used initially in previous sections.

- First, plot the response as a function of time with $1/K = 1/k = 0.5°$, and $\omega = 8\pi/s$.
- Then, plot the response as a function of $K$, with $\omega$ as a constant.
- Finally, plot the response as a function of $\omega$, with $K$ as a constant.

[10] It's not very easy to visualize 4 dimensions, so it might make more sense to visualize the evolution of a slice along one of the two spatial dimensions with time. Hint: You might find the function *squeeze* helpful. Possibly also *slice*.

[11] This is true for cells with a separable space-time receptive field, which is what we have been dealing with all along.