

The Appropriateness of Contrast Metric for Reaction Times

Beatriz M. O'Donell and Elisa M. Colombo

Departamento de Luminotecnia Luz y Visión "Ing. Herberto C. Bühler",
Facultad de Ciencias Exactas y Tecnología, Universidad Nacional de
Tucumán, Argentina
Instituto de Investigación en Luz, Ambiente y Visión (CONICET-UNT),
Tucumán, Argentina

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Abstract

We analyzed different contrast metrics to scale the stimulus strength for suprathreshold reaction times (RTs) when it is modulated along an achromatic channel (L + M) and both chromatic channels L/M and S/(L + M) considering increments and decrements along these axes. RTs were examined as a function of the Weber luminance contrast; spatial luminance ratio (SRL) and, in terms of threshold units. The results show that when there is only luminance decreasing or increasing, RTs cluster around a single RT/luminance contrast function regardless the stimulus sign and our results indicate that both SRL, Weber luminance contrast or threshold units, equate RT values. While, if the stimulus is modulated along an isoluminant plane, the appropriate contrast is Weber (RMS) or SRL for stimuli modulated along L/M axis and for stimuli modulated along S/L + M, showing an asymmetry between S-cone decrements and increments in L/M cone pathway. Threshold units are not appropriate, showing inconsistencies: The stimulus with chromatic direction equal to 90° appears as the most informative with a maximum gain. Even more so, the shared contrast gain grows as the size of the stimulus decreases.

Keywords

reaction time, metric, contrast, threshold unit, suprathreshold

Introduction

Reaction time (RT hereinafter) refers to the fastest response of a subject to the onset of a stimulus. RT has been a useful measure to analyze the behavior of visual mechanisms. Nevertheless, the choice of stimulus metric could affect the conclusions of RT differences between the visual mechanisms. Therefore, to compare the visual performance at suprathreshold conditions presents a problem as to which is the best way to express the stimulus strength (Cao, Zele, & Pokorny, 2007; Medina & Diaz, 2010; Vassilev, Murzac, Zlatkova & Anderson, 2009; Zele, Cao, & Pokorny, 2007). Any temporal difference

Corresponding author:

Beatriz M. O'Donell, Departamento de Luminotecnia Luz y Visión "Ing. Herberto C. Bühler", Facultad de Ciencias Exactas y Tecnología, Universidad Nacional de Tucumán, Av. Independencia 1800, San Miguel de Tucumán, Argentina.
Email: bodonell@herrera.unt.edu.ar

between visual pathways with different threshold sensibilities may be affected by the contrast scaling. These differences could be diminished or enlarged if the contrast scaled is not selected properly. There are many alternatives that have been proposed in terms of visibility (multiples of thresholds), Weber contrast, Michelson contrast, Whittle contrast metric, and spatial luminance ratio (SRL). Plainis and Murray (2000) also show that the slope of the RT versus $1/\text{contrast}$ function can equate the sensitivity of different detection visual mechanisms, for a fixed spatial frequency.

Whatever the case, if a single law describes the variability of the RT data as a function of a common contrast metric, this means that this metric equates the sensitivity differences between the visual mechanisms involved. Otherwise, deviations from a unique function mean that the RTs data are not well described by this common contrast metric, it does not match the neural responses of the mechanisms. A single law could be expected in the case of chromatic or achromatic stimuli with only a luminance contrast change (Burkhart, Gottesman, & Keenan, 1987; Cao et al., 2007; O'Donnell, Barraza, & Colombo, 2010; Vassilev et al., 2009; Zele et al., 2007); while a deviation from a unique law would be in the case of isoluminant chromatic stimulus with chromatic variable and no luminance change (Mc Keefry, Parry, & Murray, 2003; Medina & Diaz, 2010; O'Donnell & Colombo, 2008).

The idea that psychophysical threshold units may equate the neural responses of the mechanisms has been suggested previously (Mc Keefry et al., 2003; Mollon & Krauskopf, 1973; Smithson & Mollon, 2004). Scaling suprathreshold stimuli in multiples of threshold has been used for the purpose of comparing suprathreshold performance for stimuli modulated along different dimensions (Diaz, Barco, Jimenez, & Hita, 2001; Mc Keefry et al., 2003; Mollon & Krauskopf, 1973; Switkes & Crognale, 1999; Webster & Mollon, 1994). The question is if the differences in temporal or spatial characteristics will be preserved at suprathreshold level, while using RT as an indicator of the visual processing. An alternative scaling metric to threshold units is the contrast, where stimuli are characterized by the physical properties of the stimulus like Weber, Michelson, Whittle, or SRL.

When a change in luminance takes place between the stimulus and background, this difference generates a temporal gradient ΔL against background luminance L_b as well as a spatial gradient, $(\Delta L + L_b)$ against L_b . In a RT experiment, the stimulus is detected by luminance temporal changes or by spatial changes or by both. The Weber fraction is a measure of the stimulus temporal component. Weber contrast, (C hereinafter) scales the change in luminance, between the stimulus and the background divided by the background luminance and it is used to characterize a pulse of light in space or time while, Michelson contrast is used for periodic distributions of light in space or time and is the ratio between $L_{\max} - L_{\min}$ and $L_{\max} + L_{\min}$ where L_{\max} and L_{\min} represent the luminances of the bar and background with L_{\max} and L_{\min} representing the bars with the greater luminance and the smaller luminance, respectively.

Whittle (1986) proposed a contrast metric, $W = \Delta L / L_{\min}$, where L_{\min} is the smaller of the background luminance and ΔL is the luminance difference between L_{\max} and L_{\min} , the larger and smaller of stimuli luminance and background luminance. Vassilev et al. (2009) have used another way to quantify the luminance contrast, that is, the SRL equal to L_{\max} / L_{\min} . The relation between W and SRL is $W = \text{SRL} - 1$ (Whittle, 1986).

The SRL is associated with a spatial change. In order to determine L_{\max} / L_{\min} , Vassilev et al. (2009) used the values of Weber contrast and retinal background luminance, L_b . Since Weber contrast $\Delta L / L_b = C$ so, $\Delta L = C \cdot L_b$. The ΔL value was added to L_b in the case of increments and subtracted from L_b in the case of decrements, to obtain L_s , the luminance of the stimulus. Therefore the SRL is equal to L_s / L_b , with the larger of them as the numerator

and the smaller as the denominator. So $SRL = (1 + C)$ for increments and is equal to $(1 - C)^{-1}$ for decrements.

Cao et al. (2007) measured the RTs for contrast luminance increments and decrements under a selective stimulation of rods alone (0.002–0.2 Trolands), rods and cones (2–20 Trolands), and cones alone at 200 Trolands. The suprathreshold luminance contrasts were between 5% and 80%. The stimulus was a 2° diameter circle presented at 7.5° eccentricity in the nasal visual field in the center of a 13° background, where both stimulus and background were achromatic. For rods, RTs to decrements were faster than those to increments. RTs as a function of Weber contrast to rod Rapid-Off stimuli were shorter than those to rod Rapid-On stimuli, indicating that Weber contrast do not match the neural responses of these mechanisms. Neither the Whittle nor the Plainis and Murray transforms can equate rod Rapid-On and Rapid-Off of RTs. According to Cao et al. (2007), the postreceptoral visual signals are conveyed through ON and OFF pathways, which provide excitatory responses to light increments and decrements, respectively. Physiological investigations suggest that rod input is strong in the magnocellular pathway but weak or absent in the Parvocellular (PC) and Koniocellular (KC) pathways. From psychophysical studies, it is assumed that both rod and cone RTs to luminance stimuli are mediated by the MC pathway.

Zelev et al. (2007), using the data for rods, published previously by Cao et al. (2007), analyzed whether the multiple of threshold contrast is appropriate for equating the RTs in response to luminance increments or decrements. They found that when the RT is expressed by multiples of thresholds, the results are reversed, that is to say, Rapid-Off RTs were longer compared to the Rapid-On RT measured at the same multiple of threshold contrast. In this case, the contrast threshold ratio of decremental to incremental stimuli for each observer was equal to 2.2. Zelev et al. (2007) explained these results by saying that the threshold sensibility and RT are likely to be based on different characteristics of the internal response and, therefore, there seems to be no point in looking for a metric to equate the RT values that result from mechanisms of different sensibility. The use of a multiple of threshold as a metric can confuse the interpretation of the mechanisms involved. Expressing suprathreshold data in threshold units can produce results which are artificially biased in favor of a mechanism with low sensitivity (Zelev et al., 2007). In agreement with Mc Keefry et al. (2003) and Zelev et al. (2007), threshold units do not account for the relative contributions of postreceptoral processing to threshold. Rod incremental and decremental stimuli are detected by rod photoreceptors, however, the product of the receptor and postreceptoral processes give back different RTs. According to Zelev et al. (2007) while physiological measurements from two different cells may give different response times, which could result from a difference in either gain or conduction velocity however, the stimulus energy or contrast is the only common metric to measure the response of both cells. Threshold units would reflect the multiplicity of factors that contribute to sensitivity and confound the RTs with differences in sensitivity.

Cao et al. (2007) have also shown that there was no difference in RT to cone incremental and decremental stimuli when the RT data are plotted as a function of Weber contrast, consistent with physiological data that show symmetrical responses of MC ON and OFF cells to rapid ON or OFF sawtooth stimulus modulation (Kremers et al., 1993). However, there are reports that some observers have lower cone decrement thresholds (Bowen, Pokorny, & Smith, 1989). Cone RTs data cluster around a single RT as a function of Weber contrast function, and determined principally by the absolute value of the luminance step rather than with the background luminance and the direction of the step, a result that implies the involvement of an early linear mechanism of cone mechanism (Burkhart et al., 1987).

As a consequence, the Weber contrast metric seems to be appropriate contrast metrics for RT's cone (Burkhart et al, 1987; O'Donell, Colombo & Boyce, 2011; Rea & Oullette, 1988) but not for rods (Cao et al, 2007).

Zelev et al. (2007) have proposed, to minimize any confusion of the stimulus metric when comparing the RTs of two different systems (e.g., rod ON and OFF, S-cone and L- or M-cone), the asymptotic RT, sometimes called the irreducible minimum, which is the minimum RT value that is reached when the intensity of the stimulus is sufficiently high. While for Zelev et al. (2007), RT_0 is independent of the stimulus contrast and can be used to compare RTs, Medina and Diaz (2010) state that RT_0 depends on both the encoding time prior to the formation of the threshold and the visual latency at the contrast detection threshold.

Vassilev et al. (2009) considered this question saying that to achieve an appropriate metric for RT to suprathreshold increments and decrements it is necessary to consider both temporal and spatial luminance distribution of the stimulus against the background, mentioned earlier. They have analyzed the results from Cao et al. (2007) concluding that RT for rod vision is less sensitive to the temporal stimulus change than to its spatial gradient. The opposite occurs for cone vision, which explains why the Weber contrast is appropriate for RT for cone vision and not for rod vision. Incremental and decremental RTs for rods form two distinct RT/Weber contrast functions but they cluster around a single function when plotted as a function of the SRL.

Also, Vassilev et al. (2009) studied their own RT results for S-cone stimulation. In this case, the stimuli consisted of either a blue-light luminance increase or decrease within a 2° diameter of circular window with sharp edges presented to the right eye at 1.5° from the fovea. The SRL has been found to be a good metric for RT to increments and decrements when they involve selective stimulation of the S cones, identical to what happens with rods. In both cases, the impulse response of the visual system differs from that of achromatic photopic vision by its sluggish, monophasic time course.

Finally, when the stimuli are isoluminant and modulated along the cardinal axis [$S/(L+M)$]-cone-opponent and (L/M)-cone opponent mechanism, the longest RTs correspond to stimuli that isolate the S-cone activity and the fastest responses occur with L/M cone-isolating stimuli when the data are represented as a function of $1/\text{RMS}$, similar to the metric proposed by Plainis and Murray (2000), where RMS is the square-root of the cone contrast (Mc Keefry et al., 2003; O'Donell et al., 2010; O'Donell & Colombo, 2008; Parry, Plainis, Murray, & McKeefry, 2004). In this case, the results of RTs versus the reciprocal of RMS cluster around three lines, one corresponding to L/M cone-isolating stimuli and the others correspond to the two opposite [$S/(L+M)$]-cone-opponent mechanism. According to Sankeralli and Mullen (2001), each color signal (red, green, blue, and yellow) and luminance signal (light and dark) is subserved by a separable mechanism. Medina and Diaz (2010) too examined different contrast metrics to scale RTs for suprathreshold isoluminant stimuli: S-cone increments and decrements were isolated along two different tritan confusion lines, each one having a different luminance value. RTs were evaluated as a function of the Weber contrast and the S-cone excitation ratio—considered as being analogous to the SRL examined by Vassilev et al. (2009)—between the test stimulus and the background. RT data were fitted using a model-based version of Piéron's law and incorporates the notion of threshold units. The experimental conditions do not favor any specific contrast metric and reinforce that both the Weber S-cone contrast and the S-cone excitation ratio are plausible candidates for suprathreshold scaling at isoluminance. They conclude that S-cone RTs are not well described by a common contrast metric and are better represented by separate S-cone increments and S-cone decrements, in the same way as rod RTs (Vassilev et al., 2009; Zelev et al., 2007). S-cone RTs are better described by separate functions, reinforcing

the idea of two separate S-cone mechanisms. S-cone increments and decrements do not scale in the same manner.

Tailby et al. (2008) have studied the functional asymmetries in visual pathways carrying S-cone signals in macaque. They found that on several important dimensions, the properties of neurons that receive inhibitory input from S cones (S⁻) are quite unlike those of neurons that receive excitatory input from S-cones (S⁺). The organization of chromatic inputs differs substantially: In S⁺ cells, S-cone signals were usually opposed by those of L- and M-cones; in S⁻ cells, signals from L cones were usually opposed to those of S- and M-cones. The S⁺ and S⁻ pathways lack the symmetrical relationship that characterizes the ON-center- and OFF-center divisions of the P pathway. Even though these results were not directly dealing with RTs, these results added evidence about the asymmetry between the two separate S-cone mechanisms.

Mc Keefry et al. (2003) also showed that the difference in RTs values between the two chromatic mechanisms is highly dependent on how the chromatic stimuli are scaled. 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.

The aim of the present work is to analyze how the choice of stimulus metric affects the conclusions drawn from a RT data. In order to add evidence to this discussion, we compared the results, using the RT database previously published (O'Donell, Barraza et al., 2010; O'Donell & Colombo, 2008; O'Donell, Colombo et al., 2011), and considered different alternatives of contrast metric: multiple of threshold, Weber fraction, and SRL. The chromatic stimulus is modulated along the two chromatic-opponent-cone axes, a (L/M) axis and $[S/(L + M)]$ axis, as well as the luminance axis ($L + M$). The experimental device and the methods have been fully tested as described in these previous studies. Consequently, only a brief summary is provided here.

Experimental Procedure

O'Donell et al. (2010) have developed an empirical model of RTs from an extensive set of RT data which were collected from two experiments, using a large range of chromatic stimulus conditions. During the first experiment, O'Donell and Colombo (2008) measured RTs of chromatic stimulus as a function of luminance contrast, including the isoluminant value, for a range of purity excitation from 15% to 70% depending on the cardinal chromatic direction. The size of the stimulus was 0.17° under an adaptation luminance equal to 5 cd/m^2 .

During the second experiment, O'Donell et al. (2010) measured RTs along different chromatic directions, including both chromatic cardinal directions and intermediate ones, as a function of luminance contrast at a fixed purity excitation—expressed in terms of RMS—, using different sizes of the stimulus (0.129° , 0.258° , 0.522° , and 1.045°) and two adaptation luminances (5 and 40 cd/m^2).

In both cases, the stimulus was presented on an achromatic background. The stimulus was a Gaussian blob with a temporal cosinusoidal presentation. It took 300 ms to reach the maximum value, maintained at this condition during 300 ms and decreased during the next 300 msec. The isoluminant value was determined by heterochromatic flicker photometry. The stimulus presented was pulsed on and off at 15 Hz and, the luminance of the stimulus was adjusted until the perceptual flicker was minimized.

Once the isoluminant condition had been determined, observers began the RT experiment. They were asked to press a button on a response box as soon as they detected the presence of the stimulus. The stimulus presentation was preceded by a random time interval (between 1500 and 3500 ms), to prevent the subject from knowing when the stimulus would appear.

The time between the presentation of the stimulus and the observer's response was registered as the RT value. The stimulus was turned off by the observer's response or after 3 s if no response occurred. Once the subject responded, a fixed intertrial interval of 1500 ms was introduced during which the background luminance was presented. The stimulus parameters (adaptation luminance, color, and size) were chosen randomly from a set of values for each block of 25 trials. Only the luminance contrast sequence was randomized within a block, in order to avoid chromatic post effects. Each data point was tested 50 times.

Two observers participated in the first experiment and three in the second. They were all previously trained for this kind of experiment. The protocol of the procedure agrees with the provisions of the Declaration of Helsinki.

The chromatic coordinates of the stimuli are found on the line linking the white point—W—with each of the points with (x,y) coordinates (O'Donell, Barraza et al., 2010; O'Donell & Colombo, 2008). The stimuli were referred in terms of deg, in such a way that, stimuli 0° and 180° (the angular azimuth at MBDKL color space (Derrington, Krauskopf, & Lennie, 1984; MacLeod & Boynton, 1979) are located on the axis that only produces excitation of the L and M cones, that is the (L–M)-cone opponent mechanism or S-cone constant. The axis corresponding to the [S–(L + M)]-cone opponent mechanism or L&M-cone constant belongs to the conventional tritanopic line. The stimuli called 90° and 270° are located on this axis. The stimuli modulated in the cardinal axes appear as reddish—0°, greenish blue—80°, violet—90°, and lime—270°.

Results

As mentioned earlier, the comparison between different contrast metrics is performed by analyzing RT data published by O'Donell, Barraza et al. (2010), O'Donell and Colombo (2008), O'Donell, Colombo et al. (2011). In these works, it was shown that RT for luminance decrements and increments is equated when they are plotted as a function of Weber luminance contrast, in agreement with Vassilev et al. (2009) and Burkhardt et al. (1987): RT decreases as luminance increases, so that the behavior could be assimilated to a single RT curve as a function of Weber contrast (O'Donell et al., 2010). Nevertheless, there are other alternatives of contrast metrics that can be analyzed. The following three cases are considered: Achromatic stimuli presented on a white background, for which only the luminance varies, either in an incremental or decremental way; isoluminant stimuli with chromaticity variable along the *L/M* and *S/(L + M)* chromatic channels and, finally chromatic stimuli which are modulated only along the luminance channel *L + M*.

First Case of Analysis: Achromatic Stimuli

We have used a model that follows the Pieron's law (Vassilev et al., 2009; Zele et al., 2007):

$$RT = RT_0 + kC^{-n} \quad (1)$$

where RT_0 is the asymptotic plateau reached at very high contrasts— C —, k , and n are free parameters. The role of contrast sensitivity in RTs is expressed by the reciprocal of k or contrast gain factor (Mc Keefry et al., 2003; Medina & Diaz, 2006; Parry et al., 2004, 2007; Pins & Bonnet, 2000; Plainis & Murray, 2000; Vassilev et al., 2009; Zele et al., 2007).

The objective is to express the contrast using an appropriate metric such as that both increment and decrement contrast changes can be expressed by a single curve.

RT experimental data are adjusted according to Equation (1) as a function of contrast—Weber or SRL—and the parameters RT_0 , n , and k are calculated. The high regression coefficients ($r^2 > .9$ in all cases) indicate that this equation provides a good description of the RTs data sets. Goodness-of-fit was evaluated using the coefficient of regression R -square or R^2 , defined as the explained over the total variability of the dataset.

Parameters RT_0 , n , and k were subjected to a four-way analysis of variance with luminance contrast polarity, observer, size of the stimulus, and adaptation luminance as main effects. This analysis shows that any of these factors influences statistically the exponent n . When the luminance contrast is expressed by Weber contrast, the exponent is equal to 1, in agreement with other results (Plainis & Murray, 2000), and when luminance contrast is expressed by SRL, it is equal to 10 ± 2 . Medina and Diaz (2010) have shown that the exponent of the Pieron's law is higher for the S-cone excitation ratio (between 5 and 11) than the Weber contrast (less than 1).

RT_0 values depend on the observer ($F(2,88) = 101.4$; $p \ll .05$), stimulus size ($F(3,88) = 18.9$; $p \ll .05$), and adaptation luminance ($F(1,88) = 9.08$; $p \ll .05$) but not on the contrast polarity. RT_0 values are constant depending on each combination between observer, size, and adaptation luminance.

The k factor depends on the size of the stimulus ($F(2,32) = 9.34$; $p \ll .05$) and the adaptation luminance ($F(1, 32) = 7.28$; $p \ll .05$) when the luminance contrast is expressed by Weber. When the luminance contrast is expressed by SRL, the k factor depends only on the adaptation luminance ($F(1,88) = 7.04$; $p \ll .05$). The contrast gain factor does not depend on the contrast sign in either cases.

Figure 1(a) and (b) shows the mean RT values—calculated regarding all experimental conditions and observers—as a function of the reciprocal of the Weber luminance contrast and the reciprocal of SRL with an exponent equal to 10, indicating that both contrast Weber and SRL are suitable for scale contrast in the case of an achromatic stimulus.

Since the threshold values for luminance contrast decreases or increases were not measured, in order to scale the luminance contrast as threshold units, we have calculated them using a model proposed by Medina and Diaz (2010). They developed an alternative equation to Pieron's law, which lead to a k value expressed by the following equation

$$k = RT_0 C_t^n \quad (2)$$

where RT_0 is the asymptotic RT reached at high contrast, C_t is the luminance threshold, and n is a free exponent—the same as in the Pieron's law.

The threshold luminance data obtained in this way, using RT_0 , n , and k obtained with achromatic stimuli calculated earlier, were subjected to a four-way analysis of variance with size, adaptation luminance, contrast polarity, and observer as their main effects. This analysis shows that neither the polarity of luminance contrast nor that the observer are statistically significant but they depend on the size of the stimulus ($F(3,89) = 3.7$; $p \ll .05$) and of the adaptation luminance ($F(1,89) = 9.06$; $p \ll .05$).

Expressing the luminance contrast in terms of multiples of threshold would give similar results because, in this case, there is a single luminance threshold for both polarity and, therefore, an identical multiplication number—the luminance threshold—for each experimental situation. Figure 1(c) shows the results concluding that, this way of scaling is also suitable in the case of achromatic stimulus.

Therefore, the Weber and SRL contrasts or threshold units are suitable metrics.

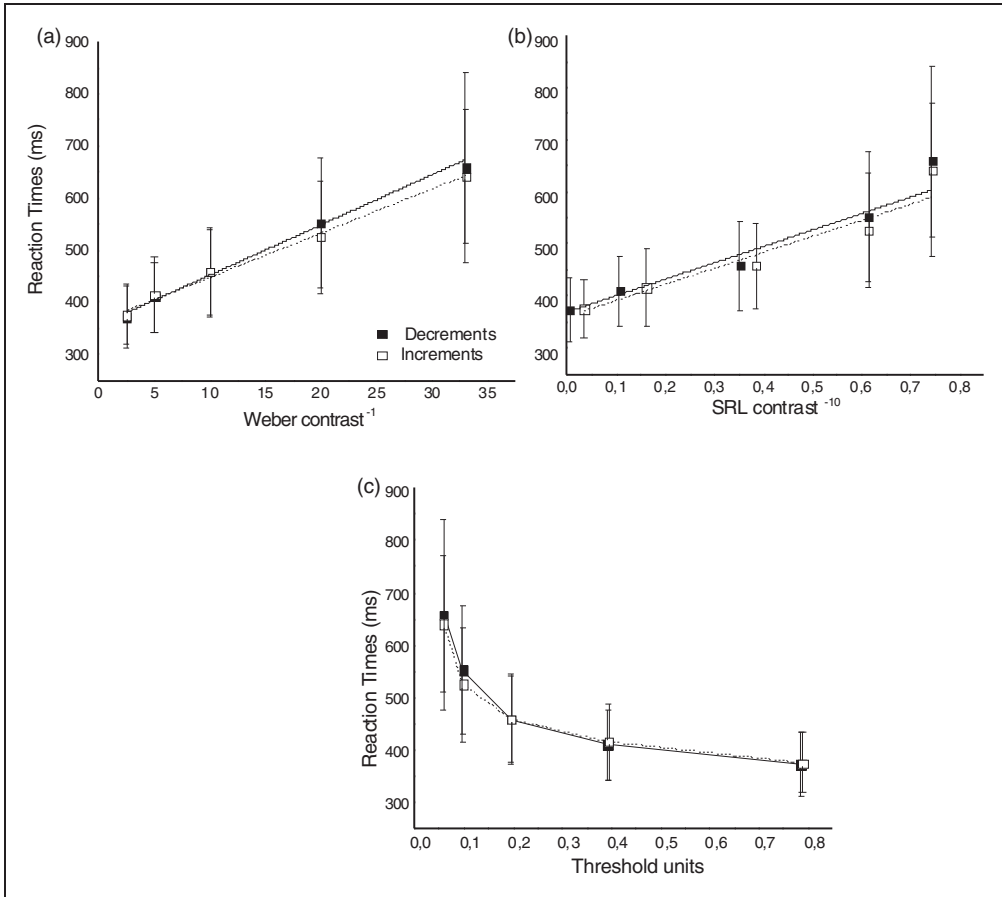


Figure 1. Mean RT values—calculated on all experimental conditions and observers—as a function of the reciprocal of Weber luminance contrast (a) the reciprocal of SRL (b) with an exponent equal to 10 and, (c) as a function of threshold units. All metric of contrast is suitable for scale contrast in the case of an achromatic stimulus.

Second Case of Analysis: Isoluminant Stimuli

We characterized the chromatic information—without luminance changes—with this RMS_i value. The square-root of the cone contrast— RMS_i —was calculated from the equation

$$RMS_i = \sqrt{((\Delta L/L_0)^2 + (\Delta M/M_0)^2 + (\Delta S/S_0)^2)/3} \tag{3}$$

where $\Delta L/L_0$, $\Delta M/M_0$, and $\Delta S/S_0$ are the Weber cone contrasts produced by each isoluminant stimulus on the background (L_0 , M_0 , and S_0).

RT data published by O’Donnell et al. (2010) corresponding to isoluminant stimuli modulated on $S/(L+M)$ and L/M chromatic channels are examined. Figure 2(a) shows RT data as a function of RMS. The gain is greater for stimuli on the L/M axis— 0° and 180° —than on $S/(L+M)$ axis— 90° and 270° —, in accordance with Mc Keefry et al. (2003), Mollon and Krauskopf (1973), and Smithson and Mollon (2004). The results show that the values on the L/M axis can be unified into a single curve while the values on the axis

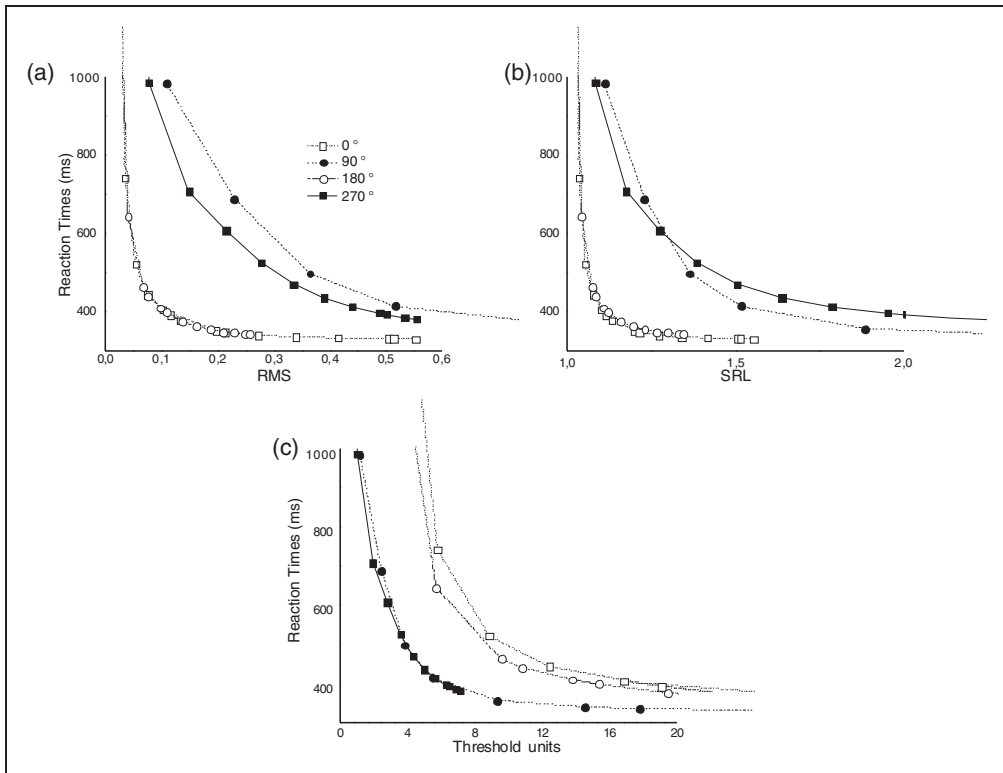


Figure 2. Mean reaction times—ms—for isoluminant stimuli 0° , 90° , 180° , and 270° as a function of (a) RMS contrast, (b) SRL contrast, and (c) contrasts expressed by threshold units— RMS/RMS_t —B). The data correspond to one observer B at adaptation luminance of 5 cd/m^2 and a stimulus size of 0.522° .

$S/(L+M)$ have different slopes. Therefore the RMS or Weber luminance contrast is not proper for the latter case.

We replotted the same RT data as a function of the SRL between stimulus and background—Figure 2(b). In this case, the slopes within the $S/(L+M)$ channel approach one another. Although Murzac and Vassilev (2004) concluded that the SRL had been found to be a better metric to RTs to S-cone selective increments and decrements, we agree with Medina and Diaz (2010) in the sense that a single function did not describe all RT data reinforcing the idea of two separate S-cone mechanisms.

In Figure 2(c) the data are plotted in terms of multiples of chromatic thresholds— RMS/RMS_t —these chromatic thresholds— RMS_t —were extracted from O'Donnell and Colombo (2011). The plotted RT values show that, although the data could be assimilated to a single curve for the $S/(L+M)$ channel, the slopes are reversed since the values corresponding to channel $S/(L+M)$ are greater than the slope corresponding to the L-M channel. The threshold units metric failed to equate RTs for increments and decrements for isoluminant stimuli.

Third Case of Analysis: Chromatic Stimuli With Luminance Change Only

We analyzed the case in which contrast luminance varies but chromaticity, expressed by RMS value, is constant. O'Donnell et al. (2010) have proposed a model for this case expressed by the

following equation

$$RT = RT_0 + \frac{g}{b|C|^{1.98} + (1-b)RMS_i^{1.98}} \quad (4)$$

where g (similar to k in equations (1) and (2)) can be understood as a parameter reflecting a shared contrast gain between chromatic and achromatic mechanisms, C is the luminance contrast, RMS_i is the pure chromatic contrast at isoluminance, and b is the relative weight between luminance and color contribution to the RT values. g and b are free parameters. O'Donell et al. (2010) show that there are differences in gain between (L/M)-cone opponent and [$S/(L+M)$]-cone opponent mechanisms and, inside this later mechanism, between stimuli at 90° and 270° . Moreover, the gain of the $S/(L+M)$ -mechanism is considerably less than that of (L/M)-mechanism. The two opposing submechanisms of the (L/M)-cone opponent mechanism have symmetry between the cones input while the same is not true for the [$S/(L+M)$]-cone opponent mechanism (Mc Keefry et al. 2003; Medina & Diaz, 2010; O'Donell & Colombo, 2008; Parry et al., 2004; Sankeralli & Mullen, 2001). In this way, it is possible to find a metric that matches the values of RT for decreases and increases on $L+M$ and $L-M$ channel but, in the case of channel S, it may not be possible to find a common metric. RMS equates RTs in the case of stimuli modulated along the (L/M)-cone opponent mechanism but not along the $S/(L+M)$ mechanism.

We can rewrite Equation (4) using a new contrast metric, which is the multiple of threshold contrast (C/C_t) in terms of Weber and (RMS_i/RMS_{it}) contrast. The chromatic thresholds, measured in terms of RMS, are equal in the L/M axis but differ along the axis $S+S$ -(O'Donell, Barraza et al., 2010; O'Donell, Colombo et al., 2011). In this way the new equation is

$$RT = RT_0 + \frac{g}{b|C/C_t|^{1.98} + (1-b)(RMS_i/RMS_{it})^{1.98}} \quad (5)$$

Figure 3(a) and (b) shows the shared contrast gain calculated from Equations (4) and (5) for each chromatic axes corresponding to a adaptation luminance of 40 cd/m^2 and two sizes of stimulus -0.129° and 1.045° . Figure 3(c) shows the gain calculated from Equation (4) using SRL as a contrast metric.

When the Weber contrast or SRL is used as a metric, the results that emerge show that the gain is higher for bigger sizes of the stimulus than for the smaller ones and that it is higher for the L/M chromatic channel than for $S/(L+M)$ channel, in agreement with Mc Keefry et al. (2003) and Parry et al. (2004). Using the multiple of threshold units, the results seem to be contradictory since this new analysis shows that color with chromatic direction equal to 90° appears to have the maximum gain and, even more, that the differences between shared contrast gains become smaller regarding the results from Equation (4). Moreover, this model shows an inconsistent trend of the shared contrast gain which grows as the size decreases.

The results show that the Weber luminance contrast and SRLs are plausible candidates for suprathreshold scaling.

The results support the idea that, when the RT data come from mechanisms with different sensitivities, the results are reversed, that is to say that RTs to increments appeared shorter than RTs to decrements, whereas, when mechanisms have similar sensitivities, this reversal does not occur when luminance changes are expressed by Weber or by SRL.

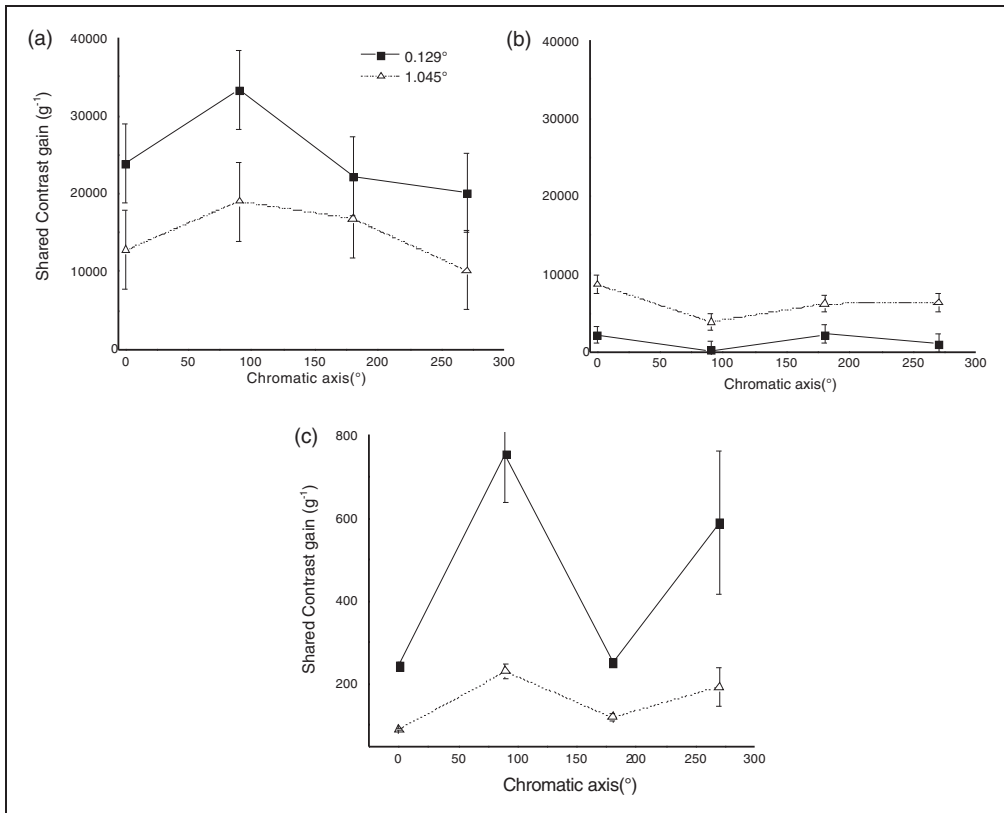


Figure 3. Shared contrast gains calculated from Equations (4) and (5) for each chromatic axes corresponding to an adaptation luminance of 40 cd/m^2 and two sizes of stimuli 0.129° and 1.045° . (a) original model using Weber contrast, (b) modified model using threshold units, and (c) model corresponding to Equation (4) using SRL as luminance contrast.

Discussion

A suitable metric contrast means that it must be able to represent the physical characteristics of the stimulus with its background without changing the relationship between the visual response and contrast or any other variable of the stimulus. The question would appear to be how it would be possible to scale the strength of a stimulus in order to equate the visual response.

In order to detect a stimulus, it is necessary to take into account both spatial and temporal luminance distribution between the stimulus and its background. Both the Weber fraction and the SRL are related to the local features of images, assuming adaptation from the background during the early stages of color processing (Cole, Hine, & McIlhagga, 1993; Whittle, 1986). While the Weber contrast is a measure of the transient stimulus component, SRL is a steady-state measure. The type of neural activity, predominantly transient or sustained, and the type of stimulus detection by temporal (successive) luminance discrimination or by spatial (simultaneous) luminance discrimination determines the appropriateness of Weber contrast or SRL contrast metric for RT. Physiological and psychophysical data show that photopic cone vision is faster and predominantly transient

while scotopic rod vision is slower and predominantly sustained (Pepperberg, 2001). Also this seems to be the case for S-cone vision (Reid & Shapley, 2002). It is important in understanding these effects to define the contrast metrics that are used.

If the sensitivities are similar, a unique metric could be found. In this case, RTs cluster around a single RT/luminance contrast function regardless of the stimulus sign, increment, or decrement. The fit of both incremental and decremental RTs by a single contrast function parallels the properties of the systems involved in stimulus detection. Our results indicate that, if there is only luminance decreasing or increasing, both SRL and Weber luminance contrast and threshold units equate RT values for cones for the background luminance range analyzed here. Assuming, and according to Vassilev et al. (2009), the Weber fraction captures the temporal change of luminance relative to the background and SRL captures the spatial discrimination, then both temporal and spatial discrimination might contribute to stimulus detection and response triggering, since all contrast metrics are adequate.

According to Tailby et al. (2008), the critical sensory event for RT is derived from the early, rising phase of a neuronal response. The critical event occurs when the stimulus-evoked response reaches some small criterion amplitude, either above or below the prevailing baseline, depending on stimulus step in visual transduction is linear, and thus equal increments and decrements will produce symmetric effects of identical time course and equal absolute magnitude. Finally, nonlinear transformations at later stages do not greatly modify incremental and decremental responses of equal absolute magnitude, so two responses that are equivalent at a first step remain equivalent at all succeeding stages. Thus, in principle, these last assumptions could be satisfied within the confines of a cone cell with only luminance change. This seems more likely in the case of contrast equivalence measurements, since all that is required is an initial linearity followed by some sort of subsequent processing that does not markedly disrupt the temporal equivalence relations represented in the early phase of the cone response. This in no way excludes the possibility that the perceptual response to decrements and increments might be mediated by different postreceptoral systems.

The difficulty arises when we try to compare results of suprathreshold visual performance through a unique metric when the mechanisms involved have different threshold sensitivities, in words of Zele et al. (2007): *Is it meaningful to search for a metric that equates the sensitivity of two mechanisms with different threshold values?*. This is the case when both the chromaticity and luminance of the stimulus or chromaticity vary only along the chromatic axis. In the model proposed by O'Donnell et al. (2010) and O'Donnell et al. (2011), the results are convincing when the contrast is scaled in terms of the Weber luminance contrast or SRL, but not with threshold units. The parameters of the model reveal satisfactorily how RT is linked to stimulus size, chromatic channels and adaptation luminance, and how they can be interpreted in terms of two chromatic mechanisms. But when the contrast is scaled in multiples of detection threshold units, the parameters of the model proposed by O'Donnell et al. (2010) cease to have any meaning. Scaling suprathreshold stimuli in multiples of each observer's color detection threshold does not seem to be appropriate for cone RTs, favoring the chromatic direction with lower sensitivity and a smaller size of the stimuli. This could be explained by saying that threshold sensitivity and RT are related to different characteristics of the internal response generated by a visual stimulus. To select the best metric, it is necessary to have previous knowledge of the threshold and suprathreshold behavior. The threshold and RTs represent different tasks and, therefore a different criterion decision. At threshold, the visual system uses all the available information to decide whether the stimulus is present or not, until a response criterion is reached. The threshold depends on the summation area, the

information necessary to detect a stimulus, but it does not take into account the contributions of the postreceptoral processes that take place after the threshold.

If the stimulus is modulated along an isoluminant plane, the appropriate contrast is Weber (RMS) or SRL for stimuli modulated along L/M axis and for stimuli modulated along $S/L + M$, showing an asymmetry between S-cone decrements and increments although not in the L/M cone pathway (Medina & Diaz, 2010; O'Donnell & Colombo, 2008).

Tailby et al. (2008) have studied the functional asymmetries in visual pathways carrying S-cone signals in macaque. They found that on several important dimensions, the properties of neurons that receive inhibitory input from S cones ("S-") are quite unlike those of neurons that receive excitatory input from S cones ("S+"). The organization of chromatic inputs differs substantially: In S+ cells, S-cone signals were usually opposed by those of L- and M cones; in S- cells, signals from L cones were usually opposed to those of S- and M cones. The S+ and S- pathways lack the symmetrical relationship that characterizes the ON-center and OFF-center divisions of the P pathway. Previous studies (Medina & Diaz, 2010) have reported different RTs for S-cone increments and S-cone decrements. These temporal asymmetries are thought to be mediated by separate excitatory and inhibitory pathways originating in the retinal ganglion cells (Calkins, 2001; Hendry & Reid, 2000; Solomon & Lennie, 2005; Tailby et al., 2008). Mullen et al. (2008) and Cottaris and De Valois (1998) suggest that S-cone RTs may support a broader dynamic range and later processing stages, possible at the cortex.

Our results reinforce the presence of specialized postreceptoral S-cone mechanisms (De Valois et al., 2000; Sankeralli & Mullen, 2001; Zlatkova et al., 2008). Departures from a single function will be compatible with separate mechanisms. S+ and S- do not scale in a similar way. Their experimental results do not favor any specific contrast metric and therefore both the Weber contrast and the SRL are plausible candidates for suprathreshold scaling at isoluminance, while maintaining two separate curves. We conclude that S-cone RTs are not well described by a common contrast metric. They are better represented by separate S-cone increments and S-cone decrements, in the same way as rod RTs.

Zele et al. (2007) have argued that the asymptotic term of Pierson's law is independent of stimulus contrast and can be used to compare RTs. Their results indicate that this is not our case, the asymptotic RT value depends on both the encoding time and the visual latency at the contrast detection threshold. The encoding time includes those processes at the earlier stages and is in agreement with the efficient coding hypothesis (Medina, 2009).

Psychophysical possibilities less frequently implemented however do exist to equate RTs, and match in behavior the suprathreshold versions of the luminance and color stimuli for salience. Walkey et al. (2006) have defined the effective achromatic contrast of a reference stimulus as the contrast that equates perceptually to the contrast of the color stimulus, in terms of RT and search time. The operational definition of equivalent contrast is any pair of negative and positive luminance contrasts that produce equivalent RTs are, by definition, an equivalent contrast. Equivalent contrast relations for RT may provide a link between the psychophysics and cellular physiology of contrast vision (Burkhart et al., 1987).

From the results presented, it can be concluded that this common metric for RT data as a function of contrast depends on the mechanisms of visual processing. None of the contrast metrics seems to give a unique answer to all the cases.

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References

- Bowen, R. W., Pokorny, J. & Smith, V. C. (1989). Sawtooth contrast sensitivity: Decrements have the edge. *Vision Research*, *29*, 1501–1509.
- Burkhardt, A. A., Gottesman J., & Keenan, R. M. (1987). Sensory latency and reaction time: Dependence on contrast polarity and early linearity in human vision. *JOSA A*, *4*, 530–539.
- Calkins, D. J. (2001) Seeing with S cones. *Progress in Retinal and Eye Research*, *20*, 255–287.
- Cao, D., Zele, J. A., & Pokorny, J. (2007). Linking impulse response functions to reaction time: Rod and cone reaction time data and a computational model. *Vision Research*, *47*, 1060–1074.
- Cole, G. R., Hine, T., & McIlhagga, W. (1993). Detection mechanisms in L-, M-, and S-cone contrast space. *Journal of the Optical Society of America*, *10*, 38–51.
- Cottaris, N. P. & De Valois, R. L. (1998) Temporal dynamics of chromatic tuning in macaque primary visual cortex. *Nature*, *395*, 896–900.
- Derrington, A., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanism in lateral geniculate nucleus of macaque. *Journal of Physiology*, *357*, 241–265.
- Diaz, J. A., Jimenez del Barco, L., Jimenez, J. R., & Hita, E. (2001). Simple reaction time to chromatic changes along L&M-constant and S-constant axes. *Color Research & Application*, *26*, 223–233.
- De Valois RL, Cottaris NP, Elfar SD, Mahon LE & Wilson JA (2000). Some transformations of color information from lateral geniculate nucleus to striate cortex. *The Proceedings of the National Academy of Sciences*, *97*, 4997–5002.
- Hendry, S. H. C. & Reid, R. C. (2000) The koniocellular pathway in primate vision. *Annu. Rev. Neurosci*, *23*, 127–153.
- Kremers J. Barry B.L., Pokorny J. & Smith V. (1993) Responses of Macaque Ganglion Cells and Human Observers to Compound Periodic Waveforms. *Vision Res*, *33*, 1997–2011.
- MacLeod, D. I. A., & Boynton, R. M. (1979). A chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America*, *69*, 1183–1186.
- Mc Keeffry, D. J., Parry, N. R., & Murray, I. J. (2003). Simple reaction times in color space: The influence of chromaticity, contrast and cone opponency. *Investigative Ophthalmology and Visual Sciences*, *44*, 2267–2276.
- Medina, J. M. (2009). 1/f (alpha) noise in reaction times: a proposed model based on Piéron's law and information processing. *Phys. Rev. E* *79*, 011902.
- Medina, J. M. & Diaz, J. A. (2006). Postreceptoral chromatic-adaptation mechanisms in the red-green and blueyellow systems using simple reaction times. *J. Opt. Soc. Am. A* *23*, 993–1007.
- Medina, J. M., & Diaz, J. A. (2010). S-cone excitation ratios for reaction times to blue-yellow suprathreshold changes at isoluminance. *Ophthalmic and Physiological Optics*, *30*, 511–517.
- Mollon, J. D., & Krauskopf, J. (1973). Reaction times as a measure of the temporal response properties of individual color mechanism. *Vision Research*, *13*, 27–40.
- Mullen, K. T., Dumoulin, S. O. & Hess, R. F. (2008). Color responses of the human lateral geniculate nucleus: selective amplification of S-cone signals between the lateral geniculate nucleus and primary visual cortex measured with high-field fMRI. *Eur. J. Neurosci*, *28*, 1911–1923.
- Murzac, A., & Vassilev, A. (2004). Reaction time to S-cone increments and decrements. 7th European conference on visual perception, Budapest, Hungary, August 22–26. *Perception*, *33*, 180 (Abstract).
- O'Donnell, B., & Colombo, E. (2008). The influence of luminance contrast and chromatic contrast on reaction times to a stimulus. *The International Journal of Lighting Research and Technology*, *40*, 359–371.

- O'Donnell, B. M., Barraza, J., & Colombo, E. M. (2010). The effect of chromatic and luminance information on reaction times. *Visual Neuroscience*, *27*, 119–129.
- O'Donnell, B. M., Colombo, E. M., & Boyce, P. (2011). Colour information improves relative visual performance. *Lighting Research & Applications*, *43*, 423–438.
- O'Donnell, B. M., & Colombo, E. M. (2011). Foveal spatial summation in human cone mechanism. *Perception*, *40*, 50–62.
- Parry, N. R. A., Murray, I. J., & McKeefry, D. J. (2007). Reaction time measures of adaptation to chromatic contrast. *Vis. Neurosci*, *25*, 405–410.
- Parry, N. R. A., Plainis, S., Murray, I. J., & McKeefry, D. J. (2004). Effect of foveal tritanopia on reaction times to chromatic stimuli. *Visual Neuroscience*, *21*, 237–242.
- Pepperberg D. R. (2001). The flash response of rods in vivo. In H. Kolb, H. Ripps, & S. Wu (Eds.). *Progress in brain Research*, *13*: 369–381.
- Pins, D., & Bonnet, C. (2000). The Pieron function in the threshold region. *Percept. Psychophysics*, *62*, 127–136.
- Plainis, S., & Murray, I. J. (2000). Neurophysiological interpretation of human visual reaction times: Effect of contrast, spatial frequency and luminance. *Neuropsychologia*, *38*, 1555–1564.
- Rea, M. S., & Ouellette, M. (1988). Visual performance using reaction times. *Lighting Research and Technology*, *20*, 139–153.
- Reid R. C., & Shapley R. M. (2002). Space and time maps of cone photoreceptor signals in macaque lateral geniculate nucleus. *Journal of Neuroscience*, *22*, 6158–6175.
- Sankeralli, M., & Mullen, K. (2001). Bipolar or rectified chromatic detection mechanism? *Visual Neuroscience*, *18*, 127–135.
- Smithson, H. E., & Mollon, J. D. (2004). Is the S-opponent chromatic sub-system sluggish? *Vision Research*, *44*, 2919–2929.
- Solomon S. G., & Lennie P. (2005). Chromatic gain controls in visual cortical neurons. *J Neurosci* *25*, 4779–4792.
- Switkes, E., & Crognale, M. A. (1999). Comparison of color and luminance contrast: Apples versus oranges? *Vision Research*, *39*, 1823–1831.
- Tailby C., Solomon S. G., & Lennie P. (2008). Functional asymmetries in visual pathways carrying S-cone signals in macaque. *J Neurosci*, *9*, 4078–4087.
- Vassilev, A., Murzac, A., Zlatkova, M. B., & Anderson, R. (2009). On the search for an appropriate metric for reaction time to suprathreshold increments and decrements. *Vision Research*, *49*, 524–529.
- Walkey, H. C., Harlow, J. A., & Barbur, J. L. (2006). Changes in reaction times and search time with luminance in the mesopic range. *Ophthalmic and Physiological Optics*, *26*, 288–299.
- Webster, M. A., & Mollon, J. D. (1994). The influence of contrast adaptation on color appearance. *Vision Research*, *34*, 1993–2020.
- Whittle, P. (1986). Increments and decrements: Luminance discrimination. *Vision Research*, *26*, 1677–1692.
- Zeile, A., Cao, D., & Pokorny, J. (2007). Threshold units: A correct metric for reaction time? *Vision Research*, *47*, 608–611.
- Zlatkova M. B., Vassilev A. & Anderson R. S. (2008). Resolution acuity for equiluminant gratings of S-cone positive or negative contrast in human vision. *Journal of Vision*, *9*, 1–10.