PERGAMON

Neuropsychologia 38 (2000) 1555–1564

NEUROPSYCHOLOGIA

www.elsevier.com/locate/neuropsychologia

Neurophysiological interpretation of human visual reaction times: effect of contrast, spatial frequency and luminance

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Received 19 January 2000; received in revised form 8 June 2000; accepted 17 July 2000

Abstract

Neurophysiological studies have demonstrated that in primates Magno and Parvo neurons have distinct contrast gain properties. Reaction Times (RTs) can be used to study supra-threshold contrast coding in humans over the same range of stimulus parameters. RTs to achromatic sinusoidal gratings were measured for a range of spatial frequencies (0.49–17.7 c/degree), stimulus luminances (0.005–20 cd/m^2) and contrasts (from threshold to 0.5). The stimuli subtended an angle of 7.2° at a viewing distance of 114 cm. RTs exhibit a linear relationship when plotted against the reciprocal of suprathreshold contrast. The slope of these functions reveals how contrast is linked to RT and can, therefore, be referred to as the RT-contrast factor with units of msec × contrast. A general equation is derived which accounts for all stimulus combinations. RT-based contrast functions resemble closely those obtained neurophysiologically for Magno (M) and Parvo (P) cells. Furthermore, the RT equivalent of contrast gain exhibits qualitatively similar gain characteristics to these neurons for a wide range of luminances and spatial frequencies. Our data support the notion that the sensory component of RTs is limited by the properties of pre-cortical neurons.

Keywords: Magno; Parvo; Visual latency; Supra-threshold; Visual physiological; Psychophysics

1. Introduction

The link between the physiological characteristics of visual neurons and reactions times (RTs) can be explored by studying the relationship between RT, spatial frequency, contrast and luminance. Although there are many reports on the effects on RT of spatial frequency and contrast [3,7,10,23,25,29,41,43], few studies have included luminance as an experimental variable and fewer still have interpreted their data in terms of the physiological characteristics of the neurons mediating the response.

All the above studies share two observations, both of which remain undisputed. First, as physical contrast is decreased then RT increases, and second, that RT is longer for high spatial frequencies (> 10 c/degree) than it is for low spatial frequencies (< 2 c/degree). These findings raise the question as to whether the same mechanisms regulate RTs and contrast sensitivity. If so, RTs would be expected to increase with spatial frequency because of the fall-off in threshold sensitivity at high spatial frequencies. That RTs increase with spatial frequency has been reported by many studies [3,20,25,29,43] and holds regardless of whether contrast is set at equal supra-threshold levels for each spatial frequency or if a compensation factor is introduced to account for reduced sensitivity at the higher spatial frequencies. At first sight this is a curious findings. It is well known, that at high contrast levels, perceived contrast does not have a band-pass function. Rather, high and low spatial frequencies are equally visible, so that the high-contrast spatial tuning function is virtually flat, as described by many reports using a matching paradigm [2,8,15,45]. These observations imply that RTs are more closely related to contrast sensitivity than to perceived supra-threshold contrast.

A point frequently overlooked in this regard is that the usually brief (transient-like) presentation paradigm of RT measurements must influence the extent to which RT spatial tuning reflects conventional contrast sensi-

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0028-3932/00/$ - see front matter
PII: S0028-3932(00)00100-7

tivity. Observers are required to respond rapidly to a temporal transient, which usually has a short presentation time. Given that the detection of higher spatial frequencies is mediated by relatively sluggish mechanisms, this will disproportionately reduce their detectability and thereby increase the corresponding RTs. On the other hand, matching experiments are not time-limited, so they would be expected to encourage the operation of sustained mechanisms.

Whatever the explanation of the relatively long visual latency for high spatial frequencies, testing a wide range of contrasts for a given spatial frequency is essential to the understanding of RTs. The relationship between RT and contrast is unclear however. Harwerth and Levi (1978) [10] and later Felipe et al. (1993) [7] showed that the decrease in reaction time as contrast increases is characterised by a discontinuity at a contrast level around 0.1, which they considered to be the result of sustained and transient channels operating at different contrast ranges. Parry et al. (1988) [31] have produced convincing evidence that there is a discontinuity in RT-contrast functions and that the different branches reflect transient- and sustained-like activity. Thomas et al. (1999) [41], on the other hand, claimed that the decrease in RT as contrast increases is smooth and without 'breaks'. They suggested that performance of the RT-task is mediated by a single, low-pass channel.

It seems highly likely that RTs are influenced by the anatomical and physiological characterisitics of the retino-cortical pathway. It is now well known that two main classes of retinal ganglion cells project to the lateral geniculate nucleus (LGN) in higher primates. These cell types are named after the laminae of the LGN to which they project; M cells project to the Magnocellular laminae and P cells to the Parvocellular laminae [35,46]. These pathways remain segregated as far as the input layers of striate cortex, where there said to be a considerable overlap between them [18,19,28]. Though there are many differences between the two processing streams, the characteristics which are relevant to the present study are their response to contrast and their different temporal properties. In general, M cells have much higher contrast sensitivity than P cells and they exhibit a slightly faster time course of responses to visual stimuli [5,11,12,22,33,39]. A corollary of their high contrast sensitivity is that M cells in the LGN have a much higher contrast gain than P cells [5,12]. Similar data are available at the retinal ganglion cell level [13,14,17]. It is evident from all physiological studies that the conspicuous difference in contrast gain provides the main distinguishing feature between M and P cells.

In this study we have tested RTs to a series of sinusoidal gratings, using a wide range of suprathreshold contrasts, spatial frequencies and luminances. We report two novel findings; first, it is possible to explain all the RT data with a simple equation linking contrast, spatial frequency and luminance. Second, we show that the RT equivalent of contrast gain corresponds closely to contrast gain values obtained neurophysiologically, in terms of both spatial frequency and luminance.

2. Methods

2.1. Stimuli

The stimuli were vertical sinusoidal gratings displayed on a Barco CCID7651 'Calibrator' colour monitor. They were composed of separate red and green patterns that were combined in phase to produce achromatic (yellow/dark-yellow) gratings. The red, green and sync inputs to the monitor were supplied by a 12-bit, two-channel grating generator card (Millipede Prisma VR1000 series 2) in a Personal Computer (PC). The refresh rate was 100 Hz. The subject viewed initially a plain yellow[1] field, which was periodically replaced by the gratings with no change in mean hue or luminance. The mean luminance of the screen [$(L = L_{max} + L_{min})/2$] was 20 cd/m^2, and this was attenuated with neutral density filters to give the lower luminances. The test field was the central area of the monitor, the peripheral area of which was occluded by black card. The circular target was presented foveally and subtended an angle of 7.13° at a viewing distance of 114 cm. For higher spatial frequencies (14.0 and 17.7 c/degree) the viewing distance was altered to 142 and 180 cm, respectively. The minimum number of cycles presented on the screen was 3.5 for the lowest spatial frequency used (0.49 c/degree). The surround was dark. The stimulus was viewed through natural pupils. Pupil size was measured for different ranges of luminances for each subject and retinal illuminations were calculated accordingly. Subjects fixated on a cross located in the centre of the illuminated area of the screen. All room lights were extinguished during the experiment.

RT data were collected for a range of contrasts from supra-threshold to threshold detection (0.5–0.006). Contrast was defined as Michelson contrast:

$$C = \frac{(L_{max} - L_{min})}{(L_{max} + L_{min})}$$

where L_{max}, maximum luminance and L_{min}, minimum luminance. Eight spatial frequencies (0.49–17.7 c/degree) and five mean screen luminance levels (20, 2, 2, 0.2 and 0.05 cd/m^2) were tested.

[1] Co-ordinates on the 1991 chromaticity diagram: $x = 0.508$; $y = 0.437$ (585 nm wavelength); calibrated with Spectrascan Photo Research 650 colorimeter, Micron Ltd, London.

3. Procedure

RTs were determined using a CED 1401 smart interface, and specifically-designed software which runs on a PC. They were measured by displaying the vertical grating for 340 ms with an abrupt onset and offset. Subjects responded by pressing a button which triggered the interface (CED 1401).

Before the RT measurement procedure began, the subjects adapted for between 5 and 15 min, depending on the luminance level. Whenever viewing the display screen, subjects were instructed to fixate a cross at the centre of the stimulus. A trial (a block of 32 presentations of the corresponding grating) consisted of the following sequence of events. A single warning tone was sounded. This was followed by a random foreperiod varying from 1000–3000 ms prior to a 340 ms presentation of the target stimulus. At the onset of the grating, a trigger probe was set and this triggered the CED 1401 to start its integral clock counter. The subject pressed the response button as soon as the stimulus appeared; the response button prompted a second event trigger which terminated the clock counter. The interval between the two probes could then be read by the PC. If no response was detected within 2000 ms after the timer was started, the computer itself responded with a time-out. Thus, 2000 ms RTs were interpreted as 'no response'. Generally, only responses between 150 and 1000 ms were accepted; RTs over 600 ms were rarely encountered.

3.1. Subjects

Two subjects (SP and LG) were used. SP was a 27-year-old male and LG a 21-year-old female. Subjects were familiarised with the range of spatial frequencies to be used in the experiment and were given a block of practice trials prior to RT recording in which different sets of spatial frequencies were presented. The subjects were optically corrected for viewing distance with spectacles (corrected VA = 6/5) and viewed the stimuli through natural pupils and binocularly.

4. Results

Fig. 1 shows mean RTs versus contrast plots (on a logarithmic axis) for the two subjects for the range of spatial frequencies used and for a wide range of contrasts. In all cases RTs have been measured at contrasts close to detection threshold. The data replicate previous findings; RT decreases with increasing contrast, levelling off at a specific contrast value for each spatial frequency, which represents the asymptote (RT_0) of the function fitted. Asymptotic reaction time (RT_0) as a function of contrast varies slightly with spatial frequency, with lower spatial frequencies having low contrast asymptotes. Moreover, for a given contrast, RT is longer for high than low spatial frequencies. The shapes of the RT-versus-contrast curves for all spatial frequencies are similar; indeed they can be described satisfactorily by the following monotonic function:

$$RT = RT_0 + k\frac{1}{C} \quad (1)$$

where, RT, reaction time, RT_0, the asymptote (absolute) RT, k, steepness of the curve and C, contrast.

It is evident that low and high spatial frequency RTs are easily distinguished by their response to low contrast stimuli. High spatial frequency gratings cannot be detected at contrast levels lower than about 0.03 whilst low spatial frequency gratings can be detected at contrast levels as low as 0.006.

Fig. 2 replots the same data as a function of 1/C. The linear relationship evident from Eq. (1) is confirmed for all spatial frequencies and for both subjects. Table 1 shows the estimated slope value, k, and the coefficient of determination, r^2, for each combination of spatial

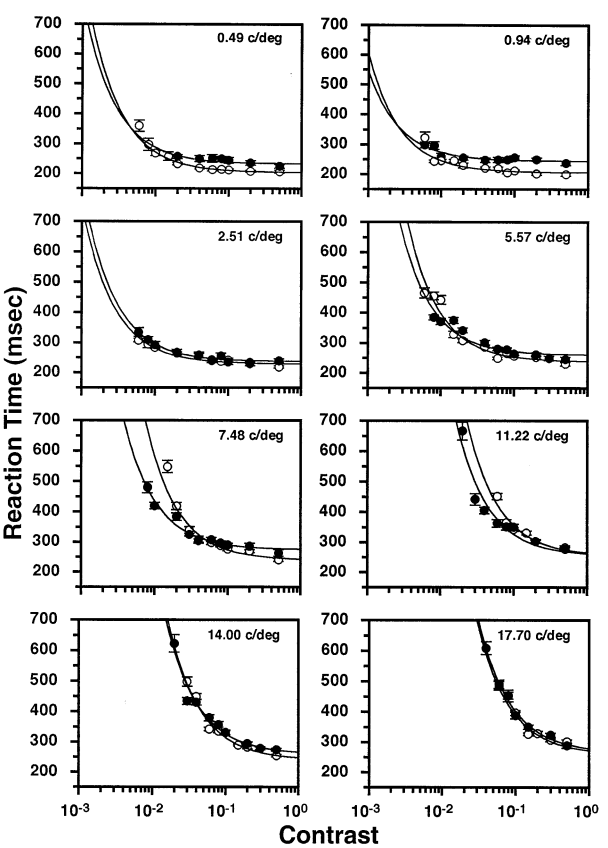

Fig. 1. Plots of reaction time vs. contrast for subject SP (open circles) and LG (filled circles). The legend indicates the spatial frequency of the grating used. Each data point represents the mean of at least 24 measurements (Maximum = 32) and the error bars ± 1 S.E. The solid curves drawn through the data are best fits of Eq. (1). Mean screen luminance was 20 cd/m^2

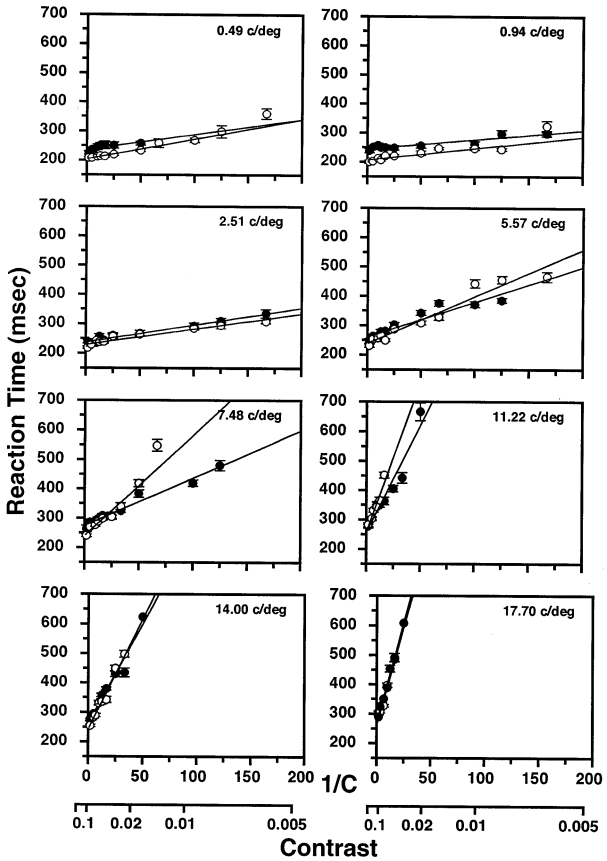

Fig. 2. Plots of reaction time vs. the reciprocal of contrast (1/C) for subjects SP (open circles) and LG (filled circles). The legend indicates the spatial frequency of the grating used. Each data point represents the mean of at least 24 measurements (maximum = 32) and the error bars ± 1 S.E. The solid lines represents the least square regression fits. Mean screen luminance was 20 cd/m^2.

frequency and luminance. The values of r^2 are high for all conditions and apart from 7.48 c/degree, there is no difference between the subjects. As seen in Fig. 2, there is a dramatic difference in the value of the slope, k, for the different spatial frequencies. Plotting RT as a function of 1/C reveals the effective contrast range of the different stimuli. At low spatial frequencies (0.49, 0.94 and 2.51 c/degree), where a unit change in contrast has only a small effect on RT, the value of k is low. Intermediate spatial frequencies (5.57 and 7.48 c/degree) have moderate values of k, whereas the group of higher spatial frequencies (11.22, 14.0 and 17.7 c/degree) is characterised by having higher values of k, because of the larger effect of contrast on RT.

In Fig. 3, RTs from a low (0.94 c/degree) and a high (11.22 c/degree) spatial frequency stimulus are plotted for the two subjects for the range of luminances used in the study. For low spatial frequencies, small increments, (or decrements) in contrast influence RT very little under photopic conditions. However, at lower luminances, visibility is reduced and small changes in contrast produce a strong effect on RT. Stimuli of lower visibility (high spatial frequencies), i.e. which have low contrast sensitivity and, therefore, a narrow dynamic range, correspond to relatively steep curves. When luminance is reduced, slopes become much steeper. It is also obvious that at low luminance levels (at and below 0.02 cd/m^2) the mechanism responsible for the detection of high spatial frequency gratings is not activated.

According to Figs. 2 and 3, the slope of the functions, k, is dependent on the effective contrast range of the stimulus and is, therefore, related to spatial frequency and luminance. Eq. (1) predicts that the value of k will reflect the behaviour of RTs for all spatial frequencies and luminances as a function of contrast. As k reveals how contrast is linked specifically to RT we have referred to it as the RT-contrast factor with units of ms × contrast. In Fig. 4, k is plotted, for both subjects, as a function of luminance for the range of spatial frequencies tested.

The functions are of the form:

$$\text{Log } k = a - e \log L \Leftrightarrow k = 10^{[a - e \log L]} \quad (2)$$

where a and e are constants derived from the best fit functions for each spatial frequency and L is luminance. Obviously, there are fewer data points for the lower luminances and these are confined to the lower spatial frequencies. For each spatial frequency, the value of k increases with decreasing luminance. It appears that, while the functions are virtually parallel to each other (the slope e varies only slightly), the y-intercept, a, varies linearly with spatial frequency. Therefore, we can approximate for Eq. (2):

$$e = \text{constant with luminance}$$

$$a = a_0 + bf \quad (3)$$

where a_0, new constant, b, slope, constant with spatial frequency and f, spatial frequency

Combining Eqs. (2) and (3) we can then write

$$k = 10^{(a_0 + bf - e \log L)} \quad (4)$$

We also need to consider the variation of RT_0 with spatial frequency, f, and luminance, L. In fact the RT_0 values vary only slightly with either spatial frequency or luminance. Similarly, we could write:

$$[RT_0] = [RT_0]_0 + df - g \log L \quad (5)$$

where d, g and $[RT_0]_0$ can be derived at each luminance and spatial frequency by appropriate fitting.

Therefore, to establish the overall link between RT, spatial frequency and contrast we can evaluate the relationship between k, f and L by combining Eqs. (1), (4) and (5) and we get:

$$RT = ([RT_0]_0 + df - g \log L) + \frac{1}{C} 10^{(a_0 + bf - e \log L)} \quad (6a)$$

Eq. (6a) was fitted to both subjects' data and co-efficients for the model derived as set out below. Note that the individual co-efficients in Eq. (6b) are the means from the two subjects. It is evident that RT can be predicted for all stimulus characteristics (contrast, luminance, spatial frequency) and a constant, $[RT_0]_0$, which is specific to the subject.

Table 1
Values of the RT-contrast factor, k (and coefficients of determination, r^2) for the range of spatial frequencies and luminances tested for each subject.

Luminance (cd/m^2)	Spatial frequency (c/degree)								
	0.49	0.94	1.71	2.51	5.57	7.48	11.22	14.00	17.70
Subject SP									
20	0.683	0.396	0.607	0.523	1.607	3.421	10.199	7.482	13.144
	(0.964)	0.839)	(0.961)	(0.937)	(0.943)	(0.945)	(0.929)	(0.978)	(0.964)
2	0.858	0.810	0.969	1.322	2.419	4.819	17.364	21.891	28.925
	(0.848)	(0.908)	(0.943)	(0.939)	0.951)	(0.984)	(0.901)	(0.998)	(0.996)
0.2	2.291	2.132	2.262	a	7.359	10.928	43.409	40.858	a
	(0.929)	(0.951)	(0.978)		(0.955)	(0.882)	(0.976)	(0.951)	
0.02	8.001	7.609	9.354	26.953	63.650	49.500	a	a	a
	(0.986)	0.964)	(0.974)	(0.974)	(0.972)	(1.000)			
0.005	16.357	20.709	25.177	a	a	a	a	a	a
	(0.960)	(0.994)	(0.962)						
Subject LG									
20	0.549	0.298	a	0.610	1.218	1.564	6.173	6.312	13.089
	(0.809)	(0.846)		(0.970)	(0.891)	(0.966)	(0.931)	(0.964)	(0.990)
2	a	0.708	a	1.011	2.834	2.960	14.023	15.466	28.263
		(0.990)		(0.951)	(0.927)	(0.935)	(0.970)	(0.891)	0.964)
0.2	a	2.428	a	2.410	8.360	11.510	35.810	53.824	a
		(0.986)		(0.941)	(0.960)	(0.980)	(0.960)	(0.986)	
0.02	a	9.878	a	11.671	22.843	36.957	a	a	a
		(0.918)		(0.951)	(0.937)	(0.984)			
0.005	19.403	18.526	a	29.495	62.670	a	a	a	a
	(0.990)	(0.966)		(0.964)	(1.000)				

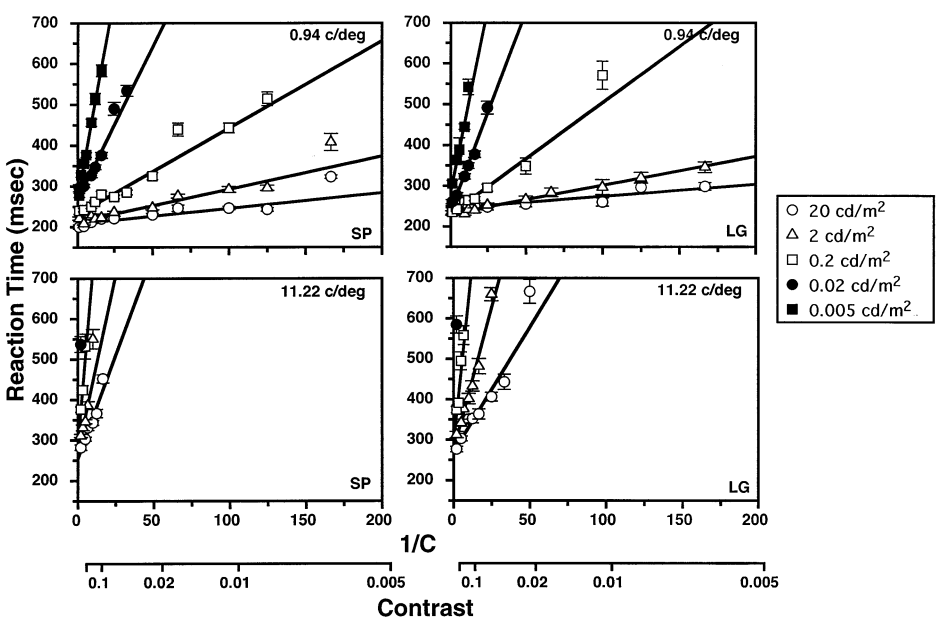

Fig. 3. Plots of reaction time vs. the reciprocal of contrast (1/C) for a low (upper) and a high (lower) spatial frequency grating, for a range of luminance levels and for both subjects. The legend indicates the spatial frequency of the grating used. Each data point represents the mean of 32 measurements and the error bars ± 1 S.E. The solid lines represent the least squares regression fits.

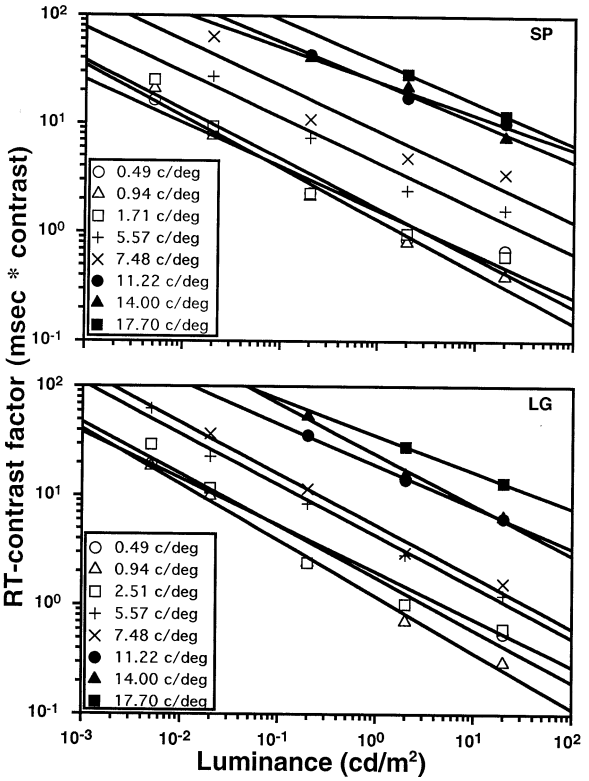

Fig. 4. RT-contrast factor, k, variation with spatial frequency for a range of luminances (in cd/m^2) and for both subjects. Effectively k is the slope of the RT vs. 1/C function (see Fig. 2). The regression coefficients of determination, r^2, are high for both subjects.

$$\mathrm{RT} \approx ([\mathrm{RT}_0]_0 + 5f - 20 \log L) + \frac{1}{C}\, 10^{(0.12 + 0.09f - 0.42 \log L)} \tag{6b}$$

In Fig. 5a (subject SP) and b (subject LG), we show how our data fit the model. Each data point shows the predicted RT derived from the model (Eq. (6b)) against the mean (n, maximum 32, see Section 2) observed RT for a particular contrast, luminance and spatial frequency. The dotted line is the idealised function when the model would exactly predict the data. Only data of $\geq 75\%$ frequency of seeing are included (see solid grey lines). The slope values are 0.942 for subject SP and 0.917 for subject LG (coefficients of determination, r^2, are 0.857 and 0.857 and 0.857, respectively). Inevitably, as RT increases there is a slight discrepancy between the predicated and measured values. For this reason we have also plotted RT equal to or less than 500 msec in order to determine whether the RTs measured are systematically longer than those predicted (see solid grey lines). In this case the slopes increases to 0.967 for subject SP and 1.003 for subject LG (r^2 are 0.834 and 0.850, respectively), which represents an improved fit between predicted and observed data.

5. Discussion

The RT data presented, agree with previous findings [3,7,10,20,25,29,41–43]. It is clear that RTs increase for higher spatial frequencies, lower constrast and lower luminances. According to Pieron's Law ($\mathrm{RT} = \mathrm{RT}_0 + kI^{\beta}$, where I is intensity) RT decreases exponentially with increasing intensity reaching an asymptotic level RT_0. For example, Mansfield 1973 [21] found the exponent β to be -0.372. It would be very surprising if the same exponent applied to contrast and any other measure of stimulus strength. In our analysis, RTs are plotted against the reciprocal of contrast (i.e. exponent $= -1$), which gives a simple linear function for each combination of spatial frequency and luminance when slope k is varied. Other way of fitting the data were evaluated; for example, if k is constant and β is

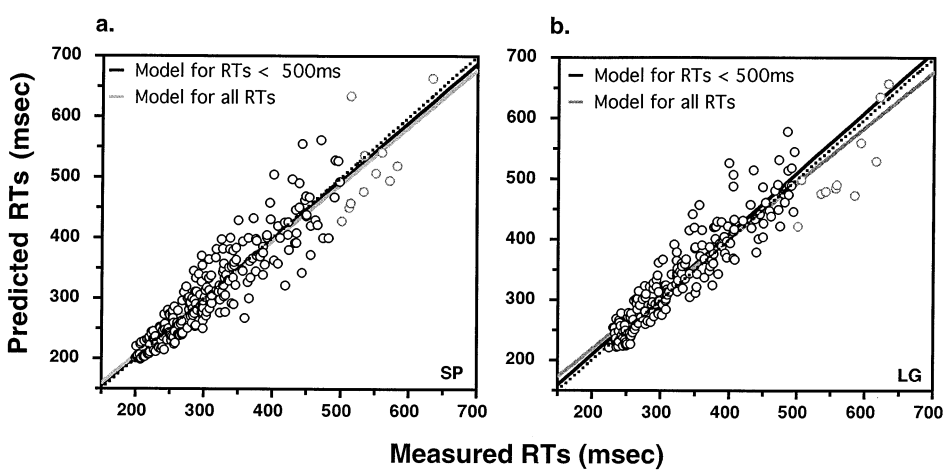

Fig. 5. Fits of predicted against measured RTs derived for subject SP (a) and subject LG (b). Data points in grey are RTs > 500 ms (see text). Each data point is the mean of at least 24 measurements. The solid grey lines are the least square regression fits to all the data points. The solid dark lines are the least squares regressions fits to the data with frequency of seeing higher than 75%. The dotted lines represent a 1:1 relationship. Between measured and predicted RTs.

varied, there is no simple relationship between β and stimulus parameters. The constant k of our model (see Eq. (1)) is crucial for interpreting RTs; this is described in the next section. From the resulting family of curves we can write a general equation which describes RT data in terms of the three variables; contrast, spatial frequency and luminance. This (Eq. (6a)) was tested by fitting the data for the two subjects. For RTs < 500 ms the equation predicts the RT measurements extremely well; when RTs > 500 ms are included, i.e. those for low visibility stimuli, there is a tendency of the equation to underestimate the measured RTs.

This raises the question of the authenticity of long RTs recorded close to threshold. Some hold the view that RTs are disproportionately long for low visibility targets because there is a difference between 'perceptual latency' and simple RTs [6,36]. Others [47] consider that central, intensity-dependent higher processes influence close-to-threshold RTs rather than retinal and pre-cortical characteristics. The association between RT and other perceptual processes remains obscure and may be related to the characteristics of the underlying detecting mechanisms (Tolhurst, 1975) [42]. The RT paradigm is inherently biased toward transient mechanisms because the stimuli usually appear and disappear abruptly (but see Parry, 2000 [30]) Certainly, probability summation alone would artificially increase RTs to close-to-threshold stimuli.

5.1. The RT-contrast factor, k

We have used the RT-contrast factor, k, to show how RT varies with contrast for different stimulus conditions. Effectively k is the slope of the RT versus $1/C$ function. Hence, the data in Figs. 2 and 3 reveal two crucial features about the relationship between RT and contrast. First, the effect of spatial frequency. At low spatial frequencies, where small increments/decrements in contrast influence RT very little, the value of k are low, whereas at high spatial frequencies, where small increments/decrements have a large effect on RT, the values of k are high. Second, the effect of luminance. The data show that as log luminance is decreased there is a systematic (almost linear) increase in the logarithm of k (Fig. 4), again revealing that it is closely linked to visibility — at low luminances, thresholds are high and the dynamic range is narrow.

5.2. Link between RTs and physiological data

When addressing the neurophysiological basis of the variation of RT with stimulus conditions it is instructive to look in detail at the physiological experiments which have used corresponding stimuli. By testing a wide range of contrasts [5,13,39] and luminances [33,34] the distinctive contrast signatures of the M and P cells have been revealed: M and P cells are most easily distinguished by their responses to low-contrast stimuli. M cells are particularly sensitive to low constrast and low luminance (but their responses saturate at relatively low constrast, around 0.1), whereas P cells respond poorly below 0.1 contrast (but saturate at much higher contrasts). It is clear from Figs. 1 and 2 that RTs to low and high spatial frequencies can be similarly distinguished by their contrast functions. At low spatial frequencies, RTs, presumably mediated by M pathways, are very short over the contrast range above 0.01, corresponding to the range, according to the single unit data, when M cells are responding most vigorously. At high spatial frequencies, RTs, presumably mediated by P pathways, are short only for the range of contrasts when P cells have a strong response; that is for values above 0.1. As contrast is reduced below 0.1, when the P cells' response is below noise levels, RTs rapidly increase.

A second approach to comparing RT and the corresponding neurophysiological subtrate is to examine the contrast gain functions for the two methods. As M cells are much more sensitive to luminance contrast than are P cells, they have a much higher contrast gain as first shown by Kaplan and Shapley (1982) and since by many others [5,13,14,17,34]. In fact Kaplan and Shapley (1986) [13] claimed that contrast sensitivity is proportional to constrast gain. Contrast gain is defined as the slope of the response amplitude-contrast function and is expressed as impulses per second per unit contrast. A similiar link exists between RTs and contrast sensitivity. RTs are reciprocally related to sensitivity; short RTs are obtained at low spatial frequencies whereas long RTs are obtained at high spatial frequencies. It follows that the RT-contrast factor should be inversely proportional to the contrast sensitivity and, therefore, is also expected to be inversely proportional to contrast gain. Fig. 6 tests this idea by comparing contrast gain values at different luminances, derived from electrophysiological responses of M and P macaque retinal ganglion cells, with the reciprocal of the RT-contrast factor for low (0.94 c/degree), medium (7.48 c/degree) and high (14.00 c/degree) spatial frequency gratings obtained in the present study. Again we have taken the simplistic view that low spatial frequency RTs (open circles) are mediated by M cells and high spatial frequency RTs (open squares) are mediated by P cells. Medium spatial frequencies show the transition from M-dominated to P-dominated stimuli and the change in the reciprocal of RT-contrast factor, effectively the RT equivalent of contrast gain, is consistent with this. M- and P-cells' contrast gains (filled circles and squares, respectively) are re-plotted from Purpura et al. (1988) [33].

The two sets of data are strikingly similar. The variation of the inverse of the RT-contrast factor values

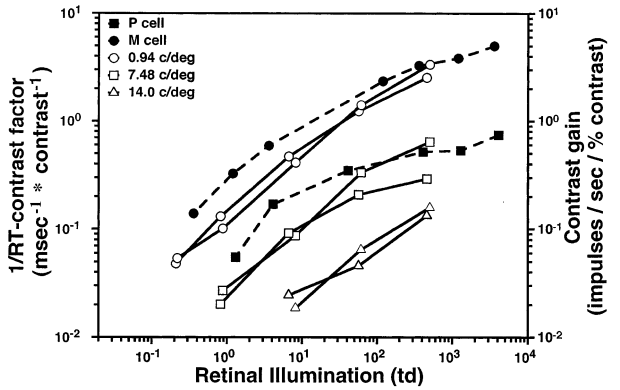

Fig. 6. Plots of the inverse of the RT-contrast factor as a function of luminance, for three spatial frequency gratings [low, (0.94 c/degree — open circles), medium (7.48 c/degree — open squares) and high (14.00 c/degree — open triangles)] and for both subjects, compared with average contrast gain values from Purpura et al.'s (1988) electrophysiological study on macaque M (filled circles; $N = 8$ and P (filled squares; $N = 15$) LGN ganglion cells. The cell responses were evoked by drifting sinusoidal gratings ranging in spatial frequency from 0.6 to 1.6 c/degree for M cells and from 1.6 to 6 c/degree for P cells.

of high and medium spatial frequencies with luminance corresponds closely to that of P-cell gain. Furthermore, the differences between the gains of M- and P-cells are very similar to the differences between high and low spatial frequency values of the RT equivalent of contrast gain (the reciprocal of RT-contrast factor in Fig. 6), throughout the range of luminances. Note also that both P-cells and the mechanism that governs high spatial frequencies (14 c/degree), do not operate when retinal illumination declines to scotopic levels (below 1 td). Although RT data and physiologically based contrast gain are derived from different experimental conditions, the qualitative comparison made in Fig. 6 hints at the neurophysiological basis of simple RTs.

5.3. RTs and achromatic contrast sensitivity

Our data show that the RT-based contrast gain exhibits similar characteristics to those of M-and P-pathways. As contrast gain has been shown to be proportional to contrast sensitivity [13] it follows that the contrast sensitivities of the input neurons of the visual cortex account for the human achromatic contrast sensitivity function. Fig. 6 implies that detection of medium (7.48 c/degree) and high (14.0 c/degree) spatial frequencies is mediated by P-cells. Moreover, all the evidence is that low spatial frequencies at threshold are detected exclusively by M-cells. Similar conclusions have been drawn by physiological studies; Derrington and Lennie (1984) [5] showed that contrast sensitivity for P-cells is lower than that of M-cells for spatial frequencies lower than 6 c/degree. Purpura et al. (1990) [34] demonstrated changes in gain with retinal illumination at low and high spatial frequencies which are similar to the changes seen in human temporal-frequency sensitivity. Lee et al. (1990) [17] provided evidence that M-cells form the most sensitive cell class for luminance modulation, and their behaviour resembles that of the Contrast Sensitivity Function (CSF) as retinal illuminance is decreased. Against this, Merigan and Eskin (1986) [24] claimed that selective damage of the P-pathway reduced contrast sensitivity for the whole range of spatial frequencies. This controversial observation, which implies that the P-pathway accounts for the CSF, has attracted much criticism [14] [16] [40]. There is also clinical evidence that M-cells mediate low spatial frequencies; Wolf and Arden (1996) [48] tested patients with a melanoma-associated retinopathy which selectively damages M-cells and showed that the low spatial frequency achromatic system was grossly impaired.

5.4. How many mechanisms determine RT?

Harwerth and Levi (1978) [10] and more recently Felipe et al. (1993) [7] have claimed that a transition in the RT-contrast plots reveals two slopes when medium spatial frequencies are tested. The high contrast region was said to show the activity of transient mechanisms, whilst the low contrast region reveals the activity of sustained mechanisms. As described above, there is now overwhelming evidence that M-cells (possibly with transient properties) have high sensitivity and P-cells have relatively low sensitivity to luminance contrast. It seems that Harwerth and Levi (1978) [10] and Felipe et al. (1993) [7] misinterpreted their data. It is not feasible that transient mechanisms account for the fast RTs at high contrasts and sustained mechanisms for the slow RTs at low contrasts. On the contrary, low contrast gratings (< 0.1) must be detected exclusively by M-cells. Obtaining fast RTs simply shows that the mechanism mediating the response has high sensitivity to the testing conditions. It is this fact that accounts for the puzzling observation of the stubborn increase in RTs with spatial frequency. High spatial frequencies are detected by low sensitivity, low gain mechanisms and will, therefore, always produce longer RTs, even at maximum contrast. It may seem paradoxical that, at low luminances, low spatial frequencies produce long RTs, but be mediated by transient (M-cell-based) mechanisms. This has also been demonstrated physiologically; Saito and Fukuda (1986) [38] showed that Y-cell responses with transient characteristics become sluggish or sustained at scotopic levels of luminance and also exhibit linear spatial summation.

In this paper we have not addressed the issue of whether there is a change in the RT-contrast slope

between high and low contrast levels, although as indicated above, there is experimental evidence that some form of transition does occur [7,10,31] and this has been demonstrated in Visual Evoked Potential (VEP) studies (see below). However, as illustrated in Fig. 2, which shows plots of the RT versus 1/C functions, the slope gradually increases with spatial frequency, indicating a gradual transition from M-dominated to P-dominated activity. It is, therefore, likely that the contribution of the P-pathway will vary with increasing contrast. Thomas et al. (1994) [41] argued that only a single mechanism (i.e. the M-system, which shows larger axons and faster conductance rates) may be responsible for the determination of the RTs, as they showed that a single, low-pass channel model fitted their data. Their model cannot be compared with ours; they used only five relatively high contrasts (one contrast level below 10%), the highest spatial frequency tested was 6.51 c/degree and they used parafoveal presentation.

It could be argued that in Fig. 2, the higher end of the scale is compressed because we used the reciprocal of contrast on the x-axis. A more detailed examination of the data, reveals that RTs produced by low and intermediate spatial frequencies tend to follow a steeper slope at high contrast levels ($>10\%$). However, we only used three contrast levels above this and it would be difficult to fit these points and derive a second function. This issue is being addressed in a separate study.

5.5. P- and M-Function in humans

The benefit of recording RTs, is that they reveal supra-threshold responses and, therefore, the operation of both M- and P-function, rather than only M-function which are usually dominant in threshold-based studies. Some psychophysical experiments reveal suprathreshold M and P activity; for example, Burbeck and Kelly (1981) [4] obtained different contrast gain measurements for low and high spatial frequencies and Pokorny and Smith (1997) [32] used discrimination thresholds to show the difference in the spatio-temporal control of adaptation between M- and P-pathways.

Human VEPs have also been used to study the P- and M-function, by testing luminance and chromatic contrast [1,9,25–27,31,37,44]. Most studies which test contrast, show a biphasic relationship between luminance contrast and VEP latency/amplitude. In common with the RT data, contrast affects VEP latency disproportionately at high spatial frequencies, reflecting M- and P-pathways. However, VEP-contrast functions are not as steep as RT-contrast functions, perhaps because they involve later stages of visual processing.

6. Concluding remarks

We have presented two new observations on the properties of simple visual RTs. First, a model is described which accounts for RTs obtained from a wide range of contrasts, spatial frequencies and luminances and a general equation linking these parameters to RTs is derived and tested. Second, using photopic and scotopic luminances and obtaining an RT equivalent of contrast gain has enabled us to compare our RT data with the neurophysiological characteristics of pre-cortical pathways in macaque monkey. The two sets of data are comparable, suggesting that the stimulus dependent, sensory component of RTs is limited by the properties of these pre-cortical neurons.

Acknowledgements

This research is part of a LINK TIO EPSRC-sponsored programme (GR/K56957). We gratefully acknowledge the support of the Department of Transport and Urbis Lighting Ltd. We thank Professor Neil Charman and Professor Janus Kulikowski for their comments on an earlier version of the manuscript. Neil Parry wrote the RT software.

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