

2.7.6

Receptive Fields

The ability to produce **sharp vision** that distinguished between various **contrasts** and **edges** is a property of receptive fields. The three major cell types of the retina (rods/cones, bipolar, ganglion) work together to form receptive fields. Receptive fields of photoreceptors are circular, with some photoreceptors located directly in the center and others making up the peripheral edges of the circle.

Light can hit any part of the circular receptive field and induce hyperpolarization and that results in reduced glutamate release.

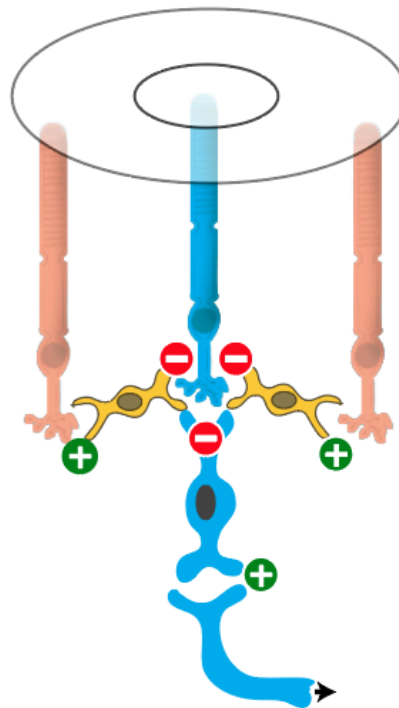
The circular nature of the photoreceptor field causes the bipolar cell to behave as if it were also circular but with an added level of complexity. This complexity is due to the fact that a bipolar cell can have one of two types of post synaptic potentials created by different glutamate receptors.

Some bipolar cells contain non-specific (cation) ionotropic glutamate receptor channels called **AMPA** channels. These channels open in response to the glutamate ligand. Bipolar cells that contain these channels are excited by glutamate release or dark conditions (see bold statement above).

*However, keep in mind that bipolar cells will be named by what light does to them. In this case, since dark conditions (more glutamate) cause excitement (or EPSPs) on the bipolar cells, light must do the opposite. Therefore, since these bipolar cells are excited by lack of light and inhibited by the presence of light, we call them **off center** bipolar cells.*

In contrast, other bipolar cells contain metabotropic glutamate receptors called mGLUR6 receptors. These receptors also respond to glutamate ligand but work through a second messenger signaling system that causes inhibition of otherwise constitutively (always open) calcium channels called **TRPM1**. These bipolar cells would then “turn on” when glutamate release is reduced (light) and “turn off” when glutamate release is increased (dark) therefore we call them **on center** bipolar cells.

For this next section you may find it helpful to refer to the following picture. Numbers on the picture will be referenced in the text. Also, as you interpret the picture, please remember that the plus and minus signs represent what the neurotransmitter coming from the presynaptic cell would do to the post synaptic cell.



Receptor field

Image by JS, 2013

In addition to synapsing directly on bipolar cells, each photoreceptor also synapses with horizontal cells.

Horizontal cells are always depolarized by glutamate.

This is represented by the green plus sign (This means that glutamate from the surround photoreceptor will cause depolarization of the horizontal cell).

Therefore you could say that horizontal cells are active in dark (more glutamate release) and inactive in light (less glutamate release). When a horizontal cell depolarizes (dark), the opposite end of this cell releases a neurotransmitter called GABA onto the terminal ends of the center photoreceptor. GABA then acts to inhibit the release of glutamate from the photoreceptor which results in less glutamate going from photoreceptor to bipolar cell.

With this complicated arrangement you will see an explanation below that explains how light focused only on the center of the receptive field associated with an "on center" bipolar cell but not the surround cells, will almost double the effect of the EPSP on the bipolar cell.

You may have to think about this a couple of times.

What we are saying is:

Light hitting the center but not the surround will result in excitation of the horizontal cells with glutamate (because its dark on the surround cells) → Causes increase GABA release from the horizontal cell → The terminal ends of the center photoreceptor receive the GABA and experience an IPSP which further lowers the amount of glutamate released from the central photoreceptor → With less Glutamate in the synapse between the central photoreceptor and the bipolar cell the on center bipolar cell will experience less inhibition → This means that the constitutively open cation channels will be uninhibited and depolarization of the bipolar cell will commence.

Even though the center photoreceptor cell is releasing less glutamate (due to light), the effect of the surround photoreceptors (due to no light and through the horizontal cell) is to slow down the release further.

Yeah, you might want to stare at the picture a few times and realize that you can have different effects with light and dark on center and surround. In fact, these different effects are what we will try to "Own" now...

To illustrate how receptive fields work we will need to make some assumptions about how the bipolar and horizontal cells work together. To do this will use the figure below. Let's assume that a photoreceptor in the center of the receptive field has a 60% effect on what the bipolar and then ganglion cell sends to the brain and that the surround located photoreceptors have a 40% effect. We can take one step further and divide the circle into three equal portions with each surrounding edge contributing 20% and the center still at 60%. In addition, let's simplify further by also assuming that there are just three photoreceptors, one in the center and one on each side (see figure). Taking this approach will "hopefully" allow us to explain the frequency of action potentials that are ultimately sent to the brain via the ganglion cell.

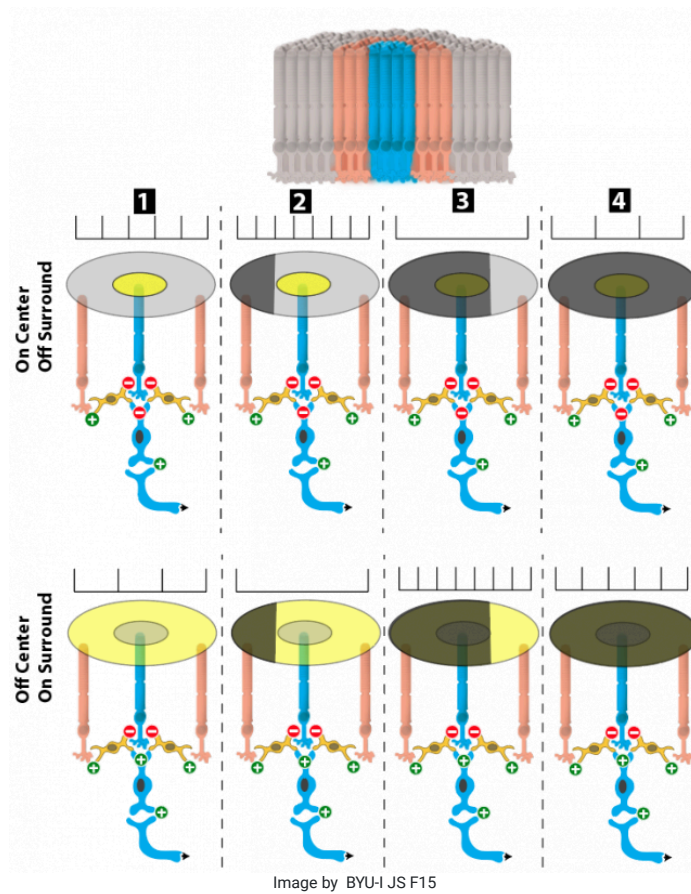
1 For on center off surround receptive fields, light hitting the entire receptive field will inhibit glutamate release from all three photoreceptors. This means that the bipolar cell will be activated as a result of the center photoreceptor (reduced glutamate) but since the horizontal cells will not be active (reduced glutamate) they won't help further reduce glutamate release from the center. Remember that activation of horizontal cells results in GABA release which further reduces glutamate. Therefore, of the 100% effect from the receptive field, 60% of the bipolar cells influence will come from the center photoreceptor and 40% from the surround (which in this case are not active). Thus, only 60% of the 100% possible influence will make it to the ganglia cell and then brain. This is represented by 6 tick marks representing an imaginary frequency of 6 action potentials.

2 If light strikes just the center and one of the surround edges, we see a different frequency. In this case, the bipolar cell will be stimulated as a result of the center photoreceptor (less glutamate) and activation of one of the horizontal cells (dark and to the left...also less glutamate). However, the surround edge to the right gets light and ends up not stimulating the bipolar cell. This results in more glutamate release from the center photoreceptor. Long story short, of the 100% effect, 60% from the center and 20% from the edge (dark) will contribute while 20% from the other edge (still in the light) will not contribute. The result is 80% of the available signal being transmitted to the brain. This is represented by 8 tick marks on the imaginary action potential frequency chart.

3 This image shows light striking only one edge. In this case, the center (dark) and one edge (light) will not contribute. Only one activated horizontal cell (dark) will contribute to the inhibition of glutamate release to the bipolar cell. Therefore, the other 80% are causing more glutamate release to the bipolar cell. This results in 20% of the available signal being transmitted to the brain. This is represented by 2 tick marks (one at beginning and one at end) on the imaginary action potential frequency chart.

4 This image shows that the entire receptive field is in the dark. In this case 40% (both activated horizontal cells) will result in the observed action potential frequency. The center photoreceptor is in the dark and will not contribute its 60% inhibition of glutamate release to the photoreceptor. This is represented by 4 tick marks on the imaginary action potential frequency chart.

The opposite effect occurs for **off center on surround** receptive fields. Remember that in these cells glutamate is stimulatory to the bipolar cell (notice the green plus sign on the bipolar cell representing the different EPSP creating inotropic glutamate receptor). Having an EPSP on the Bipolar cell instead of an IPSP receptor basically makes all the action potential frequency charts have the opposite effect. Try to work your way through the **off center on surround** receptive fields and prove to yourself that the action potential frequency graphs are correct.



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