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Contrast Gain in the Brain

Human sensory systems have the remarkable ability of adjusting sensitivity to the surrounding environment. In this issue of *Neuron*, Gardner and colleagues used fMRI to show how the visual system shifts its sensitivity to contrast. This process may be helpful for keeping the appearance of contrast constant across a range of spatial frequencies.

We've all had the experience of being temporarily blinded when walking out of a movie theater into bright sunlight. This happens because the photoreceptors in your eye have adjusted to the dark environment of the theater at the cost being unable to cope with the intensity of outdoor light levels. The bright sunlight saturates your visual system, just like an ammeter needle that pegs at maximum when the gain knob is set too low. Your eyes can tell you that there is a lot of light out there, but nothing about the differences in light intensity—at least until your photoreceptors change their gain back to daylight levels again.

It might seem that the primary purpose of the eye is to detect the *presence* of light. But the important information about the visual world is in the *differences* in light levels relative to the mean. This relative difference in light levels is called *contrast*, and it is contrast, not light level, that is the primary signal passed out of the eye into the primary visual cortex.

The primary purpose of light adaptation is to maximize sensitivity to differences in light levels around the mean level of the environment. But this process of adaptation does not occur only in the eye. It seems that a similar adaptive process happens again in the visual cortex. In this issue of *Neuron*, Gardner and colleagues used fMRI to show evidence that the visual system also adjusts itself to ambient amounts of contrast in the scene (Gardner et al., 2005).

Nearly all neurons in the visual cortex increase their firing rates with contrast, starting from a baseline response with zero contrast (a uniform field) to a maximal response with a contrast of 100%. Neural *contrast response* functions in the primary visual cortex look like the two shown in Figure 1. Notice that the blue contrast response function on the left is ideally suited to detect differences in contrast between 2% and about 25%. But for contrasts above 25% it can only respond at its maximal level.

Gardner et al. measured contrast response functions in the human visual system by using a clever method that measured both increases and decreases in fMRI responses around a mean level of contrast. They showed that, after prolonged exposure to high contrasts, the "dynamic range" of the contrast response function in early cortical visual areas shifted from something like the blue curve in Figure 1 rightward to the green curve. This process of "contrast gain" was originally found in electrophysiological studies in cats (Ohzawa et al., 1985), but this is the first evidence of it in the human visual cortex.

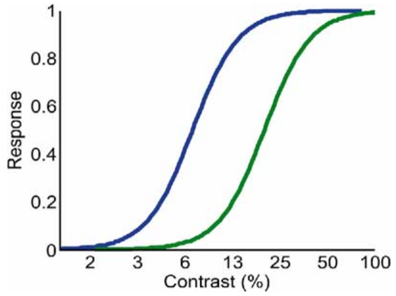

Figure 1. Example Contrast Response Functions Before (Blue) and After (Green) Adapting to High Contrasts

The visual system appears to adjust its contrast gain so that it is optimal for detecting differences in contrasts around the new average level of contrast. This means that, just as for light intensity and the eye, detecting the presence of contrast in a scene is less important to the visual cortex than detecting differences in contrast.

In fact, Gardner et al. may have discovered the part of the brain that is calculating these differences in contrast. They found U-shaped contrast response functions in cortical area V4 of the human visual system that show minimal responses at the mean level of contrast. That is, V4 responds positively to both contrast increments and decrements and therefore may be detecting changes in contrast around the mean.

What is contrast gain good for? Light adaptation is important because normal light intensities can range across more than ten orders of magnitude (but photoreceptors typically have a dynamic range of only one to two orders of magnitude). Contrast, however, ranges between a distinct maximum and minimum, and typical visual neurons cover most of that range (see Figure 1).

Perhaps, instead, contrast gain allows the visual system to compensate for its variable sensitivity across spatial frequencies. Consider the image in Figure 2, which contains a sinusoidal grating that increases in spatial frequency horizontally and decreases in contrast vertically (Campbell and Robson, 1968). Notice that, although the physical contrast is constant across any horizontal section of the image, the point at which the image fades to gray varies so that the highest and lowest spatial frequencies need a higher contrast to be seen. But note also that, along the bottom of the image where the grating is always visible, the contrast appears roughly constant and does not vary with spatial frequency.

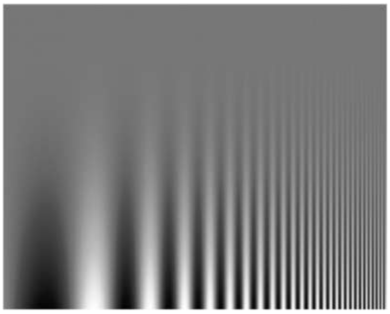

Figure 2. Contrast Sensitivity Varies with Spatial Frequency, but Contrast Appearance Does Not

Blurring by the optics of the eye and limited sampling by the eye's photoreceptors are two factors that contribute to this loss of sensitivity to high and low spatial frequencies. But even though the eye is less sensitive to high and low spatial frequencies, high-contrast stimuli are perceived correctly across a wide range of spatial frequencies—a phenomenon called "contrast constancy" (Georgeson and Sullivan, 1975). Contrast gain could support contrast constancy by boosting the apparent contrast of high and low spatial frequencies.

Contrast constancy could help us to correctly perceive the properties of objects in the world as unchanging with distance and size. As an object shrinks into the distance, its spatial frequencies shift upward. But more distant (or smaller) objects change their apparent contrast. Similarly, you might notice that although the lower rows of an eye chart may be more difficult or impossible to read, the letters in these rows do not appear lower in contrast. Also, if you step away from the image in Figure 2, the envelope marking where the image fades to gray will shift, but the bottom of the image will always appear to have the same contrast.

Gardner et al. show that contrast gain occurs within minutes of exposure to a change in ambient contrast level. This time course is consistent with a recent behavioral study showing that, after prolonged viewing of blurry images, normal images subsequently appear "too sharp" (Webster et al., 2002). However, we have only recently begun to understand some of the basic properties of contrast gain in the human visual system.

For example, contrast gain may also be long lasting. One patient, after having bilateral cataracts removed well into adulthood, perceived sharp edges as scalloped—even more than a year after his operation. This scalloping indicates that the contrast of the edges' higher spatial frequencies was overestimated by his visual system. Interestingly, before his operation, sharp edges did not appear blurry to him, despite the poor optics of his eyes (Fine et al., 2002).

Horace Barlow once wrote, "you can get used to anything," (Barlow, 1997) meaning that our sensory systems are constantly adapting to changes in the environment. Just as our eyes adapt to the incoming light levels, early visual areas in the cortex adapt to the contrast information coming in from the eye. As these contrast signals are passed further along the visual system, adaptation occurs once again in higher visual areas. Human behavioral and neuroimaging studies are now showing how our visual system adapts to higher-level visual processes such as motion (Seiffert et al., 2003), color (Engel and Furmanski, 2001), and even faces (Webster et al., 2004). Our percept of the world is not just a simple reflection of its physical properties. Instead, it is a constantly changing interpretation that is influenced by our experience over the past few minutes, days, and lifetime.

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