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Dependency of reaction times to motion onset on luminance and chromatic contrast

David C. Burr [a,b,*], Beatrice Corsale [a]

[a] *Istituto di Neurofisiologia del CNR, Via S. Zeno 51, 56127 Pisa, Italy*
[b] *Dipartimento di Psicologia, Università di Firenze, Firenze, Italy*

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Abstract

We measured reaction times for detecting the onset of motion of sinusoidal gratings of 1 c/deg, modulated in either luminance or chromatic contrast, caused to move abruptly at speeds ranging from 0.25 to 10 deg/s (0.25–10 Hz). At any given luminance or chromatic contrast, RTs varied linearly with temporal periodicity ($r^2 \cong 0.97$), yielding a Weber fraction of period. The value of the Weber fraction varied inversely with contrast, differently for luminance and chromatic contrast. The results were well simulated with a simple model that accumulated change in contrast over time until a critical threshold had been reached. Two crucial aspects of the model are a second-stage temporal integration mechanism, capable of accumulating information for periods of up to 2 s, and contrast gain control, different for luminance than for chromatic stimuli. The contrast response for luminance shows very low semi-saturating contrasts and high gain, similar to LGN M-cells and cells in MT; that for colour shows high semi-saturating contrasts and low gain, similar to LGN P-cells. The results suggest that motion onset for luminance and chromatic gratings are detected by different mechanisms, probably by the magno- and parvo-cellular systems. © 2001 Published by Elsevier Science Ltd.

Keywords: Visual motion; Reaction times; M- and P- cells; Colour; Gain control

1. Introduction

Equiluminant stimuli have often been used as a tool to differentiate parvocellular from magnocellular activity. However, although it is almost certain that chromatic aspects of stimuli must be processed through the parvo-cellular pathway, luminance modulation stimulates both pathways, so either (or both) could be used, depending on the particular task (e.g. Lennie, Pokorny, & Smith, 1993). For example, vernier acuity varies with luminance contrast in a similar way to chromatic contrast (save for a scaling constant equating the stimuli for detectability), suggesting that both are encoded by the same pathway, probably parvocellular (Krauskopf & Farell, 1991). The same holds true for orientation discrimination (Würger & Morgan, 1999) and phase discrimination (Martini, Girard, Morrone, & Burr, 1996).

For other tasks, however, such as motion discrimination, luminance and colour seem to be processed through different mechanisms, probably reflecting magno and parvocellular activity. Temporal contrast sensitivity (Kelly, 1983; Metha & Mullen, 1996) and impulse response functions (Burr & Morrone, 1993; Swanson, Uneno, Smith, & Pokorny, 1987) have quite different shape for luminance and colour, which no simple scaling operation can align. Minimal thresholds for motion detection vary considerably with chromatic contrast, but not with luminance contrast (Krauskopf & Li, 1996). The apparent speed of gratings defined by luminance and colour shows a quite different dependency on contrast, at least at slow speeds (Gegenfurtner & Hawken, 1996b; Hawken, Gegenfurtner, & Tang, 1994). There are also clear qualitative differences, such as motion at equiluminance seeming to be less smooth than that defined by luminance (Cavanagh, Tyler, & Favreau, 1984; Mullen & Boulton, 1992).

Electrophysiological evidence suggests that for slow drift speeds, only luminance modulation produces ac-

* Corresponding author. Tel.: +39-050-315-3175; fax: +39-050-315-3220.
E-mail address: dave@in.pi.cnr.it (D.C. Burr).

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tivity in the motion selective cells of MT (e.g. Gegenfurtner, Kiper, Beusmans, Cardandini, & Zaidi, 1994; Gegenfurtner & Hawken, 1996a; Thiele, Dobkins, & Albright, 1999), although at high speeds both forms of modulation provide an input.

Reaction time studies have also revealed differences in processing of luminance and chromatic stimuli, revealing differences in latencies (e.g. Bowen, 1981; Nissen & Pokorny, 1977), and different contrast dependencies for motion onset (Burr, Fiorentini, & Morrone, 1998). This current study aims to investigate further the mechanisms that detect motion onset of luminance and chromatic motion at supra-threshold levels, again taking advantage of the reaction time technique. The results point to gross differences in processing that cannot be equated by any simply scaling factor. They probably reflect the different gain control mechanisms for luminance and chromatic motion signals, corresponding well to the know contrast gain properties of parvo and magnocellular geniculate cells, and cells in MT (Sclar, Maunsell, & Lennie, 1990). These results have been published in abstract form (Corsale & Burr, 1999).

2. Methods

2.1. Stimuli

The stimuli for this study were horizontal sinusoidal gratings of 1 c/deg, modulated either in luminance or in chromaticity (red–green equiluminant), generated by framestore (Cambridge VSG) and displayed on the face of a Barco monitor at 120 frames/s. The display area was 35×25 cm, subtending 20×14 deg at the viewing distance of 1 m. Only the red and green guns of the monitor were activated, so the background colour was yellowish when viewed through Kodak 16 wratten filters (heavily attenuating wavelengths shorter than 500 nm). Chromatic gratings were constructed by combining red and green gratings of equal but opposite contrast. The mean luminance of the red gun was fixed at 50% maximum value, while the green mean-luminance could be adjusted to vary the ratio of red-to-total luminance to establish equiluminance for each observer, varying slightly the total mean luminance. At equiluminance the mean luminance was very near 20 cd/m^2.

The contrast of the chromatic gratings was expressed in RMS cone-contrast units. This was calculated by transforming the CIE co-ordinates of the stimuli into cone excitations using the primaries of Smith and Pokorny (1975). In practice it was equivalent to dividing the Michaelson contrast by 3.6.

Stimulus speed varied 0.25–10 deg/s, corresponding to a variation in temporal period τ of 100–4000 ms. Values of τ were chosen so as to span the range uniformly on a linear scale.

2.2. Reaction times

Observers were required to respond as quickly as possible to motion onset. Sinusoidal gratings were stationary on the screen, until observers initiated a trial by release of a response button. After a brief delay that varied randomly from 1 to 2 s, the grating moved abruptly upwards or downwards (at random). The observer responded to the motion as quickly as possible by button-press, and released the button to initiate the next trial when ready. The observer simply responded to the motion, irrespective of its direction (simple reaction times). Under some conditions (not shown in this study), subjects were required to report the direction of motion, and this produced essentially identical results.

In any given session, several grating speeds were randomly intermingled. Five trials were run for each condition in each session, with four separate sessions per condition, giving a total of 60 trials per condition. The mean reaction time, together with its standard error, was calculated after elimination of outliers (further than 2.5 standard deviations from the mean). Trials shorter than 100 ms or longer than 2 s were also eliminated. The reaction time distributions were inspected by eye for each condition, and were always seen to follow a reasonable approximation to Gaussian, with median similar to the mean. Indeed using the median rather than mean as the measure of central tendency did not affect the pattern of results.

Six observers were used throughout the study, three experienced observers (DCB, BC and AF), and three others naïve of the goals of the experiment.

3. Results

For each observer the equiluminance point was first established for these conditions, by measuring motion onset RTs for different red-green ratios, and choosing the ratio for which RTs were longest (see Figure 1 of Burr et al., 1998). In practice the equiluminant point varied little from subject to subject, and was always around 0.5, the point of physical equiluminance. Having established the equiluminance point, we measured RTs as a function of speed, both for the equiluminant condition and for luminance contrast of the same space-averaged chromaticity.

Figs. 1 and 2 show motion onset RTs as a function of temporal period for the six observers. It is clear that for all conditions, the data tend to follow a linear relationship, with RTs proportional to temporal period (plus a constant). The average value of the linear regression r^2 was 0.97, showing it to be an adequate approximation of the data, without the need to examine higher non-linear terms. The slopes of the linear fits to the data of Figs. 1 and 2 provide estimates of the

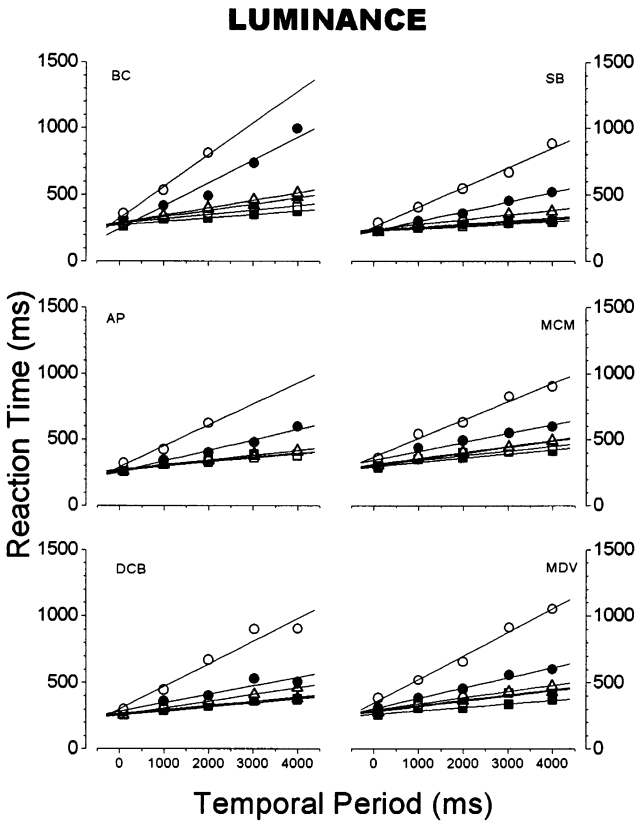

Fig. 1. Dependency of reaction times on temporal period, for gratings modulated in luminance at various contrasts: 0.007 (○), 0.015 (●), 0.03 (△), 0.06 (▲), 0.11 (□) and 0.22 (■). The curves have all been fitted by linear regression. The slope of the linear regression is the best estimate of the critical period, or Weber fraction, for each condition.

proportion, or *Weber fraction*, the period, needed to sense motion at each contrast.

Fig. 3 shows how the Weber fractions for each subject vary with luminance and chromatic contrast. For each contrast, Weber fractions were larger for chromatic than for luminance modulation. The Weber fractions depended strongly on both luminance and chromatic contrast, but the dependency was different: for chromatic modulation Weber fractions decreased steadily with contrast over the entire range, while for luminance modulation there was a strong contrast dependency only at low contrasts, with the relationship flattening off for contrasts greater than about 3%.

The results show that for a sinusoidal grating of 1 c/deg, reaction times depend on both temporal frequency (speed) and on contrast. The dependency on temporal frequency was linear over a very wide range for both luminance and chromatic gratings, while the dependency on contrast was more complicated, and was quite different for luminance and chromaticity.

3.1. Theory

Reaction time data are traditionally analysed with the Piéron (1914, 1952) equation:

$$t_R = t_0 + \alpha v^{-\beta} \quad (1)$$

Where t_R is reaction time, t_0 a stimulus independent constant (comprising motor responses and a range of other non-visual factors), and α and β are the parameters of the equation. v can refer to many aspects of the stimulus, in this case speed. The Piéron equation has been applied to reaction times to motion onset, and shown to fit the data well. For broadband stimuli such as random-dot patterns, the best fit for the equation occurs with $\beta < 1$, usually around 0.6 (e.g. Tynan & Sekuler 1982; Allik & Dzhafarov, 1984; van den Berg & van de Grind, 1989; Dzhafarov, Sekuler, & Allik, 1993). However, for narrow-band stimuli, such as the sinusoidal gratings in this and previous studies (Troscianko and Fahle, 1988; Burr et al., 1998), $\beta \cong 1$. This simplifies the equation to:

$$t_R = t_0 + \frac{\alpha}{v} = t_0 + \frac{\alpha\tau}{\lambda} \quad (2)$$

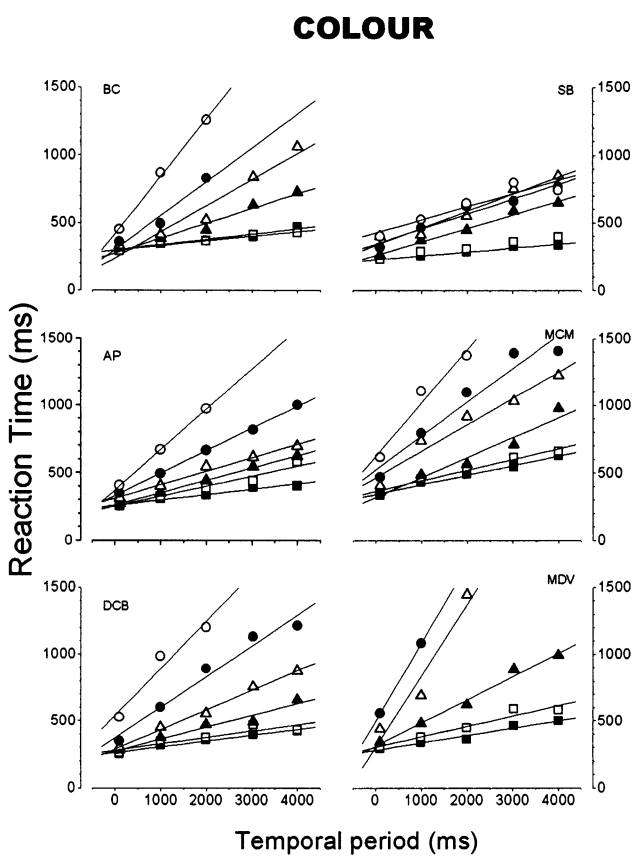

Fig. 2. Dependency of reaction time on inverse speed, for gratings modulated in chromaticity at various contrasts: 0.007 (○), 0.015 (●), 0.03 (△), 0.06 (▲), 0.11 (□) and 0.22 (■). As before, the data were fit by linear regression.

where τ and λ are the temporal and spatial periods of the grating. This has often been referred to as the '*critical distance*' model, where α is the critical distance (and α/λ the critical phase) that the stimulus must traverse to before the motion is detected, independently of drift speed. However, as mentioned above, the critical distance model does not hold in general, as for broadband stimuli, $\beta < 1$. In this study, the linear dependency at a particular contrast showed it to be an adequate description for sinusoidal gratings of fixed contrast, but the strong dependency on contrast showed that it has little general validity, even for sinusoidal gratings.

To extend the description of RTs into the contrast domain, and to try to understand why reaction times vary linearly with temporal frequency and inversely with contrast, consider the variation in instantaneous luminance as the grating moves, illustrated in Fig. 4. For a small time interval Δt, the grating will advance by $\lambda \Delta t/\tau$. The rectified space-averaged change in luminance, illustrated by the shaded areas, will vary inversely with τ (linearly if Δt is sufficiently small), and directly with the contrast of the grating. A simple model-free way to express the instantaneous local variation in luminance is

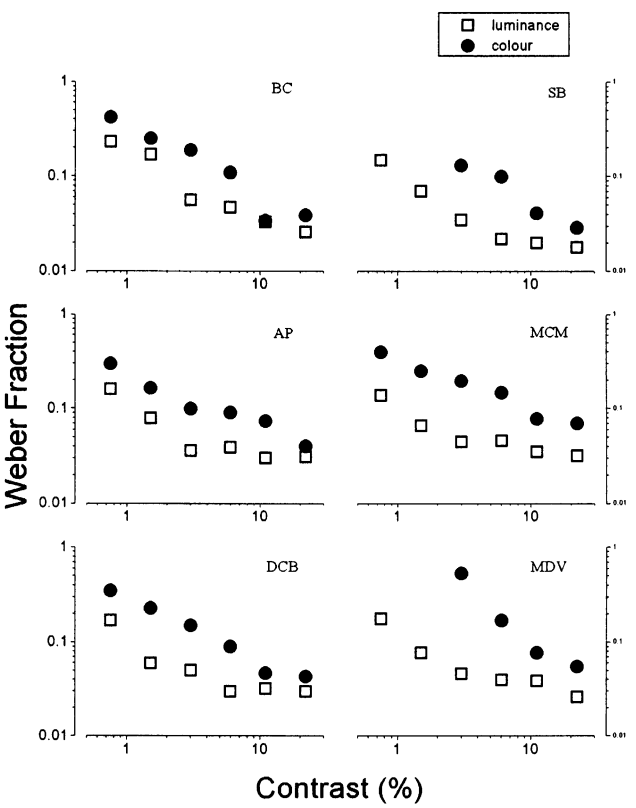

Fig. 3. Weber fraction for sensing motion, estimated from the slopes of the curves of Figs. 1 and 2, plotted as a function of contrast separately for luminance and chromatic modulation. At each contrast the Weber functions are higher for chromatic than for luminance contrast, and the dependency on contrast is clearly different for the two types of modulation.

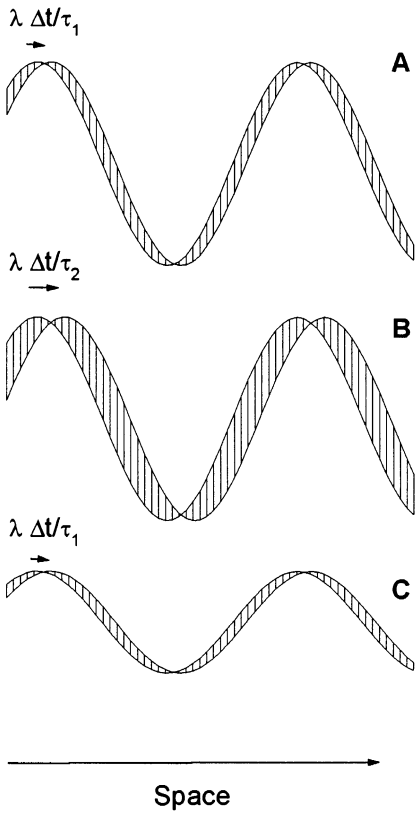

Fig. 4. Illustration of how the change in luminance over time varies with temporal period and grating contrast. For an infinitesimal increment in time, Δt, the grating will advance in phase by $\lambda \Delta t/\tau$. The shaded areas show the change in luminance for: (A) a grating of contrast c drifting with temporal period τ_1; (B) a grating of contrast c drifting with temporal period τ_2, where $\tau_2 = \tau_1/2$; (C) a grating of contrast $c/2$ drifting with temporal period τ_1. These examples illustrate schematically how the space-averaged change in instantaneous luminance will vary linearly both with temporal period τ, and spatial contrast c (for small Δt). The results of the previous figures support the linear dependence on temporal period, but not on contrast. This idea is developed more formally in the *theory* section, Eqs. (3)–(8).

as the first derivative of the luminance distribution with respect to time (although other definitions may serve equally well). This can then be used to calculate an RMS measure of *instantaneous luminance change*, by summing the square of the temporal luminance derivative over space, normalising by mean luminance and taking the square root. This is in turn is a form of instantaneous variation in contrast ($C(t)$). For a luminance distribution $L(x, t)$ of space averaged luminance L_0.

$$C^2(t) = \int_0^{\lambda} \left(\frac{\mathrm{d}L/\mathrm{d}t(x, t)}{L_0} \right)^2 \mathrm{d}x \tag{3}$$

The luminance profile $L(x, y)$ of a drifting grating is given by:

$$L(x, t) = L_0 \left(c \cos\left(\frac{2\pi x}{\lambda} + \frac{2\pi t}{\tau} \right) + 1 \right) \tag{4}$$

where c is the Michelson contrast of the grating ($c =$ amplitude/L_0). Substituting the derivative of 4 into 3:

$$C^2(t) = \frac{4\pi^2 c^2}{\tau^2} \int_0^{\lambda} \sin^2\left(\frac{2\pi x}{\lambda} + \frac{2\pi t}{\tau}\right) \mathrm{d}x \tag{5}$$

$$C(t) = \sqrt{2\lambda}\pi \frac{c}{\tau} \tag{6}$$

If one further integrates over time, up to the stimulus-dependent reaction time t_R, one can estimate C_{crit}, the accumulated dynamic contrast is at the time of response:

$$C_{crit} = \int_0^{t_R} \left(\sqrt{2\lambda}\pi \frac{c}{\tau}\right) \mathrm{d}t = \sqrt{2\lambda}\pi\, c \frac{t_R}{\tau} \tag{7}$$

Eq. (7) predicts that at any given spatial contrast c, the ratio of stimulus-dependent reaction time to temporal period (the Weber fraction t_R/τ) should be constant. This is strongly supported by the data of Figs. 1 and 2, for both luminance and chromatic contrast, for all subjects. However, Eq. (7) also predicts that the critical dynamic contrast should vary directly with the Michelson contrast of the grating, so the Weber fraction t_R/τ should be inversely proportional to contrast, which is clearly not the case, as shown in Fig. 3.

To model the observed variation in contrast, let one assume that the neural response of the mechanisms detecting the contrast change incorporates a contrast gain control. This could occur at any stage from the photo-receptor response through to the motion detection process, but for the sake of simplicity one will apply the gain control in a single stage after the dynamic contrast of Eq. (7). Gain control is typically modelled by the standard Naka–Rushton equation:

$$R(c) = R_{max} \frac{c^n}{c^n + c_{50}^n} \tag{8}$$

where R_{max} is the maximum obtainable response, n the exponent governing the steepness of the contrast dependency and C_{50} the semi-saturating contrast yielding a response of $R_{max}/2$. By substituting $R(c)$ for c in Eq. (7), one can calculate the contrast response that would cause the Weber fractions of Fig. 3 to produce a constant (arbitrarily chosen) C_{crit}.

These theoretical contrast response curves are shown in Fig. 5. The data for each subject was best fit by the Naka–Rushton equation of Eq. (8), separately for luminance and colour. The curves clearly have different form. Those of luminance contrast show a strong gain control, with low semi-saturating contrasts, indicated by the open triangles, and high exponents. On the other hand, the colour contrast curves are far more linear, with very high semi-saturating contrast (filled triangles). The scatter plots of Fig. 6 show the semi-saturating contrasts C_{50} and the exponents n for each of the six subjects, plotting colour against luminance. The differences are clear-cut. C_{50} is much higher for colour than luminance for all subjects (30 times on average), and n is much lower, about half (average 0.84 compared with 1.7 for luminance).

4. Conclusions

The results show that over a very wide range of temporal frequencies, RTs for motion onset of 1 c/deg gratings of a given contrast vary linearly with speed, being directly proportionally to temporal period, plus a stimulus invariant constant (Eq. (3)). The proportion of temporal period, or Weber fraction, varies with grating contrast non-linearly, differently for luminance and for colour. The results are well modelled by assuming that variation in contrast energy produced by motion is passed through a contrast gain control (different for luminance than for colour) and integrated over time, with detection occurring when the accumulated contrast it reaches a criterion threshold. This assumption is in line with several experiments showing motion detection and discrimination to depend on the product of the contrasts of a two-shot motion stimulus (Allik & Pulver, 1994, 1995; Morgan & Chubb, 1999).

The calculations were not based on any particular model of motion detection, but used simple, biologically plausible operations of the type that are inherent to most models. For example, temporal differentiation and spatial integration are inevitable consequences of spatio-temporal tuning of the motion detectors (Adelson & Bergen, 1985; Santen & Sperling, 1985; Watson & Ahumada, 1985; Burr, Ross, & Morrone, 1986). Other aspects of the spatio-temporal filters not modelled here, such as the spatial tuning and temporal low-pass characteristics, may produce a general attenuation of the response, will not cause any differential effects on the sinusoidal input (although they will affect broadband stimuli, as discussed below). These filters also include a rectifying stage (see in particular Adelson & Bergen, 1985; Santen & Sperling, 1985) that is modelled by the squaring of the derivative. However, it is important to note that the particular definition of change in contrast (root mean sum of squared temporal derivative) is not crucial for the model, but chosen as being a simple example. The important function governing contrast gain (Eq. (8)) occurs at many levels of the primate visual system, and will be discussed in more detail below.

The final stage of the model is an accumulation over time of the output of the motion detector, for which the physiological basis is less clear. To account for the results, this mechanism must be capable of integration of contrast energy over lengthy periods, in the order of

2 s (the slowest reaction times for both luminance and colour). There is good evidence that motion mechanisms do integrate contrast energy, but for far shorter periods of time, of the order of 100 ms (Watson, 1979; Burr, 1981). This integration, that corresponds well to the times predicted from the resonance tuning of the detector (Burr, 1981; Burr et al., 1986) is clearly far too brief to accumulate motion energy over the time-course of the longest reaction times. This suggests that the integration referred to in Eq. (7) does not occur within the mechanism that extracts the motion energy, but must reflect a second-stage integrator.

This result agrees with much previous evidence pointing to a second integration stage of motion perception. For example, Pinkus and Pantle (1997) reported motion priming effective over hundreds of milliseconds, far longer than the integration time predicted by motion energy models with appropriate temporal tuning. Other evidence also points to longer integration stages than expected from motion energy. For example, depending on the task, summation times for random dot patterns can be in the order of hundreds of milliseconds (Watamaniuk, Sekuler, & Williams, 1989; Sekular, Sekular, & Sekular, 1990; Watamaniuk & Sekuler, 1992), and far more for biological motion (Neri, Morrone, & Burr, 1998). A recent experiment in our laboratory has shown that under the same conditions that the visual system integrates contrast information for 200–300 ms, it will integrate noisy random dot motion patterns for up to 3 s (Burr & Santoro, 2001). The explanation suggested by this study is that contrast thresholds reflect the action of early mechanisms that compute motion energy, consistent with their temporal tuning (Burr, 1981; Burr et al., 1986), while increases in coherency sensitivity for

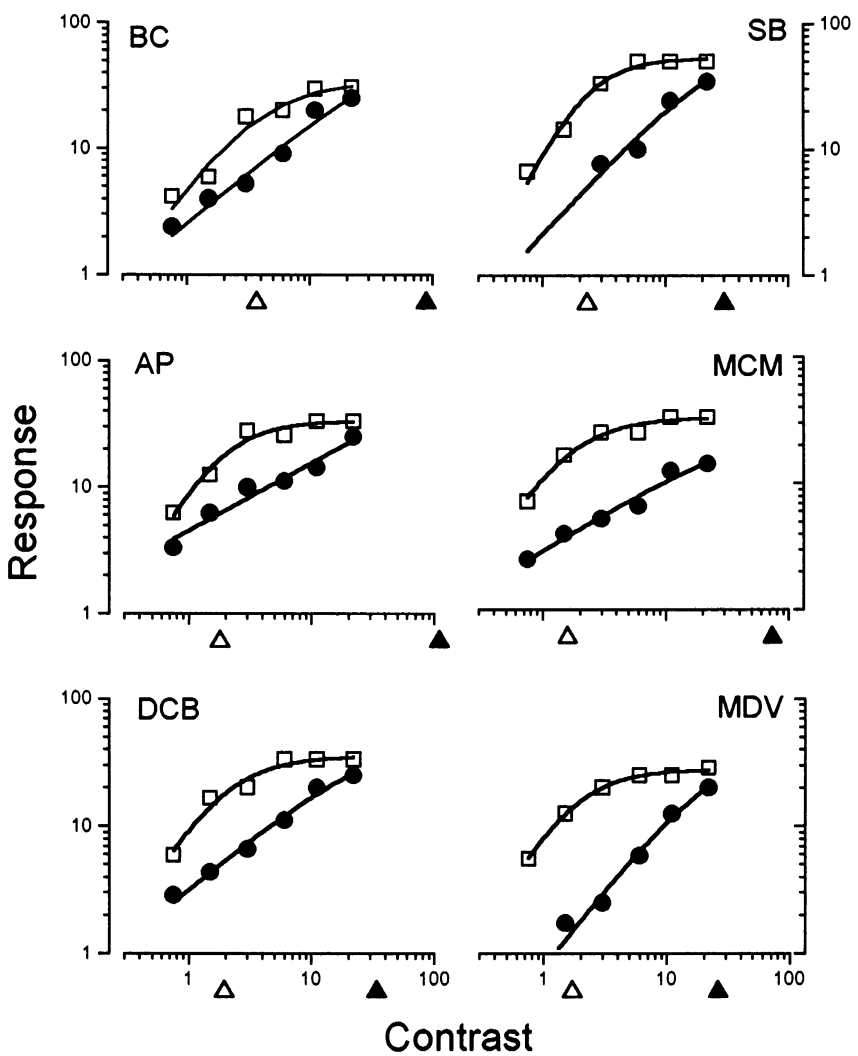

Fig. 5. Contrast response gain of the mechanisms responding to change in contrast required that predict the results of Figs. 1–3 (see text). Contrast response is plotted as the inverse of the Weber fractions ($\Delta t/\tau$) of Fig. 3. The data were fitted with the Naka–Rushton equation (Eq. (8)), with the semi-saturating contrasts C_{50} for luminance and colour for each observer are indicated by the open and closed triangles, respectively. The geometric means of the semi-saturating contrasts were 2.0 for luminance and 61 for colour.

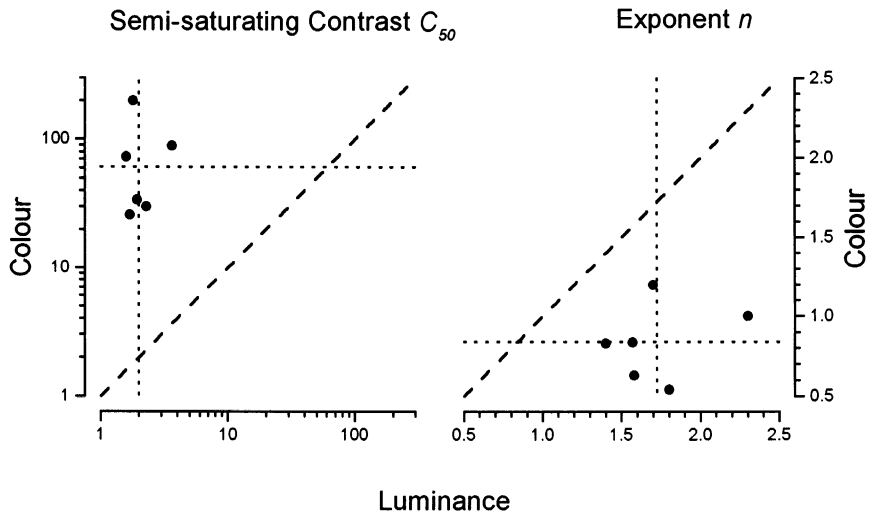

Fig. 6. Scatter plots of the two parameters of the Naka–Rushton curves of Fig. 5 for each subject. The semi-saturated contrasts are clearly much higher for colour than for luminance (geometric means 61 compared with 2.0), while the exponents were much lower (arithmetic means 0.84 compared with 1.7). The dashed lines indicate equal values for luminance and colour, and the dotted lines the averages.

random-dot patterns reflects a second stage of integration, like that proposed by Pinkus and Pantle (1997). The current study also points to the existence of this second-stage integration, with time constants of the order of seconds.

Note that the simple modelling applied here is valid only for narrow-band stimuli. For broadband stimuli, such as random dot patterns, the simplifying assumptions are no longer valid. Evidence suggests that motion mechanisms vary considerably in their spatial selectivity, with peak tuning varying from 0.1 to about 20 c/deg (Anderson & Burr, 1985). Thus broad-band stimuli, will stimulate a range of detectors, each with different spatial, and hence velocity, tuning. At slow speeds, detectors tuned to high spatial frequency will be more sensitive, at high speeds detectors tuned to low spatial frequency. How the simple equations of the model presented here should be modified to account for multiple filters of different spatial preference depends strongly on what assumptions are used for combining their outputs. However, it is clear that allowing for filters tuned to higher spatial frequencies, hence lower speeds, will privilege the detection of lower speeds, reducing the exponent β of the Piéron Eq. (1), as has been observed with broad-band stimuli (Tynan & Sekuler, 1982; Allik & Dzhafarov 1984; Dzhafarov et al., 1993). This idea could be readily tested by measuring reaction times to motion onset for sinusoidal gratings of different spatial frequency, and for compound gratings.

Although motion detectors vary considerably in spatial selectivity, the variation in temporal frequency seems to be far more limited, with all detectors tuned around 10 Hz (Anderson & Burr, 1985). This is an important part of the model. If there existed a range of detectors with widely different temporal tuning, allowing for selectivity to low velocities (even of narrow-band stimuli) the linear relationship with temporal period would no longer be predicted. The results reported here provide further support for limited temporal tuning.

One of the more interesting aspects of this study is that to explain the data at all contrasts, it is necessary to assume a contrast-gain control mechanism, of the type demonstrated by both psychophysical (e.g. Legge & Foley, 1980; Ross & Speed, 1991; Wilson & Humanski, 1993) and neurophysiological (e.g. Ohzawa, Schlar, & Freeman, 1985; Schlar, Maunsell, & DePriest, 1989) techniques. Contrast gain is typically modelled by the Naka–Rushton Eq. (8), determined by two parameters, the semi-saturating constant C_{50} and the exponent n. C_{50} is the contrast at which the curve attains half its maximum value, and the exponent n governs the steepness of the curve. The fitted values of C_{50} and n are clearly different for the data with luminance and colour contrast: the luminance curves had average semi-saturating constants of 2.0%, compared with 61% for colour contrast; and the exponent for luminance was twice that for colour, 1.7 compared with 0.84. The gain control for luminance is clearly stronger than that for colour.

These results find interesting parallels in the contrast response curves of neurones at various stages in the macaque visual pathway. Sclar, Maunsell and Lennie (1990) measured contrast response curves for neurones in the magno- and parvo-cellular layers of LGN, in V1 and in MT (all for stimulation by luminance modulated gratings), showing that the gain curves varied considerably from area to area. Table 1 summarizes the median semi-saturating constants and exponents of the cells

recorded in the four areas. The most linear were the P-cells, with median $C_0 = 50\%$ and $n = 1.6$; the least linear were the cells of MT, with $C_0 = 7\%$ and $n = 3$. While it is difficult to make direct comparisons from psychophysics to neurophysiology for many reasons (such as the problem of relating average spike count to psychophysical performance), these numbers are quite similar to those reported here. Although the exponents are uniformly higher than those of this study, the median value for MT cells was twice that of the P-cells, as luminance was twice that of colour in this study (if the square of the spike were the relevant measure, the numbers would coincide almost exactly). The semi-saturating constants are also similar: MT cells showed a median value of 7% (but a mode nearer 3%), compared with the mean of 2% measured here, and that for P-cells was 50% compared with 61% of this study. Note that the contrast response curves for P-cells in Sclar et al. (1989) study were measured with luminance, not chromatic, gratings. Unfortunately there do not exist comparable curves for chromatic stimuli, but measurements of Lee, Pokorny, Smith and Kremers (1994) suggest that the response of P-cells to chromatic modulation is at least as linear, if not more, than that to luminance modulation

Accepting the due precaution advised when relating physiology to psychophysics, the strong similarity in contrast response curves suggests that reaction times to motion onset of luminance stimuli may mediated by the magno-cellular system and MT, while those of chromatic stimuli by the parvo-cellular system. Even if one has reservations about making these comparisons, it is clear that the curves of Fig. 5 reflect the operation of different neural systems. There is no simple scaling operation of either contrast or Weber fractions that can cause the contrast response curves of luminance and colour to coincide. The most probably reason for this is that luminance gratings are detected by the magno-cellular system, and chromatic gratings by the parvo-cellular system. This result is highly consistent with neurophysiological evidence showing that the motion of equiluminant gratings of slow to moderate velocities is not processed by MT (Gegenfurtner et al., 1994; Gegenfurtner & Hawken, 1996a; Thiele et al., 1999).

Table 1
Median values of Naka–Rushton fits to the contrast response curves of cells in various visual structures (adapted from Schlar et al. (1989), table 1).

Visual structure	C_{50} (%)	N
Parvocellular LGN	50	1.6
Magnocellular LGN	11	1.2
V1	33	2.4
MT	7	3.0

The results are also consistent with previous psychophysical studies. Direction discrimination (Nakayama & Silverman, 1985), speed discrimination (McKee, Silverman, & Nakayama, 1986) and signal detection measures of motion performance (Edwards, Badcock, & Nishida, 1996) are little affected by contrast, except near threshold. Furthermore, Keck, Palella and Pantle (1986) have shown that the motion aftereffect shows strong contrast dependency up to 3% contrast, but is virtually independent of contrast at higher contrasts. Unfortunately, there are no comparable data with equiluminant gratings, where then prediction is for strong dependency over a wide range.

Although the results reported here strongly suggest that slowly moving luminance and chromatic gratings are processed through different pathways, there also exists good evidence to suggest that the motion of colour and luminance stimuli share a common site of analysis. For example, luminance and chromatic gratings drifting in opposite directions do not appear to slide over each other, as one would expect if they stimulated completely different detectors (as occurs for different spatial frequencies: Adelson & Movshon, 1982), but when of appropriately matched contrast, one grating annuls the other, cancelling the sensation of motion (Cavanagh & Anstis, 1991). Furthermore, adaptation to drifting luminance gratings produces motion after-effects on subsequent inspection of equiluminant gratings, and vice versa, implying a common site of directional adaptation (Cavanagh & Favreau, 1985; Derrington & Badcock, 1985; Mullen & Baker, 1985). One possibility is that the initial encoding occurs through different pathways (with different gain controls) and that the output of these separate pathways is pooled by a higher-order mechanism that integrates both types of motion signals. This integrating mechanism may correspond to the second-stage temporal integrator of the model proposed here (Eq. (7)). Some suggestion that this integration stage could pool both luminance and colour signals is given by the fact that both luminance and chromatic stimuli can lead to very long stimulus-dependent reaction times, 1–2 s, both requiring temporal integration over relatively long periods.

One consequence of the invariance of luminance with contrast may be to keep motion signals from luminance information relatively invariant in the face of variable constant. Indeed perceived speed varies strongly with the contrast of chromatic gratings (Gegenfurtner & Hawken, 1996b; Hawken, Gegenfurtner, & Tang, 1994), but much less with that of luminance gratings (Thompson, 1982; Stone, Watson, & Mulligan, 1990; Allik & Pulver, 1995). Furthermore, with techniques very similar to those used in this paper, it has been shown that the RTs to both luminance and chromatic gratings are well predicted by their perceived, rather

physical speed (Burr et al., 1998). It would seem that while the visual system will take advantage of any potential information about motion, including that from chromatic modulation, it depends more heavily on the information derived from luminance sources, that these work veridically over a wide contrast range. Indeed when both colour and luminance motion signals are available, the system relies on the luminance signals, at least for 'natural' two-dimensional stimuli (Farell, 1999).

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