

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

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**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 sinusoidally ramped onset of small, equiluminant, colored Gaussian 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  $RT = RT_0 + k \cdot C^{-1}$ .

**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, precortically at least, 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).<sup>1-3</sup> 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 mecha-

nisms.<sup>4,5</sup> 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.<sup>6,7</sup> This means that the information flow along color-opponent channels must undergo several transformations that culminate in color appearance.<sup>8</sup> The number of these mechanisms and where they arise in the visual pathway are matters of some conjecture.<sup>9,10</sup> 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.<sup>11,12</sup>

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.<sup>13</sup> 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.<sup>14-16</sup>

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.<sup>17-24</sup> In some of these, RT has been shown to be independent of wavelength,<sup>17,19,20</sup> but this has tended to occur when chromatic stimuli have been confounded with luminance increments<sup>19,20</sup> embedded within a surround<sup>17</sup> or flickered at fast temporal rates ( $\geq 15$  Hz).<sup>24</sup> Better isolation of the chromatic visual system is achieved by the use of selective adaptation<sup>21</sup> or equiluminant stimuli<sup>22</sup> or by the manipulation of temporal presentation profiles.<sup>23-25</sup> Under these conditions, the RT has been shown to vary as a function of stimulus chromaticity.<sup>18,25</sup> Piéron, for example, found that RTs to red stimuli were shorter than those to green or blue stimuli,<sup>19</sup> whereas Nissen and Pokorny<sup>22</sup> 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.<sup>22,24</sup> 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

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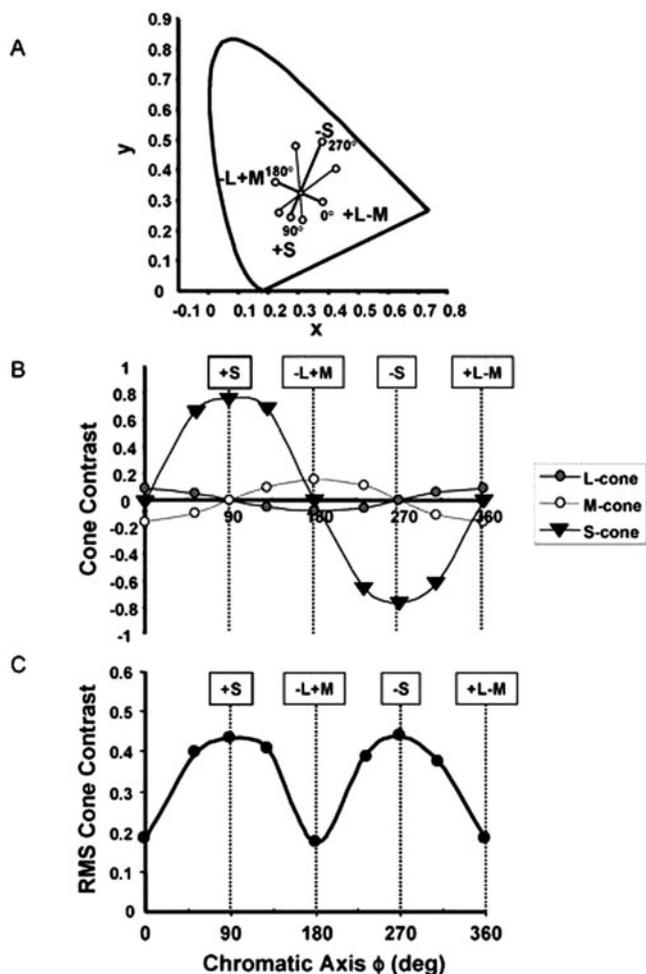
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**FIGURE 1.** (A) The 1931 CIE chromaticity diagram showing the location in color space of the eight chromatic axes that were tested. (○) Gamut limit in each direction. The background (illuminant C,  $x = 0.310, y = 0.316$ ) is located at the intersection of the axes. (B) Individual L, M, and S-cone modulations produced by the stimuli (at the gamut limit) as a function of chromatic axis. (C) The variation of cone contrast as a function of chromatic axis expressed as a pooled RMS metric ( $\text{RMS cone contrast} = \sqrt{[(L_c^2 + M_c^2 + S_c^2)/3]}$ ).

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).<sup>26</sup>

**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.<sup>29,30</sup> 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 ( $SD = 0.2^\circ$ ) 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  $\text{cd/m}^2$ . The background subtended  $22^\circ$  in width and  $17^\circ$  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<sup>29</sup> fundamentals. To produce a single value for the specification of cone contrast for each stimulus we computed the pooled root mean square (RMS).<sup>30,31</sup> Thus

$$\text{RMS cone contrast} = \sqrt{[(L_c^2 + M_c^2 + S_c^2)/3]} \quad (1)$$

where  $L_c, M_c$  and  $S_c$  are the Weber cone contrasts for the L, M, and S cones against the neutral background. Figure 1C 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 sinusoidal 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 sinusoidally over the final 190 ms of the presentation (Fig. 2B).

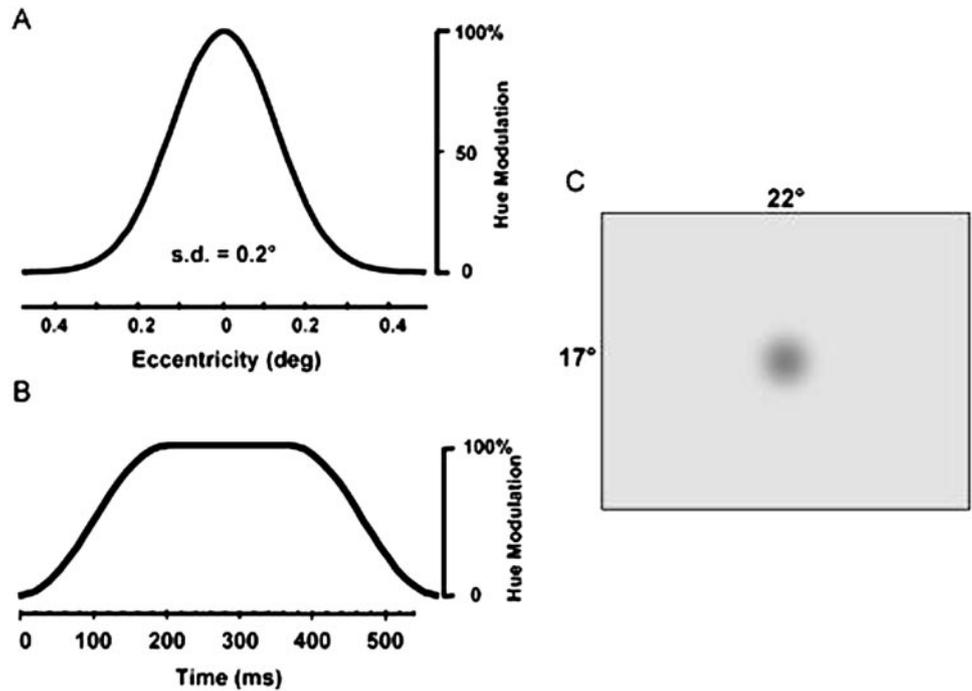
**Procedure**

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

**TABLE 1.** Chromaticity Coordinates of the Stimuli Used in the Experiments

Color Axis ( $\phi$ )	Chromaticity Coordinates*	
	$x$	$y$
0	0.386	0.285
53	0.319	0.231
90	0.274	0.230
130	0.235	0.263
180	0.226	0.355
233	0.298	0.518
270	0.396	0.517
310	0.434	0.410
Background	0.310	0.316

The values represent the stimuli at maximum modulation.  
\* CIE 1931.



**FIGURE 2.** The spatial and temporal configuration of the stimulus. (A) The Gaussian spatial profile of the hue modulation (SD = 0.2°) (B) The cosinusoidal temporal presentation profile of the stimulus. The spot took 190 ms to reach full modulation, remained at this level for a further 190 ms, and then decayed over 190 ms. (C) In this black-and-white representation of the stimulus, the change in chromaticity at the center is represented by a change in luminance.

etry. 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

$$\text{LUM}_i / 2\text{LUM}_b \quad (2)$$

where  $\text{LUM}_i$  is the peak luminance at the center of the test spot and  $\text{LUM}_b$  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 after the subject's response, or after 5 seconds if no response was made. At the completion of a trial, the mean and SE of the RTs were calculated, omitting responses outside the range of 150 to 1200 ms. In other studies in our laboratory and in particular in pilot studies for 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 Anomaloscope, 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 naïve to the purposes of this particular experiment. The protocol complied with the provisions of the Declaration of Helsinki.

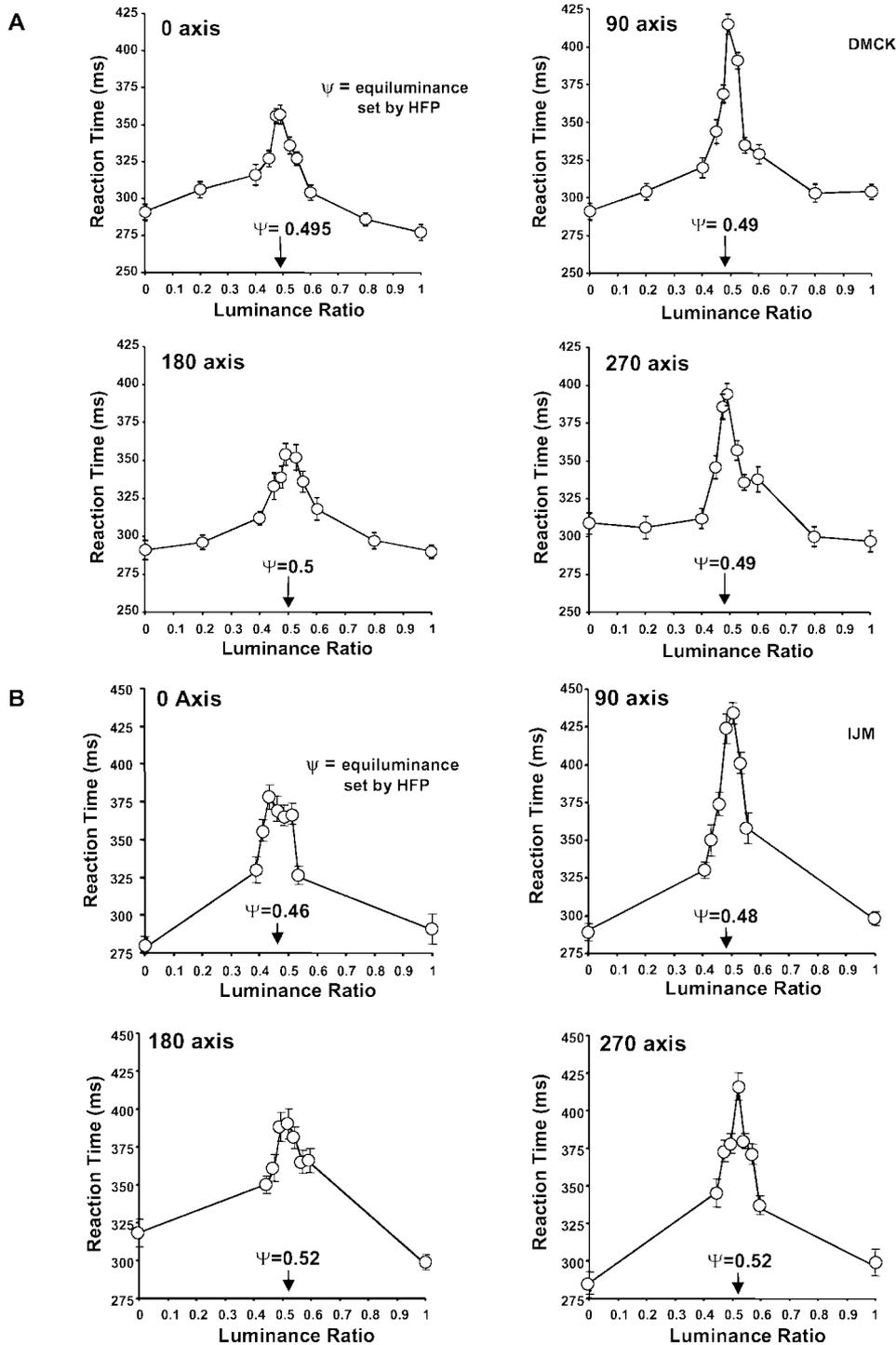
## RESULTS

### 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.<sup>24</sup> Many of these studies were based on the assumption that photometrically matched stimuli constitute equiluminant stimuli. However, few subjects conform to the ideal  $V\lambda$  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



**FIGURE 3.** The variation in simple RT as a function of luminance ratio for stimuli that modulate along four different chromatic axes ( $\phi = 0^\circ, 90^\circ, 180^\circ, 270^\circ$ ). Data are shown for two subjects DMCK (A) and IJM (B). Also shown on the plots are the luminance ratio settings ( $\psi$ ) for subjective equiluminance made by heterochromatic flicker photometry. Note the good correlation between the subjects' equiluminant point and the slowest RT obtained.

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<sup>32</sup> has described a general equation that relates RT to stimulus intensity (I)

$$RT = RT_0 + k \cdot I^\beta \quad (3)$$

where RT is the reaction time,  $RT_0$  is the asymptotic RT (i.e., absolute RT), and  $k$  is the slope. Plainis and Murray<sup>33</sup> 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

$$RT = RT_0 + k \cdot 1/C \quad (4)$$

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  $1/\text{contrast}$ ). 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

**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

Subject	Measure	Chromatic Axis (deg)							
		0	53	90	130	180	233	270	310
DMcK	Lum ratio	0.5	0.49	0.49	0.5	0.51	0.49	0.48	0.49
	Threshold	0.0022	0.0121	0.0341	0.0161	0.0022	0.0093	0.0256	0.0108
	$k$	0.86	5.72	11.66	6.85	0.69	4.30	6.26	4.04
	RT <sub>0</sub>	377	345	408	355	353	342	410	340
	$r^2$	0.96	0.98	0.99	0.96	0.97	0.92	0.96	0.98
NRAP	Lum ratio	0.52	0.49	0.50	0.51	0.51	0.52	0.51	0.50
	Threshold	0.0058	0.0338	0.0937	0.0407	0.0071	0.0190	0.0559	0.0274
	$k$	1.05	7.20	18.06	4.99	0.87	4.08	7.58	4.14
	RT <sub>0</sub>	348	360	396	404	378	387	416	384
	$r^2$	0.94	0.93	0.96	0.95	0.97	0.90	0.94	0.97
IJM	Lum ratio	0.46	0.47	0.50	0.52	0.53	0.53	0.51	0.48
	Threshold	0.0059	0.0390	0.0861	0.0372	0.0073	0.0244	0.0402	0.0209
	$k$	1.44	7.87	15.74	8.60	1.08	3.51	6.30	5.35
	RT <sub>0</sub>	389	372	423	387	383	397	402	370
	$r^2$	0.91	0.97	0.92	0.99	0.97	0.96	0.93	0.96
PVM	Lum ratio	0.48		0.47					
	Threshold	0.0059		0.0510					
	$k$	0.97		13.17					
	RT <sub>0</sub>	340		401					
	$r^2$	0.94		0.90					

Lum ratio, luminance ratio.

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<sub>0</sub> is likely to be differences in absolute transmission times for specific stimuli along the visual pathway. The fact that RT<sub>0</sub> 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).

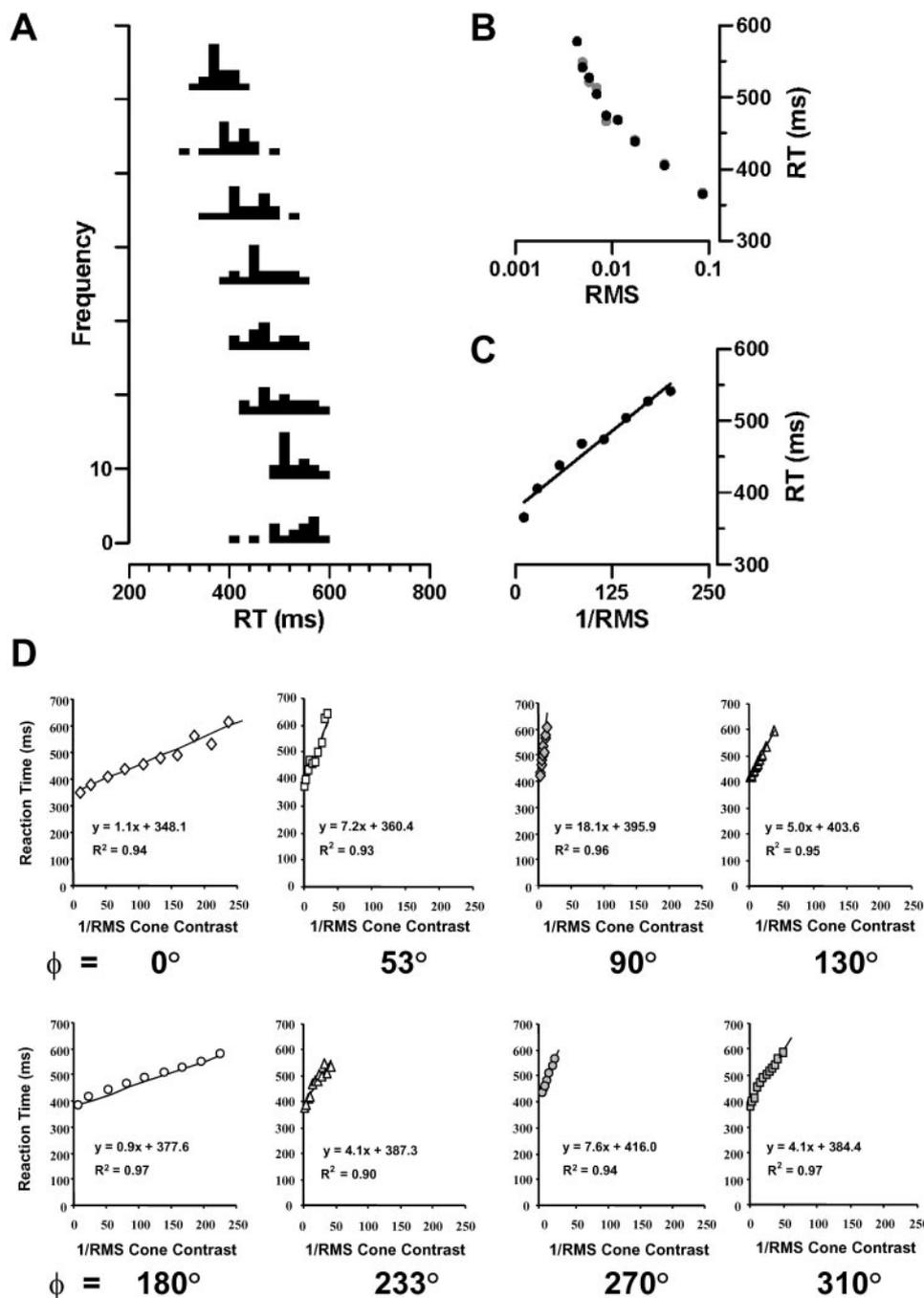
In Figure 5, the equations derived from empiric data have been used to compute the RTs that would be produced by stimuli having the same RMS cone contrast across all color axes. Four levels of contrast (0.1, 0.15, 0.2, and 0.25) have been arbitrarily chosen but illustrate the point that, for the same amount of cone contrast, the longest RTs are elicited by the 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 ( $\phi = 90^\circ$ ) and -S ( $\phi = 270^\circ$ ) 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  $r^2$ ,

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 Crognale<sup>34</sup> 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.<sup>34</sup> Another means of characterizing chromatic stimuli across different axes in color space is to scale them according to equal multiples above detection threshold.<sup>5</sup> 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



**FIGURE 4.** (A) RT histogram to a series of contrasts at a single chromatic axis ( $\phi = 180^\circ$ , subject, NRAP). Bin-width = 20 ms. (B) Mean (●) and median (⊙) RTs as a function of RMS contrast derived for the data in (A). (C) The  $180^\circ$  data in (B) replotted on a reciprocal contrast scale. (D) RTs plotted as a function of RMS cone contrast for eight different axes in color space at the  $\phi$  noted. The data were fitted by the function  $RT = RT_0 + k \cdot 1/C$  and plotted as a function of  $1/\text{RMS}$  cone contrast. Linear regression lines have been fitted to provide a unique description of the RT variation for each chromatic axis. See Table 2 for the parameters of these functions.

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  $90^\circ$  axis produces an increase in RT of the order of 300 ms in comparison with stimulation along the  $180^\circ$  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

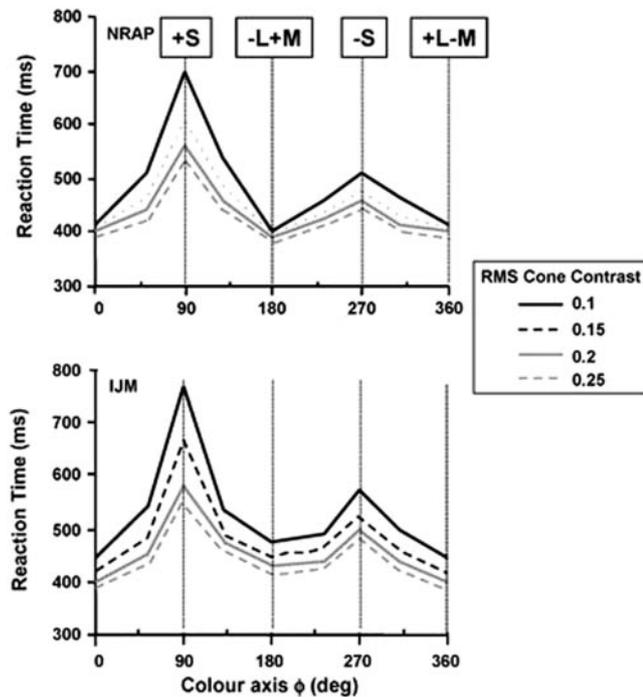


FIGURE 5. The linear equations that model the behavior of RT as a function of cone contrast (Fig. 4, Table 2) have been used to calculate how RT varies as a function of chromatic axis. At each axis, the RT that is produced by a specific amount of cone contrast has been computed for several arbitrarily 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).

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 exaggerate the temporal processing differences between S and L-M cone-isolating stimuli.

Other studies have investigated simple RTs to chromatic stimuli. Parry et al.,<sup>35</sup> for example, demonstrated that RTs to red-green equiluminant gratings are much longer than those obtained for equivalent achromatic stimuli and that their contrast dependence differs. The observation that targets modulating the S-cone driven pathway yield longer RTs is not new. Mollon and Krauskopf<sup>21</sup> showed that the  $\pi_1$  mechanism has a long integration time and Nissen and Pokorny<sup>22</sup> demonstrated the operation of chromatic mechanisms in RT functions obtained from a hue substitution paradigm. Ueno et al.<sup>24</sup> manipulated the background of an incrementally presented monochromatic stimulus to reveal the contributions of chromatic and achromatic mechanisms. The RTs were chromatically dominated when a steady relatively bright background was used and was dominated by luminance mechanisms when the background 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

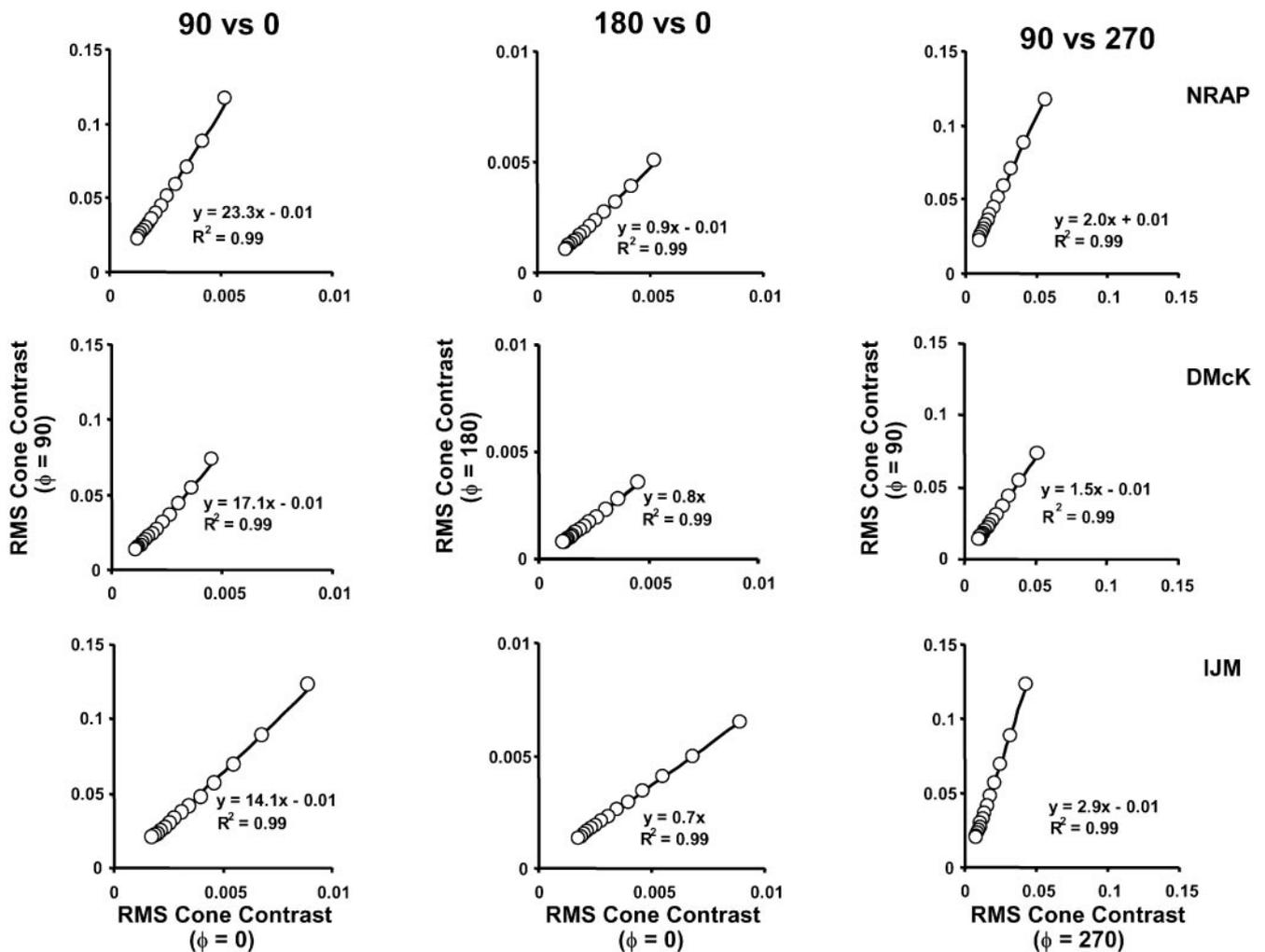
Contemporary models of post-receptoral color vision suggest the existence of precortical L-M and S-(L+M) cone-opponent channels,<sup>28</sup> whereas in the cortex there are many more chromatic mechanisms tuned to a variety of different directions in color space.<sup>5,6,11</sup> Our observations that 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 isoresponse (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 findings<sup>36,37</sup> 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.<sup>8,11</sup>

Recent psychophysical investigations have pointed to the existence of separable ON and OFF processing pathways within the cone-opponency mechanisms.<sup>38-40</sup> Thus color vision 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 Mullen<sup>41</sup> found that the two opposing submechanisms 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 asymmetry 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 between the responses of the +S-(L+M) or blue-on and the +(L+M)-S or blue-off system have been noted in some psychophysical studies,<sup>39-41</sup> but not in others.<sup>42-44</sup> It can be speculated that the existence of differences in response properties may be indicative of physiological-anatomic differences between the blue-on and -off pathways,<sup>45,46</sup> 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 systematically as a function of color axis. Chromatic stimuli that modulate along the +S axis ( $\phi = 90^\circ$ ) are the least effective in generating a response, that is, greater amounts of cone contrast are necessary to generate a specific RT, whereas stimuli that modulate along the L-M axes ( $\phi = 0, 180^\circ$ ) are the most effective. This relative insensitivity along the S axis has also been found in suprathreshold contrast-matching paradigms. Switkes and Crognale<sup>34</sup> found that S-to-LM cone contrast ratios of approximately 8:1 were necessary to produce suprathreshold contrast matches. Our RT data suggest that an even higher cone contrast ratio of 18:1 is needed to produce perceptual equivalence (at least as far as the RT is concerned).



**FIGURE 6.** A comparison of the perceptual strength of stimuli along different chromatic axes. From the modified Piéron equations used to fit the RT data the RMS cone contrast necessary to generate a specific RT along one chromatic axis was computed and plotted against the cone contrast required to produce the same RT along another axis. An estimate of the slope of these functions provides a measure of the relative perceptual strength of one chromatic stimulus in comparison with another. The figure shows the analyses for the comparison of selected stimuli:  $\phi = 90^\circ$  (+S) versus  $\phi = 0^\circ$  (+L-M);  $\phi = 180^\circ$  (-L+M) versus  $\phi = 0^\circ$  (+L-M); and  $\phi = 90^\circ$  (+S) versus  $\phi = 270^\circ$  (-S) for the three observers. The mean of the slopes for the three observers are  $90^\circ$  vs.  $0^\circ = 18.2$ ,  $180^\circ$  vs.  $0^\circ = 0.84$ , and  $90^\circ$  vs.  $270^\circ = 2.15$ .

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<sup>47</sup> 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.<sup>5</sup> 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 magno- 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.<sup>48</sup> 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.<sup>49</sup> Recent single-unit studies tend to invoke

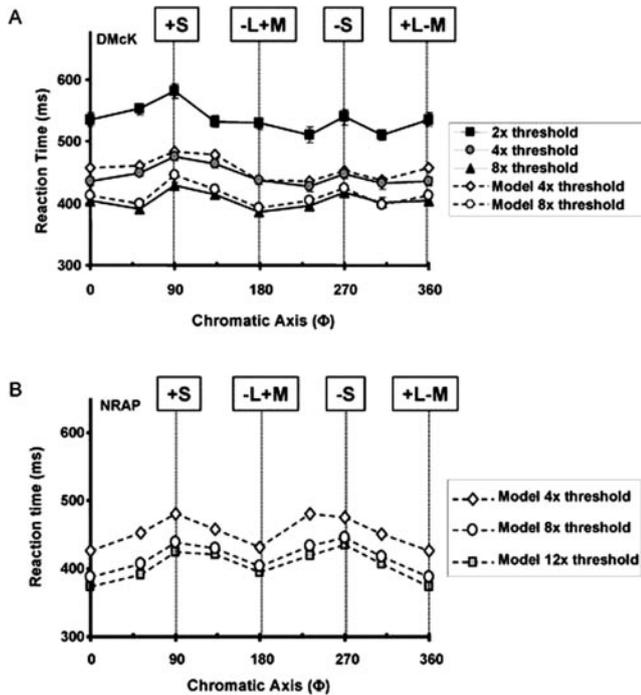


FIGURE 7. (A) The variations in RTs measured as a function of chromatic axis for stimuli that have been scaled in terms of equal multiples (2 $\times$ , 4 $\times$ , 8 $\times$ ) above detection threshold (subject DMcK). Also shown (dashed lines, open symbols) are the predicted RTs based on the modified Piéron equation ( $\hat{\tau}$ ), which adopts a contrast metric scaled according to multiples above detection threshold.

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.<sup>50</sup> 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.<sup>13,46,51-53</sup> 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 equiluminance, L-M cone-isolating stimuli are highly effective in generating nonlinear responses from magnocellular neurons.<sup>14,54</sup> Furthermore, it has been shown that the differences in sensitivity to "equivalent" tritan and red-green stimuli are generated by an additional transient mechanism that contributes to the detection of equiluminant red-green patterns that probably arises as a result of magnocellular responses to such stimuli.<sup>55</sup> It is argued that, if this transient component is masked, the remaining, purely chromatic, L-M cone mechanism is no faster than the S cone mechanism (Smithson HE, Mollon JD, ARVO Abstract 532, 2001).<sup>56</sup> 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.<sup>57</sup>

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