Where in the brain do after-effects occur?

So far in this chapter we have talked about channels for orientation and size and have made implicit (and occasionally explicit) references to cells in area V1. The assumption behind this is that the after-effects we have described are due to adaptation in these cells. Can we back up such a claim? Here, we provide two lines of evidence that support this idea—however, as we have said before, beware simplistic ideas.

First, one of the major features of area V1 is that many of its cells are binocular (driven by both eyes). So, are our after-effects also binocular? The experiments are fairly easy. We view the adaptation pattern with one eye and then test for the after-effects in the same eye or in the other eye. If all the cells adapted were binocular, we should get perfect transfer of the effect from one eye to the other. If all the cells adapted were monocular (driven only by one eye), we should get no transfer of the effect from one eye to the other. The results depend a little upon exactly how the experiments are done but, on the whole, we get about 70% transfer for the tilt and size after-effects (Mitchell and Ware, 1974). This fits nicely with the idea that most, but not all, the V1 cells are binocular. Interestingly, in people who lack binocular cells the after-effects do not transfer between the eyes.

⇛ See Box 3.3

⇛ See Chapter 11

The most direct evidence that adaptation of cells in V1 underlies after-effects should be from experiments that look at the responses of single cells after adaptation. In our model of adaptation (Figure 4.4), channels (or neurons) become desensitized by adaptation. Can we illustrate this in single cells? Experiments have been performed which examine a cell's response after having been exposed to a high-contrast grating for some time. The results are that cells in the retina and LGN do not show any adaptation—their response is the same before and after the high-contrast adapting pattern (Movshon and Lennie, 1979). However, cells in the cortex, commencing in area V1, do indeed show a change in response so that they fire less after exposure to the high-contrast pattern.

The advent of imaging techniques like fMRI has enabled us to discover that adaptation effects are widespread in the cortex. Adaptation effects occur not only in areas close to V1, like V2, V4, and V5, but also in 'higher visual areas' like the fusiform face area in inferotemporal cortex (Grill-Spector and Malach, 2001).

⇛ See Chapter 12

Contrast sensitivity

We might wonder if all our bar detectors are equally sensitive. Are we as good at seeing little skinny stripes as we are at seeing big fat stripes—whoops, we mean as good at seeing high spatial frequencies as we are at seeing low spatial frequencies? We can answer this question by measuring how much contrast (i.e. the difference between the lightest and darkest parts of the image) we need to see bars of different sizes. You might think that we are best at seeing the low spatial frequency (big) bars and less

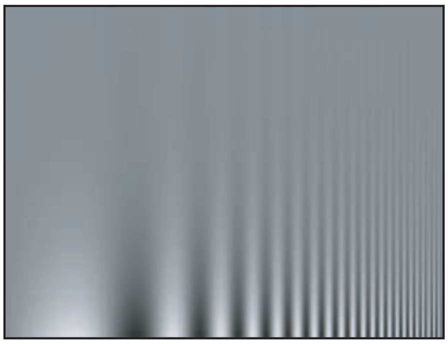

Figure 4.17 Contrast sensitivity at various spatial frequencies. The spatial frequency of this grating increases from low at the left to high at the right, and the contrast increases from top to bottom. Clearly, we are most sensitive to some middle spatial frequency, with lower sensitivity to both high and low spatial frequencies.

good at seeing high spatial frequency (skinny) bars; after all, we can make a pattern with bars so thin that we can't see them at all. Look at Figure 4.17; it shows a set of bars of different sizes, big on the left and getting thinner as you move across the figure to the right. Notice that we have changed our bars from having sharp edges to having blurry edges. We have done this because any sharp edge, even if it is the edge of a fat bar, is really skinny—or, as we should say, sharp edges contain many high spatial frequencies—and we want just low spatial frequencies on the left-hand side of our picture. At the bottom of the figure the bars have high contrast, but as you go up the figure the contrast reduces. At some point on the figure you should discover that you can no longer see the bar at all. The higher up the picture you can see the bar, the more sensitive to the bar you are. Do you find that the bars all disappear at the same height on the picture? No. The most obvious feature is that our sensitivity goes down at the right-hand side of the picture, where the high spatial frequencies are; indeed, eventually the bars are so close together that we cannot resolve them at all no matter how high the contrast. Now look at the left-hand side of the picture, where the low spatial frequencies are. Here, we can see that it is not the case that biggest is best; we are actually most sensitive to the bars in the middle of the picture, at medium spatial frequencies.

Figure 4.18 shows the approximate height at which the bars disappear—a measure of how sensitive we are to contrast at that particular spatial frequency. This graph is known, not unreasonably, as the **spatial contrast sensitivity function** (Campbell and Maffei, 1974) and it can tell us a great deal about how we see objects of different sizes. Look at the point marked 'resolution limit', which marks the highest spatial frequency that we can see. This is the point where the bars of a high-contrast stimulus (i.e. one that goes from black to white rather than shades of grey) become so small that you can no longer tell them apart. So if the world out there contains all different spatial frequencies there will be lots that we can't see, particularly those that fall above our resolution limit.

When we look at someone a long way away we can't tell much about them, but as they come closer their image gets bigger on our retinas, and more and more of the spatial frequency content of their image falls on the visible side of the resolution limit.

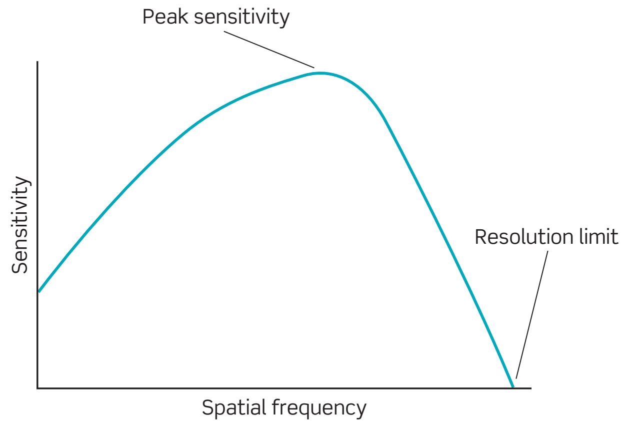

Figure 4.18 The contrast sensitivity function (CSF). The curve shows the point at which we fail to see the grating in Figure 4.17. We can see all spatial frequencies below the curve, but all information outside this 'window of visibility' remains unseen.

Details that were invisible now come into view. So a small figure becomes recognizable as a friend, and eventually we can see that she has a big red pimple on her nose and her mascara is all smeared. Of course, the pimple was always there as she approached, but when we first saw her, the spatial frequencies that defined the zit were beyond our resolution limit. So all the information that lies above our resolution limit is invisible to us, but so is any information that lies at lower spatial frequencies if its contrast is too low. The contrast sensitivity function describes our **window of visibility**; any information that lies above the curve is invisible, we can only see stuff below the curve.

The resolution limit—often termed **visual acuity**—is the point that conventional eye charts try to determine. You may be familiar with the Snellen chart used by opticians, with high-contrast letters of diminishing size (Figure 4.19). This is a good test for opticians to use, because it is a measure of the smallest thing that we can resolve. Many problems of early vision, such as a lens that is not able to focus the light coming into the eye, will cause the fine detail (the high spatial frequencies) to be lost. Hence, a test that measures our ability to detect the high frequencies is sensible. However, much of what your visual system is required to do has little to do with the fine detail. When driving down a motorway (freeway) it is rare that you will need to read the number plate of a car at some distance (a measure of your ability to see high spatial frequencies), but spotting a pedestrian about to step out on to the road, or a truck emerging from a fog bank, could be vital for your (and their) survival. These tasks are accomplished by detectors tuned to much lower spatial frequencies, and measuring contrast sensitivity to gratings of various spatial frequencies allows us a simple measure of performance at whatever spatial scale we wish. We shall see in other sections of the book that this method can be used to understand vision in many situations, such as what another animal or human infant can see.

In most images, there is information at many spatial frequencies, and therefore we need **channels** (a channel is a collection of neurons all with the same tuning characteristics) at lots of spatial frequencies to get this information. We are not normally aware of all these channels (be they spatial frequency or orientation) and the conscious perception we have is of a single image. However, we can illustrate the existence of such

Figure 4.19 The Snellen eye chart. High-contrast letters of progressively smaller size allow us to determine the resolution limit of the visual system. To have 20:20 vision means that you can see at 20 feet what a 'normal' person can see at 20 feet. The metric equivalent is 6:6 vision—20 feet is about 6 metres. Someone with 20:200 vision can see at 20 feet what a normal person can see at 200 feet. Such a person would be legally blind. If you are a young, fit, bright-eyed student and it's after 3 o'clock in the afternoon, your vision could well be 20:10—better than normal.

information by some simple demonstrations. Figure 4.20 has been made by blending two pictures into one. Two pictures were taken, one of the actor Anthony Hopkins and one of a skull (not Anthony Hopkins' skull). The two images were then filtered so that the high spatial frequency information was split from the low spatial frequency information (a bit like we did for our retinal ganglion receptive fields—remember Chapter 2?). The information from the high spatial frequencies of one image was then blended with the low spatial frequencies from the other (and vice versa for the other image). So, Figure 4.20a is made up of the blurry bits of Anthony Hopkins and the sharp edges of the skull, whilst Figure 4.20b is made up of the blurry skull and the sharp edges of Anthony Hopkins. What we see from a fairly close viewing distance, such as the distance the book is away from you now, is dominated by the higher spatial frequencies—you should see a skull in the image to the left and Tony to the right. However, we can do various manipulations that should make it hard to see the high spatial frequencies while still keeping the low ones. The easiest is simply to screw up your eyes (i.e. squint); alternatively, place tracing paper over the image. Both methods should have the same effect—the high spatial frequencies become less visible and you see the lower ones. The skull becomes Tony, and Tony becomes the skull.

⇛ See Chapter 2

What we have done here is that we have low-pass filtered the image. Remember straining the potatoes in Chapter 3? Blurring an image removes the high spatial frequencies, and they are the frequencies that contain the fine detail of a picture. But

⇛ See Chapter 3

(a) (b)

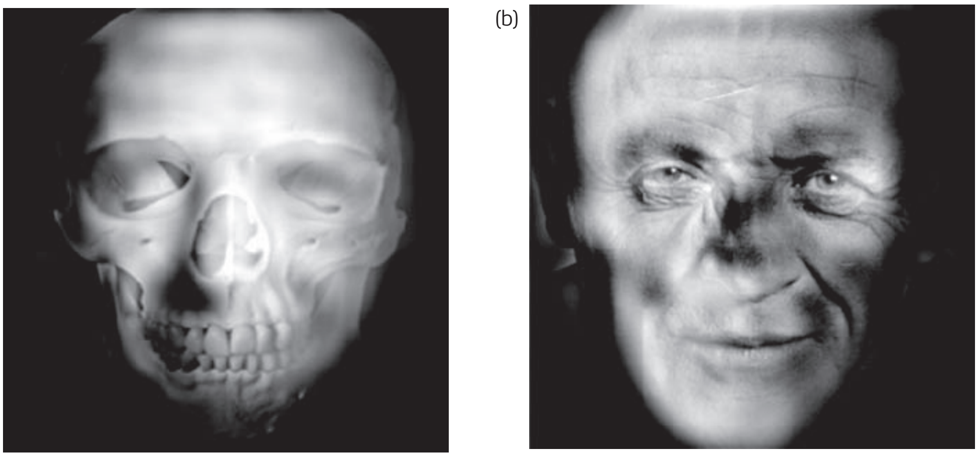

Figure 4.20 Sir Anthony Hopkins on the right and a skull on the left, or is it Hopkins on the left and a skull on the right? Look at these pictures close up and then from a distance: the skull and Sir Anthony will swap places.

perhaps a word of warning is in order here. You may have noticed that your bathroom window has blurry glass in it to protect your modesty from the prying eyes of the world. However, the next time you're cavorting naked in the shower, remember that the glass is only a low-pass filter; so it gets rid of just the high spatial frequencies. Therefore, although it will prevent your small fine details from being seen, your big blurry bits will still be on view to all.

So what is the point of all this spatial frequency stuff? What it means is that the image we see is actually broken up by our visual system into different channels that are handling information at different scales. You will remember that we have already described the way in which our visual system breaks up the image into different orientation channels, so it seems that the early part of the visual system is interested in the orientation of lines and edges and their size (see Figure 4.21). Psychophysical demonstrations (like the tilt after-effect or the simultaneous size illusion) show that the image that enters our eye is actually filtered by our visual system into discrete channels of activity at each point on the scene. This is a very efficient way of encoding the information and can be done by quite 'simple' cells that are biologically feasible. However, the problem is to go from this rather strange code of 'energy at particular spatial frequencies and orientations' to the objects that we really think we see.

Peripheral vision

Try viewing Figure 4.17 again, but now fixate a point about 10 cm below the pattern. The image of the grating no longer falls on a point in the centre of our vision (the fovea) but on a more peripheral part of our retina. You should now find it harder to see the high spatial frequency gratings, but the low frequencies appear to suffer very little. If high spatial frequencies are detected by small receptive fields, then this must mean that as we move into the peripheral parts of our vision we don't have very small

⇛ See Chapter 1

Figure 4.21 Two children on holiday. The three lower images show the information from this picture in the low, middle, and high spatial frequency bands.

receptive fields; indeed, when we go far into the periphery we are eventually left with just the large receptive fields. So, in our far peripheral vision we can only detect low spatial frequencies. Figure 4.22 shows what happens to contrast sensitivity across the visual field. Clearly, in the periphery we only see low spatial frequencies, and even those must be of a high contrast for us to see them. One influential idea is that peripheral vision is actually just like foveal vision, only coarser. So we could actually make our peripheral vision as good as our central vision by simply magnifying the image. This idea is illustrated in Figure 4.23. Here, an 'eye chart' has been constructed where

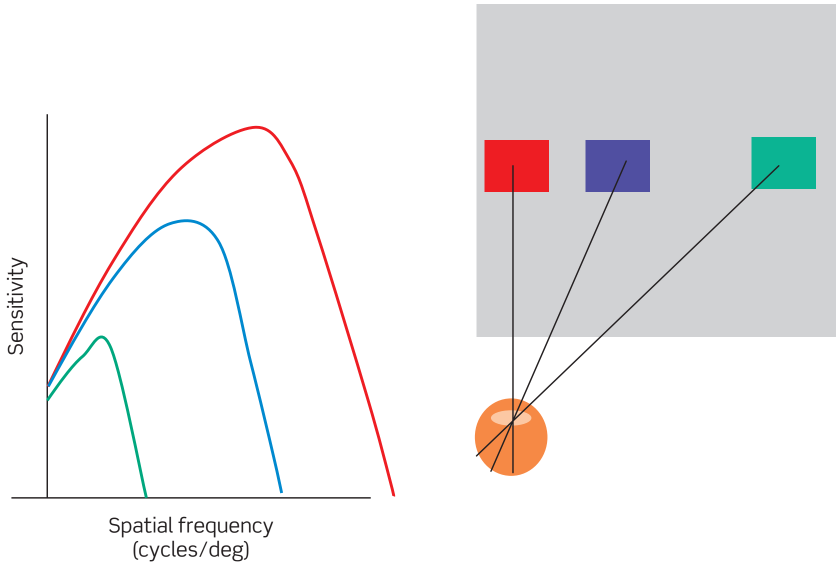

Figure 4.22 Contrast sensitivity in peripheral vision. As we move away from central vision we lose the ability to see high spatial frequencies.