

# Forward and Backward Masking with Brief Chromatic Stimuli

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*Abstract:* Visual masking typically occurs when mask and target are separated in time by less than 100 ms, and the form of this interaction might be expected to depend on the latency of the target and mask signals. We track psychophysically the time course of signals from the two colour-opponent channels by using forward and backward masking, in which mask and target each stimulate only one colour channel. Stimuli resemble those used in the Cambridge Colour Test,<sup>1</sup> in that spatial luminance noise is used to ensure that neither edge artifacts nor luminance differences can be used as a cue to discrimination of the stimulus against the field. Additionally, we introduce temporal luminance noise in order to ensure that our very brief chromatic modulations are not detected via the magnocellular pathway. Our data suggest that there is no large latency difference between the two chromatic channels of the early visual system, and that previous evidence for such a difference may instead reflect a difference between chromatic and achromatic pathways. © 2000 John Wiley & Sons, Inc. *Col Res Appl*, 26, S165–S169, 2001

*Key words:* latency; masking; colour opponent; koniocellular; magnocellular; luminance noise

## INTRODUCTION

Current models of the early stages of human colour vision assume that the initial trichromatic stage feeds into one or more achromatic channels and two chromatic channels: one comparing the long-wave (L) and middle-wave (M) cone signals, and the other comparing signals from short-wave (S) cones and some combination of L- and M-cone signals.<sup>2</sup> The two chromatic channels are thought to have evolved at

different times and their substrates remain morphologically distinct.<sup>3–5</sup>

There is a strong tradition of suggestions that the short-wave chromatic response has disproportionately long time constants.<sup>6</sup> When critical durations or reaction times were measured for liminal increments under conditions that isolate Stiles'  $\pi$  mechanisms,<sup>7</sup> both integration times and latencies were found to vary with the adaptive state of the mechanism responsible for detection and did not depend on the adaptive state of the retina as a whole.<sup>8–10</sup> In particular, latencies were longest for the short-wave system: the largest latency difference occurred with liminal stimuli, but even asymptotic reaction times to suprathreshold stimuli were as much as 50 ms slower in the case of  $\pi_1$ , the short-wave mechanism.<sup>10</sup> Mollon and Polden<sup>11</sup> described a phenomenological demonstration of the longer latency of the  $\pi_1$  mechanism: objectively colinear red and blue bars appear out of phase when swept across a yellow adapting field.

Robson and Kulikowski<sup>12</sup> reported particularly long VEP latencies for chromatic modulations along a tritan axis, a result that they ascribe to the relative slowness of the S-cone driven pathway. And very recently Cottaris and DeValois<sup>13</sup> claimed that the "sluggish" S-opponent signals become available in V1 only at a latency of 96–135 ms compared to the L/M-opponent signals, which are available at a latency of 68–95 ms.

A modern explanation for this latency difference might be found in the morphology of the S-cone driven pathway. Conduction velocity is proportional to axon diameter and, in so far as axon diameter reflects soma size, we might attribute the relative delay of the short-wave pathway to the koniocellular units that we now know to carry its signals.<sup>5,14,15</sup>

Our masking experiments were designed to track psychophysically the time course of signals from the two chromatic channels. A masking stimulus typically raises threshold for detection of the target when the two stimuli are separated in time by less than 100 ms. The form of this interaction might be expected to depend on the relative latency of the target

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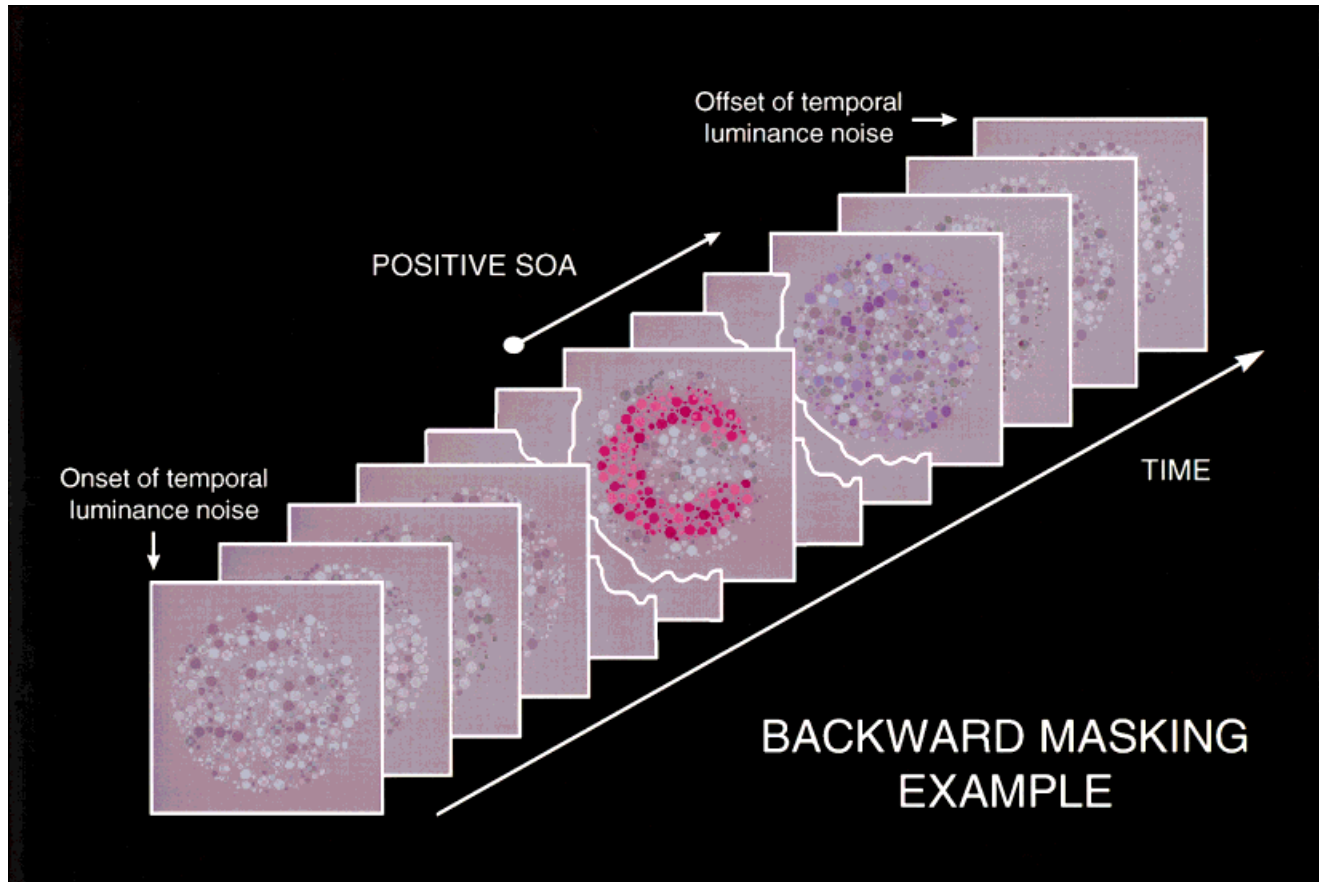


FIG. 1. A schematic representation of the sequence of visual events in a backward masking trial, where the violet-coloured noise mask followed the cherry-coloured target in time. In forward masking trials, the mask preceded the target in time. In the experiments, stimuli were embedded in 61 frames of temporal luminance noise, though in this diagram many of the uniform chromaticity buffer frames have been omitted from the beginning and end of the train. Stimulus-onset asynchrony (SOA) was manipulated: the shortest interval used was a single frame (10 ms) such that target and mask were presented on consecutive frames. The longest interval used was 10 frames (100 ms). The target was always presented in the center of the noise train and, at longer intervals, the mask was displaced closer to the end of the train. A new spatial pattern was drawn for each trial, and temporal luminance noise began 500 ms after this appeared. After the offset of temporal luminance noise, the pattern remained until the subject's response was recorded.

and mask signals and we might suppose, for example, that in order to mask an L/M opponent signal a sluggish S-opponent signal would need a head-start.

The chromatic channels of the human visual system are difficult to isolate. Unwanted luminance differences may arise from nonlinearities in the display or from variations among observers and retinal positions. Edge artifacts may occur at the boundaries between two hues owing, for example, to misconvergence of the guns of a monitor or to chromatic aberration of the eye. In addition, temporal transients are keenly detected by the visual system and even at equiluminance chromatic modulations may be detected by the magnocellular pathway.<sup>16</sup> In the masking experiments presented here, we use spatial luminance noise<sup>17,18</sup> and temporal luminance noise<sup>19,20</sup> to ensure that achromatic pathways cannot detect our chromatic stimuli.

#### METHODS

Stimuli were presented on a Sony Multiscan colour monitor (17se II), running at a frame rate of 100 Hz and controlled

from the host PC via a Cambridge Research Systems (CRS) Visual Stimulus Generator graphics board (VSG/2.3). The monitor had been gamma corrected using the CRS OptiCAL system. The MacLeod–Boynton chromaticity coordinates<sup>21</sup> of each of the phosphors were derived from spectral radiance measurements of the phosphor multiplied by the Smith and Pokorny cone fundamentals.<sup>22</sup> Gun weightings for chromaticities defined in MacLeod–Boynton space were then calculated via the center of gravity rule. Phosphor decays were measured, and the time taken for discharge of half the energy of a single frame presentation of a 20 cd/m<sup>2</sup> patch was estimated at 0.5, 1.0, and 1.2 ms for the R, G, and B guns, respectively.

Figure 1 shows a schematic representation of our stimuli. As in pseudo-isochromatic plates, the stimulus area in our experiments was broken down into many small, circular elements and, instead of trying to equate the luminance of target and field, we varied the luminance of the individual elements: each element was randomly assigned a luminance between  $\pm 2$  cd/m<sup>2</sup> of the average luminance of 18 cd/m<sup>2</sup>.

The initial chromaticity of the individual patches of the

## (A) Observer JDM

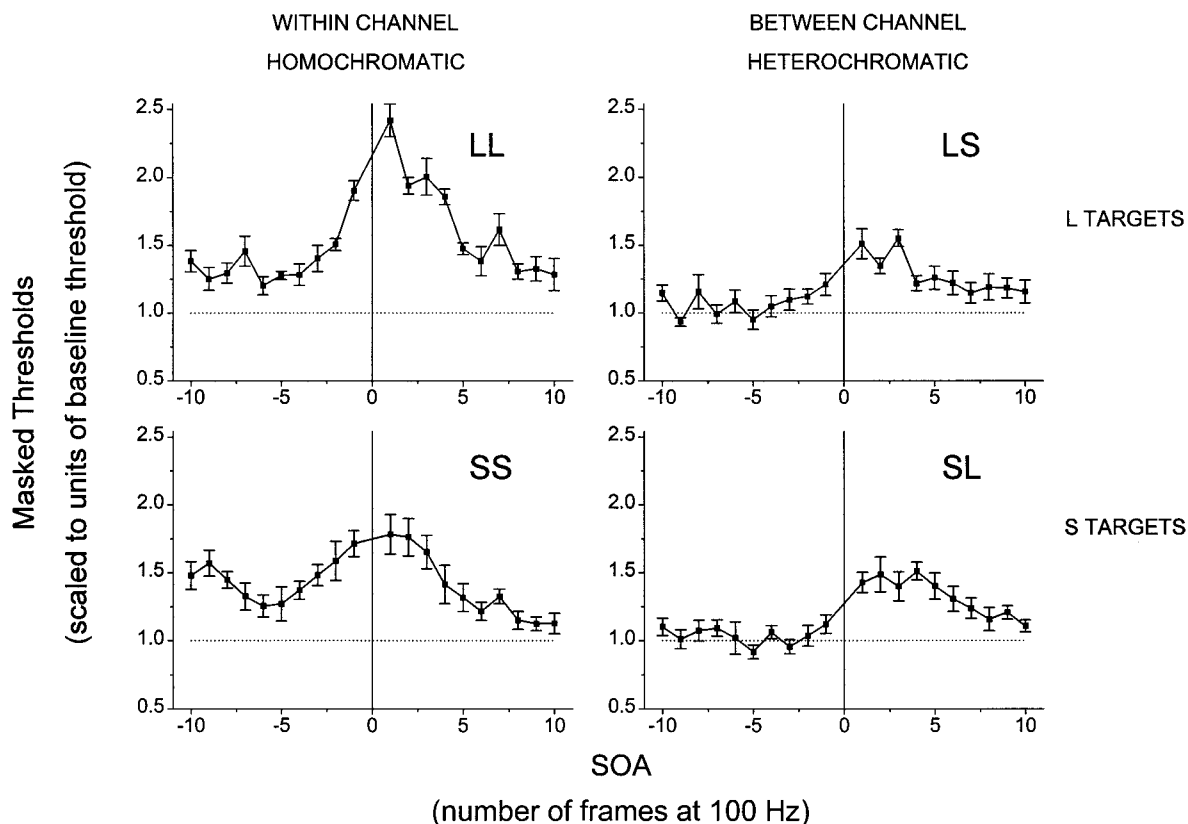


FIG. 2. (A) Data from observer JDM. Masked thresholds, scaled to units of baseline threshold, are plotted against SOA. A higher value on the ordinate indicates more masking. The labels, LL, LS, SS, and SL identify the conditions by the order of chromaticities in a backward masking trial (i.e., target followed by mask). Each data point is the average of the end-points of 8 staircases, and error bars show  $\pm 1$  standard error. (Figure continued on next page.)

array was approximately that of equal-energy white, and they were set within a steady field of the same chromaticity. For mask and target, a subset of elements was changed to the required chromaticity for a single frame only. To prevent the magnocellular pathway from mediating detection of these brief chromatic modulations, we embedded them in a train of temporal luminance noise: the luminance of each patch changed from frame to frame and the chromaticity of each patch could be modulated independently of luminance changes.

Targets comprised a coloured ring with a gap at one of four possible locations (similar to the stimuli used in the Cambridge Colour Test<sup>1</sup>) and the subjects' task was to indicate, by pressing one of four buttons, the location of the gap. In a masked discrimination task, as used here, the subject may be able to learn a set of consistent local features in the compound percept of mask + target, and Watson<sup>23</sup> has shown that successful masking is a function of the observer's ignorance about the stimuli. In our experiments, the spatial properties of the masks were random and were different from trial to trial: for each mask, random elements of the stimulus area were coloured such that the area of coloured elements was equal to the area of coloured elements in a C-shaped target stimulus.

To study the relative latencies of the two chromatic channels, we used the 4 possible permutations of masks and targets defined by chromaticity vectors along the +L direction of the l/m-axis of MacLeod-Boynton space and along the +S direction of the s-axis of MacLeod-Boynton space. We defined equivalent masks along the two axes in terms of multiples of threshold relative to the reference chromaticity.<sup>24</sup>

Figure 1 shows a between-channels, backward masking example, where the violet-coloured noise mask follows the cherry-coloured target in time. The test sequence of target-blank-mask for backward masking or mask-blank-target for forward masking was embedded in 61 frames of temporal luminance noise, and the target was always presented in the center of the noise train. The shortest stimulus-onset asynchrony (SOA) used was a single frame (10 ms at the frame rate of 100 Hz) such that target and mask were presented on consecutive frames. The longest interval used was 10 frames (100 ms). For a baseline threshold measurement, a similar noise train was used but with no chromatic masking stimulus.

During an experimental session, the mask chromaticity was held constant while the chromaticity of the target was modified adaptively until a threshold chromaticity differ-

## (B) Observer HES

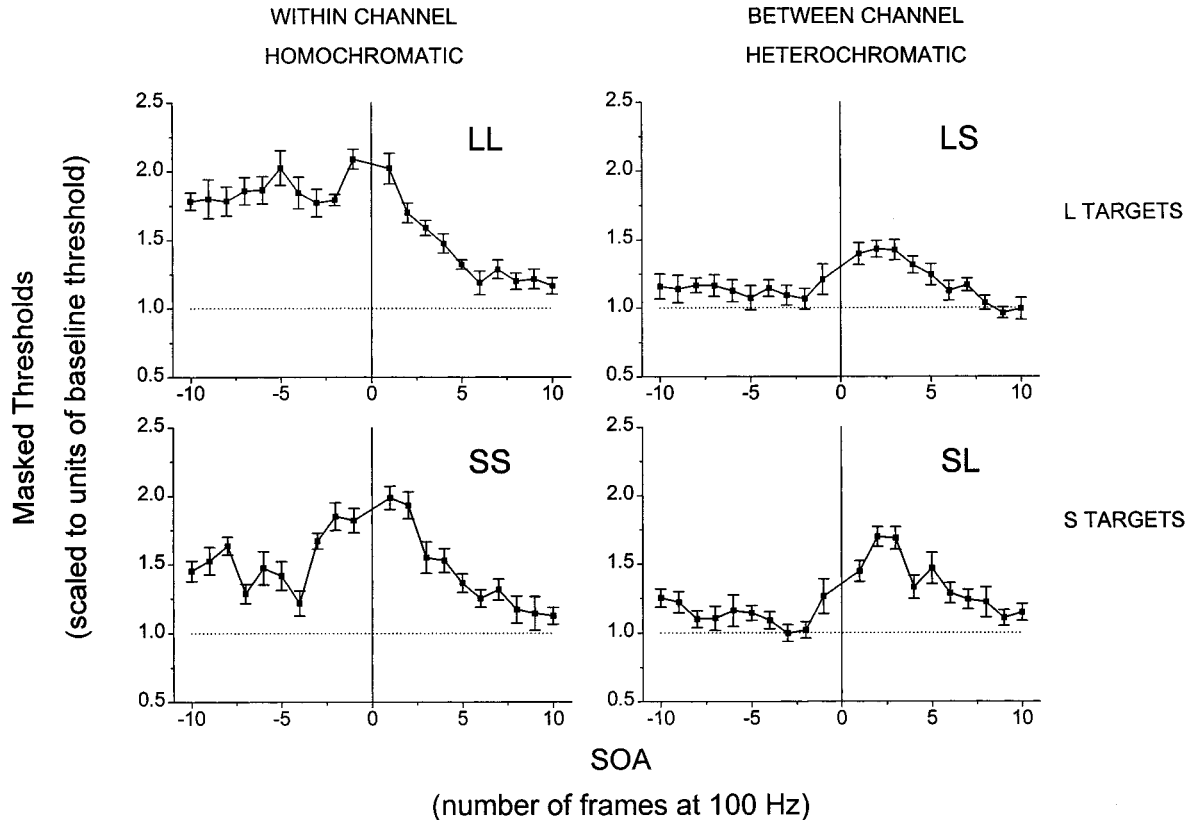


FIG. 2. (Continued) (B) Data from a second observer, HES.

ence between background and target was found. All threshold measurements were grouped in blocks of 6 randomly interleaved staircases. Each staircase in the block used the same target and mask chromaticity combination, though the temporal separation between mask and target was different for each staircase. One staircase was always used to measure baseline thresholds to allow us to control for effects of practice.

### RESULTS

The masking function relates the threshold in the presence of the mask to the time course of the stimulus presentation. Data from two observers with normal colour vision are plotted in Fig. 2. We see that there is significant forward masking when mask and target excite the same subsystem (LL and SS) and virtually no forward masking in the between-channel cases (LS and SL). This selectivity of forward masking is consistent with Krauskopf's theory of independent, cardinal directions, where modulation along one axis does not affect performance along the other.<sup>25</sup>

Particularly important for the latency question is that, for both S and L targets, the peak of the between-channel masking function is shifted in time relative to the peak of the within-channel masking function. In both within-channel conditions, the masking is greatest when mask and target

are presented close together in time. This is consistent with a model where mask and target signals have the same time course. The between-channel conditions are the key to the relative latencies of the two subsystems. If we suppose that Cottaris and DeValois<sup>13</sup> are correct and S-opponent signals are tens of ms slower than L/M-opponent signals, then the maximum masking of S targets by L masks should occur at positive SOAs and, conversely, the maximum masking of L targets by S masks should occur at negative SOAs. For S targets and L masks (bottom right) our data are consistent with the sluggish S-signals being most effectively masked by a delayed L mask. On the other hand, for L targets and S masks (top right), we should expect the maximum masking effect to occur with negative SOAs, when the sluggish S mask was given a head start. There is no evidence for this.

### DISCUSSION

It is not easy to isolate the chromatic channels of the human visual system, owing to the individual variations in luminance setting, the variations in settings across the visual field, and the edge artifacts that arise from chromatic aberration and imperfections of monitors. In addition, if the response is to be made to a temporal transition from one chromaticity to another, the nominally equiluminant transition may be visible to the magnocellular pathway, as Lee,

Martin, and Valberg<sup>16</sup> have demonstrated in recordings from macaque ganglion cells (although, significantly, the contamination may be absent if the modulation is along a tritan line). By using our flickering pseudo-isochromatic plates, we believe we can produce brief stimuli that do isolate the chromatic channels.

Historically, experiments that used either Stiles' method or hue substitution may have failed to isolate chromatic channels when the L- and M-cones were modulated, but may have succeeded in isolating a chromatic channel when only the S-cones were modulated. The contrast is between the L- and M-cones, which have access to a variety of post-receptor channels, and the S-cones, whose response is thought to be intrinsically confined to a chromatically opponent pathway. The present results suggest that little variation in latency is present when the neural signals are securely corralled in chromatic channels.

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1. Mollon JD, Reffin JP. A computer-controlled colour vision test that combines the principles of Chibret and of Stilling. *J Physiol* 1989;414:5P.
2. Kaiser PK, Boynton RM. Human color vision. Washington, DC: Opt Soc Am; 1996.
3. Mollon JD. "Tho' she kneel'd in that Place where they grew. . ." The uses and origins of primate colour vision. *J Exp Biol* 1989;146:21–38.
4. Dacey DM, Lee BB. The 'blue-on' opponent pathway in primate retina originates from a distinct bistratified ganglion cell type. *Nature* 1994;367:731–735.
5. Hendry SH, Yoshioka T. A neurochemically distinct third channel in the macaque dorsal lateral geniculate nucleus. *Science* 1994;264:575–577.
6. Stromeyer CE. The perception of colour. *Nature* 1887;36:246.
7. Stiles WS. The directional sensitivity of the retina and the spectral sensitivities of the rods and cones. *Proc R Soc (Lond) B* 1939;127:64–105.
8. Krauskopf J, Mollon JD. The independence of the temporal integration properties of individual chromatic mechanisms in the human eye. *J Physiol* 1971;219:611–623.
9. Uetsuki T, Ikeda M. Adaptation and critical duration for Stiles  $\pi$  mechanisms. *J Opt Soc Am* 1971;61:821–828.
10. Mollon JD, Krauskopf J. Reaction time as a measure of the temporal response properties of individual colour mechanisms. *Vision Res* 1973;13:27–40.
11. Mollon JD, Polden PG. Some properties of the blue cone mechanism of the eye. *J Physiol (Lond)* 1976;254:1P–2P.
12. Robson AG, Kulikowski JJ. Objective specification of tritanopic confusion lines using visual evoked potentials. *Vision Res* 1998;38:3499–3503.
13. Cottaris NP, De Valois RL. Temporal dynamics of chromatic tuning in macaque primary visual cortex. *Nature* 1998;395:896–900.
14. Martin PR, White AJ, Goodchild AK, Wilder HD, Sefton AE. Evidence that blue-on cells are part of the third geniculocortical pathway in primates. *Eur J Neurosci* 1997;9:1536–1541.
15. Calkins DJ, Meszler LB, Henry SHC. Multiple ganglion cell pathways provide input to the koniocellular neurons of macaque LGN. *Invest Ophthalmol Vis Sci* 1998;39:S238.
16. Lee BB, Martin PR, Valberg A. Nonlinear summation of M- and L-cone inputs to phasic retinal ganglion cells of the macaque. *J Neurosci* 1989;9:1433–1442.
17. Stilling J. Die Prüfung des Farbensinnes beim Eisenbahn- und Marinepersonal. Cassel: Theodor Fischer; 1877.
18. Regan BC, Reffin JP, Mollon JD. Luminance noise and the rapid determination of discrimination ellipses in colour deficiency. *Vision Res* 1994;34:1279–1299.
19. Mollon JD. Color vision. *Ann Rev Psychol* 1982;33:41–85.
20. Birch J, Barbur JL, Harlow AJ. New method based on random luminance masking for measuring isochromatic zones using high resolution colour displays. *Ophthalmic Physiol Opt* 1992;12:133–136.
21. MacLeod DIA, Boynton RM. Chromaticity diagram showing cone excitation by stimuli of equal luminance. *J Opt Soc Am* 1979;69:1183–1186.
22. Smith VC, Pokorny J. Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Res* 1975;15:161–171.
23. Watson AB. Entropy masking. *Perception* 1997;26:S2.
24. Boynton RM, Nagy AL, Olson CX. A flaw in equations for predicting chromatic differences. *Col Res Appl* 1983;8:69–74.
25. Krauskopf J, Williams DR, Heeley DW. Cardinal directions of color space. *Vision Res* 1982;22:1123–1131.