

Color Vision: How the Cortex Represents Color

Dispatch

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Our understanding of how we see color has benefited from the long tradition of visual psychophysics. More recently, models and methods from psychophysics are guiding modern neuroimaging experiments on color vision. Combining the two techniques can lead to discoveries that neither can make alone.

Why are stars not visible in the sky during the day, even though they give off just as much light as they do at night? In general, the ability to see a faint target decreases with increasing background intensity. This phenomenon, called light adaptation, shifts the operating range of the visual system to match the intensity of the environment. One view of light adaptation is that it is primarily the result of changes in the 'gain', or sensitivity, of the cone photoreceptors in the eye. The normal eye has three classes of cone photoreceptors, each sensitive to a different — but overlapping — range within the spectrum of visible light. The idea is that each cone changes its sensitivity in proportion to the average light level it receives. This hypothesis is supported by a simple psychophysical experiment: increasing the background to adapt the short-wavelength (S) sensitive cones alone makes a target detected by the S cones harder to see, but does not affect the ability to see targets detected by the long (L) and medium (M) wavelength cones.

Psychophysical experiments such as this require a model that links the underlying neuronal response to an observer's percept. A classic model of color perception incorporates stages of processing at the levels of the photoreceptors, the ganglion cells that transmit information from the eyes to the brain, and the primary visual cortex (V1) [1,2] (Figure 1). Neuronal signals in the cortex are assumed to be noisy, so that the response varies from trial to trial. When comparing a weak target against a background to the background alone, noise in the response to the background can occasionally exceed the response to the target, causing an ideal observer to make a mistake [3].

Such models make quantitative predictions about neuronal responses along the cascade of events leading to perception. Indeed, psychophysicists are proud to point out that many 'discoveries' made by physiologists were in fact already predicted from models of behavioral performance. But as psychophysical experiments only measure the final perceptual and decision stages of a visual event, psychophysics alone cannot confirm *where* the underlying brain responses occur.

Functional magnetic resonance imaging (fMRI) is therefore an ideal companion for psychophysics. fMRI measurements reflect blood-oxygen-level-dependent (BOLD) changes in cerebral vasculature associated with changes in underlying neuronal responses [4]. Although the cascade of events from neuronal response to the BOLD effect is not well understood, it appears that the BOLD response is roughly proportional to underlying neuronal activity averaged over a few millimeters in space, and several seconds in time [5,6]. Thus fMRI measures the response across a neuronal population, much like the predicted responses in typical psychophysical models. fMRI is complementary to psychophysics because it can tell *where* a neuronal event occurs, but it provides little information about how these responses relate to our experience and behavior.

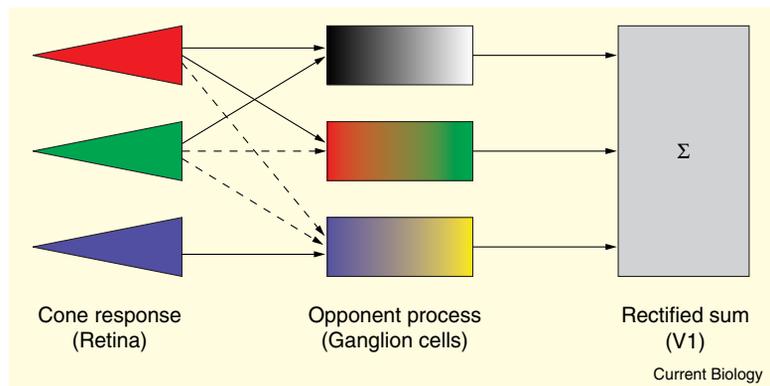
An excellent example of a useful combination of psychophysics and fMRI is a recent study by Wade and Wandell [7] on chromatic light adaptation. In their psychophysical and fMRI experiments, target stimuli designed to excite either the S cones alone, or the L and M cones alone, were presented on a variable background. When the background was changed to increase the input to the S cones alone, the fMRI response *and* the ability to detect an S cone target decreased. Similarly, when the background was changed to increase the input to the L and M cones, then L and M cone targets produced lower fMRI responses and were harder to detect. Most importantly, behavioral measurements and fMRI responses to S cone targets were not strongly affected when changes in the background affected only the L and M cones, and *vice versa*.

Wade and Wandell [7] then made a quantitative comparison of the psychophysical and fMRI measurements by applying the classic model of color perception. In their experimental design, the target intensity was held constant as the background intensity increased (Figure 2A). When changes in target and background affected the same cone type, the decrease in gain with increasing background intensity caused a decreasing response to the target (Figure 2B). This led to poorer performance, as predicted by the ideal observer (Figure 2C). By assuming that the response to the target is reflected in the fMRI response in V1, Wade and Wandell [7] found that the changes in gain estimated from the fMRI responses closely predict the changes in the observer's performance.

My colleagues and I [8] used a similar approach to study the role of V1 responses in the ability to discriminate contrast. Keeping the background constant, black and white (luminance) stimuli were presented to subjects who were asked to detect an increment in contrast above a baseline contrast. The task is similar to Wade and Wandell's [7] if the baseline contrast stimulus is thought of as the background, so the increment in contrast acts as a superimposed target.

Figure 1. A classic model of color perception.

Light with a given spectrum differentially excites the S, L and M cones in the retina. These three signals are added (dark lines) and subtracted (dashed lines) in the retina to form three opponent mechanisms — the red–green, blue–yellow, and luminance mechanisms — which are relayed by the ganglion cells to the cortex. V1 responses in the cortex reflect a rectified and summed response from the three opponent mechanisms.



Unlike Wade and Wandell [7], we adjusted the contrast increment for each background level so that the subject's performance would always be 80% correct (Figure 2F). Keeping the performance level of an ideal observer constant keeps the response to the target constant across baseline intensities (Figure 2E).

As in earlier studies of contrast discrimination [9], we found that the contrast increment needed to maintain constant performance increased with baseline contrast (Figure 2D) [8]. These behavioral results were then compared to fMRI responses to stimuli across a range of contrasts. fMRI contrast–response functions in V1 were found to increase monotonically, but with decreasing slope. This is qualitatively consistent with the behavioral performance because it means that, as the baseline contrast increases, a larger contrast increment is needed to increase the V1 response to a level that leads to constant discrimination performance. As in Wade and Wandell's [7] study, a quantitative model of V1 responses was able to predict both fMRI responses and contrast discrimination thresholds.

The ability of fMRI responses in V1 to predict the effects of both chromatic adaptation and contrast-gain control is interesting because, while chromatic adaptation appears to occur mainly within the photoreceptors [10], contrast gain control is believed to be carried out within the cortex [11]. Thus responses in V1 can not only predict changes in behavioral performance caused by gain changes in the input signals

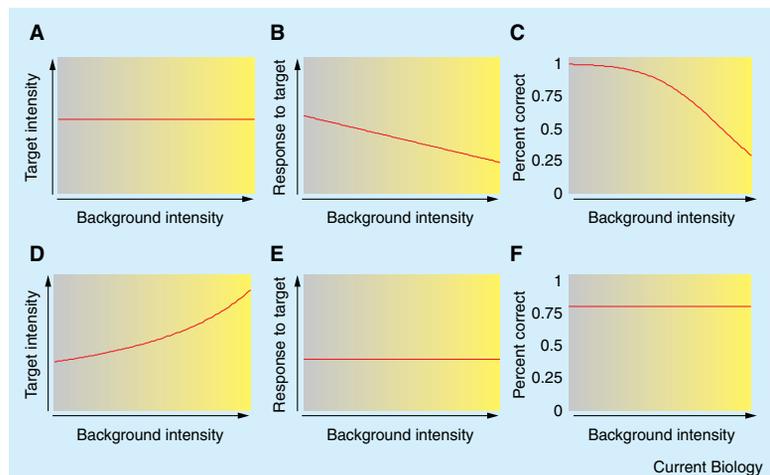
to V1, they are also consistent with gain changes occurring within V1 itself.

Over the past few years there have been an increasing number of studies combining fMRI and visual psychophysics. In a study closely related to the two described above, Engel and Furmanski [12] showed that V1 responses adapted to chromatic contrast in a manner that qualitatively matched changes in the perceived contrast after adaptation. In an earlier study, Engel *et al.* [13] found that evidence of opponent color mechanisms measured psychophysically was consistent with V1 responses measured with fMRI. Also, a pair of papers [14,15] on the efficacy of S cones on motion processing reported that, compared to luminance stimuli, stimuli that only excited the S cones reduced the fMRI response in a motion-sensitive area of the brain — the medio-temporal area, MT — in a manner that qualitatively matched the reduction in the perceived speed of the same moving stimuli.

Psychophysics and functional imaging may seem at first to be totally unrelated, if not opposing methods for studying the brain. fMRI is only about a decade old, while psychophysics has been around for well over a century; fMRI requires specialized, expensive equipment with a staff of physicists to maintain it, while psychophysics can be done in your own garage with a home computer. But these recent studies that combine the two techniques show how the application of psychophysical models and behavioral measurements can serve as a great supplement to fMRI.

Figure 2. The relationship between gain control and psychophysical performance.

Given a fixed target intensity across all background intensities (A), gain changes in response to the increasing background will decrease the response to the target (B), thereby resulting in poorer performance for detecting the target against the background (C). If the target intensity is increased with the background (D) in such a way to keep the response to the target constant (E), then psychophysical performance will remain constant across all background intensities (F).



Glowing fire-colored patches superimposed on a computerized rendered brain may look impressive, but simply knowing where the brain becomes active to a given stimulus is not always enough. Ultimately, we would like to know how these brain responses relate to our perceptual experience, thereby closing the gap between brain and behavior.

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