Simple Reaction Times in Color Space: The Influence of Chromaticity, Contrast, and Cone Opponency

Declan J. McKeefry, Neil R. A. Parry, and Ian J. Murray

PURPOSE. This study examined the influence of stimulus chromaticity on simple reaction times (RTs) to determine the stage of chromatic processing that is most influential in their generation.

METHODS. Simple RTs were measured in response to the cosinusoidally ramped onset of small, equiluminant, colored Gauss–ian spots. The chromaticity of these stimuli was varied, to modulate along a series of vectors in color space that included red-green (L-M) and blue-yellow (S-[L+M]) opponent axes.

RESULTS. RTs are highly sensitive to small departures from subjective equiluminance. They are also dependent on stimulus chromaticity. The longest RTs are generated in response to equiluminant stimuli that isolate S-cone activity, whereas the shortest are generated by stimuli that modulate the L-M opponent axis. However, temporal processing differences are highly dependent on how the chromatic stimuli are scaled in relation to one another. The differences are reduced when scaling is based on detection threshold. The relationship between chromatic contrast and RT can be described by the modified Piéron equation $RT = RT_0 + k \times C^{-1}$.

CONCLUSIONS. Simple RTs generated in this study conform to the idea that they are largely determined by cone-opponency mechanisms. The use of cone contrast as a metric for scaling chromatic stimuli exaggerates differences between the temporal responsiveness of L-M and S-(L+M) opponency mechanisms. (Invest Ophthalmol Vis Sci. 2003;44:2267–2276) DOI:10.1167/iovs.02-0772

Contemporary models of color vision assume that, preconsciously, chromatic information is extracted through two independent postreceptoral cone-opponency channels, processing red-green (L-M) and blue-yellow (S-[L+M]) information (where S, M, and L represent input from short-, middle-, and long-wavelength sensitive cones, respectively). However, this cone-opponency model is not entirely satisfactory when it comes to explaining various adaptation effects that point to the existence of more than two chromatic mechanisms. Furthermore, cone opponency is unable to account for the fact that the sensations of “pure” red, green, and blue, the so-called unique hues, do not match the stimuli that isolate the (L-M) and S-(L+M) channels. This means that the information flow along color-opponent channels must undergo several transformations that culminate in color appearance. The number of these mechanisms and where they arise in the visual pathway are matters of some conjecture. Nevertheless, it seems likely that a major role is played by the primary visual cortex (V1), at a site beyond the laminae, that receive input from the lateral geniculate nuclei (LGN). There is a broad distribution of chromatic preferences in the cortex and there are a number of neurons that respond equally well to modulation of luminance and chrominance.

In contrast to the cortex, the LGN has only two kinds of chromatic cells, coding red-green or blue-yellow information. Blue-yellow information is transmitted along a separate pathway composed of small, bistratified ganglion cells. The red-green- and blue-yellow-coded cells provide the substrate for simple color opponency. Nonchromatic (luminance) information is processed along the magnocellular pathway, the retinal neurons of which project to the two dorsal magnocellular layers of the LGN. There is overwhelming evidence that these cells provide the neural basis for a luminance channel.

One of the basic goals of the present study was to establish whether variation in simple reaction time (RT) can be explained in terms of the simple cone-opponency model described earlier or whether it reflects the higher-order mechanisms known to operate at cortical levels. Many studies have been undertaken to examine the influence of color on the simple RT. In some of these, RT has been shown to be independent of wavelength, but this has tended to oc- cur when chromatic stimuli have been confounded with luminance increments embedded within a surround or flickered at fast temporal rates (≥15 Hz). Better isolation of the chromatic visual system is achieved by the use of selective adaptation or equiluminant stimuli, or by the manipulation of temporal presentation profiles. Under these conditions, the RT has been shown to vary as a function of stimulus chromaticity, for example, that RTs to red stimuli were shorter than those to green or blue stimuli, whereas Nissen and Pokorny have demonstrated that RTs to 570-nm stimuli are much longer than for other regions of the visible spectrum. The broad consensus that appears to emerge from these studies is that when the stimuli used to elicit RTs have poor chromatic selectivity and incorporate luminance changes that can be detected by achromatic mechanisms, then RTs are independent of stimulus chromaticity. If, however, stimuli possess good chromatic selectivity and minimize achromatic intrusions, then there is a strong dependence of RT on stimulus color. This agreement may prove to be short lived. Recent work by Smithson and Mollon (Smithson HE, Mollon JD. ARVO Abstract 532, 2001) has shown that when luminance intrusion is controlled by masking, RTs to chromatic stimuli exhibit little change as a function of stimulus chromaticity.

The issue of variation in RT with changing stimulus chromaticity therefore merits reexamination. In early studies, the
relationship between simple RT and color was explored by using highly saturated monochromatic stimuli at discrete intervals along the visible spectrum. We were particularly interested in the contribution of color-opponency mechanisms to the generation of the RT. To this end, stimuli were chosen to lie at specific points in color space to allow more precise control of the degree of cone excitation. This approach was adopted with a view to ascertaining whether the mechanisms that lead to the generation of RTs are extracted at an early precortical stage and are dominated by cone-opponency mechanisms or whether they occur at a later stage in the visual system (Parry NRA, McKeefry DJ, Murray IJ, ARVO Abstract 3988, 2002).

METHODS

Stimuli

Simple reaction times (RTs) were measured to the onset of a colored Gaussian patch on a white equiluminant background. These stimuli were presented on a high-resolution color graphics monitor (GDM500; Sony, Tokyo, Japan) under the control of a video graphics card (VSG 2/5; Cambridge Research Systems, Rochester, UK) that has an on-board timer allowing RTs to be measured with a resolution of less than 1 ms.

All the chromatic stimuli lay on an equiluminant plane in CIE color space (Fig. 1A), which is analogous to the MBDKL color space.\(^25,30\) The angle \(\phi\) defines a specific chromatic axis and thus defines the chromaticity of the stimulus. Eight axes in total were investigated, four of which are of particular importance. The 0° (+L−M) and 180° (−L+M) axes produce stimuli that minimally activate S cones and produce only L- and M-cone excitation. Conversely, the 90° (+S−[L+M] or +S) and 270° (−S+[L+M] or −S) axes isolate S-cone activity while minimally activating L and M cones. Four other axes were also used where the relative activation of the L, M, and S cones varied. The chromaticity coordinates of the stimuli used are given in Table 1.

Each stimulus had a radially symmetrical Gaussian spatial profile (SD = 0.2") with hue modulation maximum at the center (Fig. 2A). The stimuli were presented on an equiluminant background (chromaticity coordinates, \(x = 0.310, y = 0.316\)) with a mean luminance of 12.5 cd/m\(^2\). The background subtended 22' in width and 17' in height at the viewing distance of 100 cm. Stimuli were viewed binocularly.

Cone contrast has been widely adopted as a metric for the specification of chromatic stimuli. Figure 1B shows how individual L-, M- and S-cone contrasts varied with each of the chromatic stimuli. These data were computed as Weber cone contrasts produced by each stimulus on the neutral background. Cone excitations were calculated using the Judd-modified 1931 CIE values in conjunction with the Smith and Pokorny\(^29\) fundamentals. To produce a single value for the specification of cone contrast for each stimulus we computed the pooled root mean square (RMS).\(^30,31\) Thus

\[
\text{RMS cone contrast} = \sqrt{\left|Lc^2 + Mc^2 + Sc^2\right|/3}
\]

where \(Lc, Mc\), and \(Sc\) are the Weber cone contrasts for the L, M, and S cones against the neutral background. Equation 1 plots the maximum available (i.e., limited by the gamut) computed RMS cone contrast for each stimulus as a function of color axis. Stimuli were calibrated with a spectral photometer (model PR650; PhotoResearch, Chatsworth, CA).

The effects of temporal transients were minimized by presenting the stimulus with a raised cosinusoidal temporal profile, so that hue modulation reached a maximum at 190 ms after stimulus onset. The stimulus then remained at the set chromatic contrast for a further 190 ms and was reduced cosinuosoidally over the final 190 ms of the presentation (Fig. 2B).

**Procedure**

Each chromatic axis was tested in turn starting with \(\phi = 0\)°, using the following protocol. After 5 minutes of adaptation to the background, equiluminance was determined with heterochromatic flicker photom-

<table>
<thead>
<tr>
<th>Color Axis ((\phi))</th>
<th>(x)</th>
<th>(y)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.386</td>
<td>0.285</td>
</tr>
<tr>
<td>53</td>
<td>0.349</td>
<td>0.231</td>
</tr>
<tr>
<td>90</td>
<td>0.274</td>
<td>0.250</td>
</tr>
<tr>
<td>130</td>
<td>0.235</td>
<td>0.263</td>
</tr>
<tr>
<td>180</td>
<td>0.226</td>
<td>0.355</td>
</tr>
<tr>
<td>235</td>
<td>0.298</td>
<td>0.518</td>
</tr>
<tr>
<td>270</td>
<td>0.396</td>
<td>0.517</td>
</tr>
<tr>
<td>510</td>
<td>0.434</td>
<td>0.410</td>
</tr>
<tr>
<td>Background</td>
<td>0.310</td>
<td>0.316</td>
</tr>
</tbody>
</table>

The values represent the stimuli at maximum modulation.

\(^*\) CIE 1931.
The stimulus was flickered on and off at 16 Hz, and luminance of the stimulus was adjusted until perceptual flicker was minimized. Luminance ratio was calculated by

\[ \frac{LUM_t}{2LUM_b} \]

where \( LUM_t \) is the peak luminance at the center of the test spot and \( LUM_b \) is the background luminance. Thus the luminance ratio at photometric equiluminance was 0.5, with 0 denoting black at the center and 1 denoting twice the background luminance. Detection threshold for the chromatic stimulus was then measured using a temporal two-alternative, forced-choice procedure. Stimuli were presented in the same temporal envelope as in the RT paradigm, with the 75% correct level taken as an estimate of threshold.

For each axis, a series of RT trials were conducted at different contrasts, ranging from near threshold to gamut maximum. The interval between contrasts was evenly spaced on a 1/contrast scale. Subjects were instructed to press a nonlatching spring-loaded lever switch incorporated into a response box (model CB3; Cambridge Research Systems) as soon as they perceived the onset of the stimulus. In a single trial, at least 20 RTs were recorded to the same stimulus with successive stimuli being randomly presented between 1000 and 3000 ms. We found that number of RTs for each contrast value (typically 128). We found that these experiments, we sampled contrast more finely and have a higher number of RTs for each contrast value (typically 128). We found that this had no noticeable influence on the present results. RT histograms with 20-ms bins were computed, and the shape of the distributions tested for normality (one-sample Kolmogorov-Smirnov test; SPSS for Windows, ver. 6.0; SPSS Sciences, Chicago, IL). All distributions were normal, and mean RT was therefore taken as a measure of central tendency.

Experiments were performed with three of the authors: DMcK, a 34 year-old myope; NRAP, a 46 year-old low hypermetrope; and IJM, a 51 year-old emmetrope. Color vision of all participants was normal according to standard clinical tests (Ishihara, Nagel model 1 Anomalouscope, City University Color Vision Test). All subjects wore appropriate refractive correction for the testing distance. Key points were also tested on a fourth observer (PVM, a 32 year-old emmetrope) who, while being an experienced psychophysical observer, was naive to the purposes of this particular experiment. The protocol complied with the provisions of the Declaration of Helsinki.

**RESULTS**

**Reaction Times to Equiluminant and Non-equiluminant Stimuli**

Previous studies have demonstrated that the variation of RT as a function of chromaticity is highly dependent on the degree to which contributions from achromatic or luminance-based mechanisms are minimized. Many of these studies were based on the assumption that photometrically matched stimuli constitute equiluminant stimuli. However, few subjects conform to the ideal VA function, and there is wide intersubject variability of equiluminant points. We approached problem by investigating the variation in RT with luminance ratio. Figures 3A and 3B show the variation of RT as a function of luminance ratio for the 0°, 90°, 180°, and 270° chromatic axes for two subjects (DMcK, IJM). The corresponding subjective equiluminant points are also indicated (see also Table 2). In each case, the longest reaction times are obtained around this equiluminant point, and the shortest RTs are obtained when the luminance ratios are 0 or 1. The increase in RT at equiluminance is greater for stimuli that isolate S-cone activity (90° and 270°) and these functions seem to peak much more sharply. Therefore RTs to S cone-isolating stimuli are more likely to be susceptible to luminance contributions, which will have the effect of shortening the RT if the appropriate equiluminant settings are not used. For L-M cone-isolating stimuli, the consequences of departure from equiluminance seem less marked.

**The Influence of Chromatic Axis on Reaction Time**

RTs were measured for equiluminant stimuli that were modulated along the eight different axes in color space described in the Methods section. Along each axis, RTs were measured as a
function of RMS cone contrast, levels of which were chosen to extend from threshold to the maximum suprathreshold contrast possible for that particular axis. Piéron\textsuperscript{32} has described a general equation that relates RT to stimulus intensity (I)

$$RT = RT_0 + k \cdot I^\beta$$  \hspace{1cm} \text{(5)}

where RT is the reaction time, $RT_0$ is the asymptotic RT (i.e., absolute RT), and $k$ is the slope. Plainis and Murray\textsuperscript{33} have shown that RT is a linear function of contrast when plotted on a reciprocal contrast scale (i.e., $\beta = -1.0$), and can be expressed as

$$RT = RT_0 + k \cdot \frac{1}{C}$$  \hspace{1cm} \text{(4)}

where $C$ is the RMS cone contrast. This modification of Piéron’s general equation has been used to fit the data in Figure 4 for subject NRAP ($k$ and $RT_0$ for the other subjects are given in Table 2; all showed the same linear relationship with 1/contrast). The high regression coefficients ($r^2$) indicate that this equation provides a good description of the data sets for each axis. Thus, for each color axis we now have a unique equation that describes the relationship between RT and cone contrast. Both $k$ and $RT_0$ reach maxima with stimuli at and around the $90^\circ$ and $270^\circ$ axes. The latter parameter represents the RT that
would occur for a stimulus of contrast approaching infinity (1/C = 0) and as such represents a theoretical minimum RT to that stimulus. A major contribution to the variation in RT is likely to be differences in absolute transmission times for specific stimuli along the visual pathway. The fact that RT is longest for S cone-isolating axes and shortest for L-M cone-isolating axes is consistent with neurophysiological measures of the visual latencies for these opponent mechanisms (see the Discussion section and Ref. 48).

In Figure 5, the equations derived from empiric data have been used to compute the RTs that would be produced by stimuli having the same RMS cone contrast across all color axes. Four levels of contrast (0.1, 0.15, 0.2, and 0.25) have been arbitrarily chosen but illustrate the point that, for the same amount of cone contrast, the longest RTs are elicited by stimuli that lie along the S cone-isolating axes (RTs along the 90° axis being longer than those along the 270° axis). The shortest RTs are generated by stimuli that lie on the L-M cone-isolating axes and, for intermediate axes, the RTs lie between these two extremes. Thus, there appears to be a difference in the perceptual strength of a unit of cone contrast as a function of color axis. A unit of L or M cone contrast appears to be more effective in generating a faster response than a unit of S cone contrast. Furthermore, a noticeable feature of the plots shown in Figure 5 is the asymmetry between the +S (ϕ = 90°) and −S (ϕ = 270°) cone axes. In all three subjects, cone modulation along the +S axis generated a longer RT than the same degree of modulation along the −S axis, implying a difference in perceptual strength of opposing +S and −S inputs.

This issue of the perceptual strength or effectiveness of a unit of cone contrast is explored more thoroughly in Figure 6, where the cone contrasts that are required to produce a range of RTs from threshold to suprathreshold levels are plotted against the cone contrasts required along another axis to produce the same RTs. The plots are restricted to comparisons between the cardinal axes and three graphs are shown for each subject (90° vs. 0°, 180° vs. 0°, and 90° vs. 270°). The data have been fitted by linear functions, which in view of the high r², provide a good description of the data. The slope of these functions can be taken as a measure of the relative effectiveness of cone contrast along the two axes (see Switkes and Crognale54 for a similar approach). These functions are essentially a measure of the relative contrast gain along two chromatic axes. The first column in Figure 6 plots the cone contrast required along the 90° (+S) axis to produce a certain RT against the cone contrast required along the 0° (+L−M) axis to give the same RT. The mean slope for the three observers is 18.2, which is a measure of how much less sensitive the visual system is to the unit of cone contrast along the 90° axis compared with the 0° axis. The slope of the function fitted to the data from the +L−M (0°) and −L+M (180°) axes is closer to unity (mean slope = 0.84), whereas that fitted to the +S (90°) and −S (270°) axis has an average value of 2.15 for the three subjects.

### Scaling to Multiples of Detection Threshold

Although the use of cone contrast has been widely adopted as a metric for the specification of chromatic stimuli, the foregoing sections raise questions as to its suitability in equating the perceptual strength of color stimuli, as do other studies.34

Another means of characterizing chromatic stimuli across different axes in color space is to scale them according to equal multiples above detection threshold.5 We were interested in determining the extent to which the long RTs generated by S-cone stimuli in comparison with L-M cone stimuli were dependent on the metric used to equate chromatic stimuli. The thresholds for each axis and each subject are presented in Table 2. Figure 7 illustrates how RT varied as a function of chromatic axis when the stimuli were scaled in relation to multiples above detection threshold rather than RMS cone contrast, as used previously. Figure 7 shows empiric data obtained from stimuli at 2 and 8 times above their respective detection thresholds, as well as functions derived from fits of data using equation 4. Note that we have now expressed contrast in terms of multiples above detection threshold. The values of RT derived from these equations correspond well to

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**Table 2. Luminance Ratio, Threshold Contrast (RMS Cone Contrast) and Statistics of the RT Versus 1/RMS Contrast Function for Each Subject and Each Chromatic Axis**

<table>
<thead>
<tr>
<th>Subject</th>
<th>Measure</th>
<th>0</th>
<th>53</th>
<th>90</th>
<th>130</th>
<th>180</th>
<th>233</th>
<th>270</th>
<th>310</th>
</tr>
</thead>
<tbody>
<tr>
<td>DMcK</td>
<td>Lum ratio</td>
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<td>0.49</td>
<td>0.49</td>
<td>0.5</td>
<td>0.51</td>
<td>0.49</td>
<td>0.48</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>Threshold</td>
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<td>0.0121</td>
<td>0.0541</td>
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<td>0.0022</td>
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<tr>
<td></td>
<td>k</td>
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<td>5.72</td>
<td>11.66</td>
<td>6.85</td>
<td>0.69</td>
<td>4.30</td>
<td>6.26</td>
<td>4.04</td>
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<tr>
<td></td>
<td>RT₀</td>
<td>377</td>
<td>345</td>
<td>408</td>
<td>355</td>
<td>553</td>
<td>342</td>
<td>410</td>
<td>340</td>
</tr>
<tr>
<td></td>
<td>r²</td>
<td>0.96</td>
<td>0.98</td>
<td>0.99</td>
<td>0.96</td>
<td>0.97</td>
<td>0.92</td>
<td>0.96</td>
<td>0.98</td>
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<tr>
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<td>Lum ratio</td>
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<td>0.51</td>
<td>0.52</td>
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<tr>
<td></td>
<td>k</td>
<td>1.05</td>
<td>7.20</td>
<td>18.06</td>
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<td>4.08</td>
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<tr>
<td></td>
<td>r²</td>
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<td>0.93</td>
<td>0.96</td>
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<td>r²</td>
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<td>0.97</td>
<td>0.92</td>
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<tr>
<td>PVM</td>
<td>Lum ratio</td>
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</tr>
</tbody>
</table>

Lum ratio, luminance ratio.
the actual measures of RT across chromatic axes for stimuli at 4 times threshold and above.

Evidently, with the adoption of a metric that scales contrast in comparison with detection threshold, RT varies much less as a function of chromatic axis than in previous cases. Note that in Figure 5, for absolute cone contrasts of 0.1, stimulation along the 90° axis produces an increase in RT of the order of 300 ms in comparison with stimulation along the 180° axis. Differences persist, however, when the stimuli are scaled with reference to detection threshold. RTs to stimuli along the S cone–isolating axis are significantly longer than those to L-M stimuli (\( P < 0.05 \), ANOVA combined with a post hoc Tukey honest-significant-difference [HSD] test), but the increase in RT for the former is only approximately 40 ms longer than for the latter (Fig. 7).

**DISCUSSION**

**Summary and Relation to Previous Work**

We have investigated the extent to which simple RTs are dependent on stimulus chromaticity and that postreceptoral L-M and S-(L+M) cone–opponent pathways are influential in their generation. Our findings can be summarized as follows: (1) RTs are highly sensitive to small departures from equiluminance, and for each color vector the longest RTs are obtained at luminance ratios that match the individual’s subjective equiluminance point. (2) The relationship between chromatic contrast and RT can be well described by a modified Piéron equation: \( RT = RT_0 + k \cdot C^{-1} \). (3) Simple RTs generated in response to S cone–isolating stimuli are longest, whereas the shortest RTs are generated by L-M cone–isolating stimuli. This
last observation implies that the visual system has a faster 
processing capability for information encoded by the L-M 
system than that encoded by the S-(L+M) system. The difference 
between the two, however, is highly dependent on how the 
chromatic stimuli are scaled in relation to one another. The use 
of cone contrast as an absolute metric tends to greatly exag-
gerate the temporal processing differences between S and L-M 
cone-isolating stimuli.

Other studies have investigated simple RTs to chromatic 
stimuli. Parry et al.,55 for example, demonstrated that RTs to 
red-green equiluminant gratings are much longer than those 
obtained for equivalent achromatic stimuli and that their con-
trast dependence differs. The observation that targets modu-
lating the S-cone driven pathway yield longer RTs is not new. 
Mollon and Krauskopf21 showed that the \( \pi_1 \) mechanism has a long integration time and Nissen and Pokorny56 also demonstrated the operation of chromatic mechanisms in RT functions ob-
tained from a hue substitution paradigm. Ueno et al.55 manip-
ulated the background of an incrementally presented mono-
chromatic stimulus to reveal the contributions of chromatic 
and achromatic mechanisms. The RTs were chromatically dom-
inated when a steady relatively bright background was used and 
was dominated by luminance mechanisms when the back-
ground was flickered at 15 Hz. They found the longest RTs at 
570 nm, corresponding closely to our 270° yellow stimulus, 
but did not extend their measurements to wavelengths below 
450 nm.

RTs and Chromatic Processing Models

Contemporary models of post-receptoral color vision suggest 
the existence of precortical L-M and S-(L+M) cone–opponent 
channels,28 whereas in the cortex there are many more chro-
matic mechanisms tuned to a variety of different directions in 
color space.5,6,11 Our observations that RTs polarize around 
the L-M and S-(L+M) opponent axes imply that it is cone 
opponency that plays a predominant role in dictating the 
rapidity of the simple RT. Furthermore, preliminary analysis of 
isoreception (RT) contours suggests that performance along 
intermediate (i.e., noncardinal) axes can be well described by 
a probability-summation model that assumes the operation of 
two functionally independent L-M and S-(L+M) opponent 
mechanisms. This seems to be consistent with other find-
ings,46–57 and more in keeping with models of precortical color 
processing, rather than cortical processing (at least beyond the 
LGN input layers), where cardinal opponent mechanisms seem 
less influential.8,11

Recent psychophysical investigations have pointed to the 
existence of separable ON and OFF processing pathways 
within the cone-opponency mechanisms.58–60 Thus color vi-
sion may be more accurately thought of as comprising four 
separate monopolar mechanisms (+L–M, red-on/green-off; 
+M–L, green-on/red-off; +S–(L+M), blue-on/yellow-off; and 
+(L+M)–S, yellow-on/blue-off). To what extent do the RT 
data reported in the current study reflect this “rectified” model of 
chromatic processing? Using a noise-masking paradigm, 
Sankeralli and Mullen41 found that the two opposing sub-
mechanisms of the red-green system possess a close degree of 
symmetry in the weighting of their cone inputs. The RT data 
shown in the current study appear to suggest that this balance 
is maintained at suprathreshold contrast levels. This is revealed 
by the fact that when we plotted the cone contrasts of the 
+L–M (\( \phi = 0^\circ \)) and +M–L (\( \phi = 180^\circ \)) stimuli required to 
generate the same RT, we obtained a slope close to unity (see 
Fig. 6). This symmetry between the RT data for the +L–M and 
+M–L stimuli may suggest a balanced weighting of cone 
inputs between these submechanisms. The plots for 
+S–(L+M) (+S) and +(L+M)–S (–S) reveal a marked asym-
metry in the variation of RTs with, on average, more than 
twice as much cone contrast being required by the former 
stimuli to generate the same RT as the latter. RTs generated by 
–S stimuli also tended to be shorter than for +S stimuli at 
equal multiples above detection threshold. Asymmetries be-
tween the responses of the +S–(L+M) or blue-on and the 
+(L+M)–S or blue-off system have been noted in some psy-
chophysical studies,39–41 but not in others.42–44 It can be 
speculated that the existence of differences in response prop-
erties may be indicative of physiological-anatomic differences 
between the blue-on and -off pathways,45,46 but this has yet to 
receive firm electrophysiological support.

Effectiveness of Chromatic Stimuli across 
Color Axes

The use of RTs provides a means by which we can make an 
objective measure of the perceptual strength or effectiveness 
of suprathreshold chromatic stimuli across different axes in 
color space, in a manner that is relatively free from subjective 
criteria. Initially, chromatic stimuli were defined according to 
cone contrast. We have shown that their perceptual strength, 
expressed in terms of effectiveness in generating an RT, varies 
steadily, and that an objective measure of the perceptual strength 
of the stimulus can be obtained by measuring the RT to a 
given stimulus. This RT is then compared to the RT produced 
by a standard stimulus, and the two RTs are plotted as a func-
tion of cone contrast (Fig. 4, Table 2) have been used to calculate 
the RTs polarize around

![Image](53x476 to 293x734)

**Figure 5.** The linear equations that model the behavior of RT as a function of cone contrast (Fig. 4, Table 2) have been used to calculate how RT varies as a function of chromatic axis. At each axis, the RT that is produced by a specific amount of cone contrast has been computed for several arbitrarily chosen levels of RMS cone contrast (0.1, 0.15, 0.2, 0.25) and plotted as a function of \( \phi \) for each subject (NRAP, IJM).
This higher sensitivity difference, however, closely mirrors that found between the S-(L+M) and L-M mechanisms at detection threshold in psychophysical experiments. Sankeralli and Mullen found a cone contrast threshold ratio of 16:1 for the detection of S-(L+M) grating stimuli compared with L-M stimuli. Regardless of the absolute magnitude of this sensitivity difference between the S and L-M opponent axes, the existence of a difference in sensitivity confirms previous opinion that cone contrast is not a good measure of suprathreshold stimulus strength. It is clear that a unit of cone contrast for a stimulus modulating one particular color axis does not have the same perceptual strength as a unit of cone contrast along a different axis. This raises serious questions as to the suitability of cone contrast as a measure of the visibility of chromatic stimuli.

Arguably, a better means of equating suprathreshold chromatic stimuli is to scale them in terms of equal multiples above detection threshold. This is because absolute cone contrasts are not equivalent in strength: S-cone contrast of 0.1 is barely above threshold, whereas L-M contrast of 0.1 is a highly suprathreshold stimulus. A central finding in this study is that, regardless of how the chromatic stimuli are scaled, signals carried by the S cone pathway appear to be subject to a slightly increased processing time, a critical point is that the sluggishness of the S cone system is greatly exaggerated if cone contrast is used as a stimulus metric. If, conversely, the stimuli are normalized with reference to detection threshold, then the differences between the S and L-M mechanisms are much less pronounced. Scaling with reference to detection threshold is not without its own limitations. In particular, this approach takes no account of the relative contributions of the magnocellular and parvocellular systems to the threshold measures themselves. Thus, apparent differences in suprathreshold performance may possibly be attributable to threshold based contributions.

As far as the physiology is concerned, recent single-unit studies in the macaque monkey have demonstrated that information mediated by the S-cone system takes longer to reach the primary visual cortex than information mediated by the L-M cone system. However, it would be too simplistic to explain variation in RT solely in terms of differences in the transmission times of underlying neurons. This approach takes no account of the probabilistic dynamics of the activities of larger populations of neurons. Recent single-unit studies tend to invoke
the existence of additional comparative stages of neural processing. These enable the extraction of information concerning when the onset of stimulus actually occurs by comparison with the overall activity of neural populations. The analysis of the temporal structure of neural spike trains seems important in this processing, particularly for low contrast stimuli. The differences in processing delays may reflect genuine physiological differences between the parvo- and koniocellular pathways that carry the S(L+M) and L-M opponent signals. However, it remains unclear to what extent the different methods of scaling or equating chromatic stimuli may affect response latencies of neurons receiving S and L-M cone input in V1.

Another possibility is that any temporal advantage that the L-M-cone system has over the S-cone system is gained through the inherent ability of nontritan stimuli to use activity from nonchromatic, nonparvocellular mechanisms. Even at equiluminant and cone specific luminances, the inherent ability of nontritan stimuli to use activity from lateral geniculate nucleus to striate cortex is no faster than the S cone mechanism (Smithson HE, Mollon JD, ARVO Abstract 532, 2001). In the present study, however, we have taken care to minimize transient or magnocellular intrusions by blurring the stimuli in both space and time. This fact, coupled with the highly linear RT-contrast functions, casts doubt on the possibility that magnocellular activity contributes to the generation of RT differences with S and L-M cone-isolating stimuli. This point seems apt in the light of recent single-unit recordings from the macaque LGN which demonstrate the existence of S cone input to magnocellular neurons, a contribution which had previously been thought to be the preserve of L and M cones.55

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References


