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Magnocellular channel subserves the human contrast-sensitivity function

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Abstract. There is evidence that the human contrast-sensitivity function (CSF) is mediated by the spatiotemporal characteristics of magno and parvo neurons early in the visual pathway. In this study we use a measure of contrast gain derived from simple reaction times, to investigate the neural substrates of suprathreshold performance. The results reveal the activity of two mechanisms having distinctly different contrast-gain characteristics. Comparing these to neurophysiological data, we find that the magnocellular system dominates close-to-threshold detection and probably forms the basis of the achromatic CSF, whereas the parvocellular system dominates detection at higher contrasts, when the magnocellular system saturates.

1 Introduction

There is compelling physiological evidence that in the primate retino-cortical pathway there are at least two distinct channels, originating from the two main classes of retinal ganglion cells, the magno and parvo cells, which project, respectively, to the magnocellular (M) and parvocellular (P) layers of the lateral geniculate nucleus (LGN) (Rodieck et al 1985; Wiesel and Hubel 1966). Beside the highlighted differences in several anatomical and functional characteristics (Kaplan and Benardete 2001; Kaplan et al 1990; Lee 1996; Lund et al 1995; Perry et al 1984; Yeh et al 1995), the two detecting channels show characteristic signatures in the processing of luminance contrast: M neurons have high sensitivity to luminance contrast (ie high contrast gain; Kaplan and Shapley 1986), but their responses saturate at fairly low contrasts, whereas P neurons have relatively poor sensitivity to achromatic contrast, but show a higher degree of spatial and temporal linearity (Hicks et al 1983; Kaplan and Shapley 1986; Lee et al 1990; Sclar et al 1990). This constellation of different properties has led to the notion that these two streams of visual information remain largely segregated in the striate cortex V1 and possibly beyond, and are engaged in parallel processing of different and complementary aspects of the visual scene (DeYoe et al 1994; Livingstone and Hubel 1988).

Psychophysical studies that rely on threshold detection, eg the contrast-sensitivity function (CSF), are considered to reflect the spatiotemporal properties of the neurons in the retino-cortical pathways. There has been an extensive literature regarding the neuronal substrate of the CSF. It is now well accepted that the M cells provide the neural basis of the luminance channel (Lee et al 1989; Shapley and Hawken 1999), mediating most of the CSF to achromatic patterns (Kulikowski 1989), although the opposing view that the P-cell channel could support luminance, at higher spatial frequencies, had also been advanced (Derrington and Lennie 1984; Lennie and D'Zmura 1988; Merigan and Maunsell 1993). This controversy is fully discussed in Plainis and Murray (2000) and is the main topic for Lennie et al (1993).

Recently, simple reaction times (RTs) have been employed to derive achromatic (Murray and Plainis 2003; Plainis and Murray 2000) and chromatic (McKeefry et al

2003) CSFs, and Plainis and Murray (2000) have described a wide range of stimulus characteristics in which the RT is a linear function of the reciprocal of contrast, so that

$$\tau = \tau_0 + kC^{-1}, \quad (1)$$

where τ = reaction time, τ_0 = the asymptotic reaction time, k = slope, C = contrast. Effectively this means the exponent in Pieron's famous reaction time equation is -1. The advantage of using RTs is that sensitivity can be obtained over a range of suprathreshold contrasts and thereby provide a direct measure of contrast gain. Using a derivation of the well-known Naka–Rushton equation to obtain gains at high and low contrasts, Murray and Plainis (2003) have described a biphasic relationship, revealing the transition between two physiological mechanisms identified as reflecting M and P pathways. Inevitably, this characteristic change in gain occurred only for low spatial frequencies where, because of the high sensitivity, more than one mechanism operates (see Appendix, figure A1). At high spatial frequencies and under low luminances the biphasic function is replaced by a simple straight line. Although this was not the first time the biphasic function for RT versus contrast had been described (see Harwerth and Levi 1978; Parry 2001), the interpretation in terms of P and M pathways was novel.

In this paper we develop this interpretation of RT data further by comparing the RT-based contrast gains obtained under conditions where it might be speculated that either M or P pathways dominate detection. To make this comparison we have taken the ratio of contrast gains obtained for M (low contrast range) and P (high contrast range) dominated conditions for a range of spatial frequencies.

2 Methods

Two young subjects aged 29 (SP) and 23 (LG) participated in the experiments. Subjects were optically corrected for the viewing distance with spectacles (corrected VA was $\geqslant 6/5$) and viewed the stimuli through natural pupils and binocularly. Subjects were familiarised with the range of conditions to be used in the experiment and were given a block of practice trials prior to RT recording.

The stimuli were vertical sinusoidal gratings, modulated in luminance, and displayed on a high-resolution monitor (for details, see Murray and Plainis 2003). Stimuli appeared/disappeared with a square-wave temporal profile. Mean luminance was 20 cd m^{-2}. Contrast was defined as equal to the Michelson contrast. The test field was a circular target subtending an angle of 7.13 deg. The minimum number of cycles presented on the screen was 3.5 for the lowest spatial frequency used (0.49 cycle deg^{-1}).

RTs were determined with 1 ms resolution with a CED 1401 smart interface, linked to a PC, and a purpose-designed computer program. Subjects were instructed to respond by pressing a button, which triggered the CED 1401. A trial consisted of the following sequence of events. A single warning tone was sounded. This was followed by a random foreperiod varying from 1000 to 3000 ms prior to the presentation of the target stimulus. If the subject did not respond, the next stimulus was presented after 5000 ms. At the onset of the grating, a trigger probe was set which prompted the CED 1401 to start its integral clock counter. This was terminated when the response button was pressed. Only responses between 150 and 1000 ms were accepted; RTs over 600 ms were rarely encountered. When a grating was not present, the screen remained blank, with the same space-averaged luminance as the stimulus.

Subjects fixated on a cross, located at the centre of the illuminated area of the screen, for central viewing and on a series of red LEDs when eccentric viewing was tested. RT data were collected for a range of contrasts from suprathreshold (0.5) to threshold (C_0) detection. A block of about 28–32 RTs was recorded for a single contrast level. A series of spatial frequencies (0.49 to 17.7 cycles deg^{-1}) and eccentricities (0°, 5°, 10°, and 15°) for both hemifields was tested. Stimulus duration varied between 20, 50, and 500 ms.

3 Results

RT data for both subjects and all conditions were initially plotted as a function of the reciprocal of contrast (C^{-1}). The resulting slopes revealed a linear relationship in conditions where a single mechanism operating over the whole contrast range, and a bi-linear function for conditions where sensitivity was high (an example of a bi-linear function is given in the Appendix, figure A1; for the complete data see figures 3 and 4 in Murray and Plainis 2003). In the latter paper, the transition point between the two segments occurred at around $C = 0.1$, indicating the presence of two distinct neural mechanisms with different sensitivities (gains): a low-sensitivity P-dominated channel at high contrasts and a high-sensitivity M-dominated channel at low contrasts (below 10%). In this paper, the RT contrast sensitivities of the two subserving neural mechanisms, derived from the regression analysis of RT-contrast functions, as described in the Appendix, are plotted for a range of stimulus conditions.

Figure 1 shows plots of the M-dominated and P-dominated RT-derived sensitivities as a function of spatial frequency for three stimulus presentation times. It is clear that when presentation time is long (500 ms), the sensitivity function of the M-dominated channel shows a band-pass shape, resembling the characteristics of the sensitivity of M neurons. On the other hand, the P-dominated channel exhibits a low-pass frequency characteristic, which also holds for the P-pathway neurons. Moreover, for the longest presentation used, the ratio of M over P sensitivity is maximal (between 5 and 10) for middle spatial frequencies ($\sim 2-5$ cycles deg^{-1}). The ratio between the two neural mechanisms is reduced for the low and the higher spatial frequencies and for short presentation times (20 and 50 ms). Higher spatial frequency gratings (>10 cycles deg^{-1}) produce monotonic RT versus $1/C$ functions, resulting in a single slope of lower contrast-gain characteristics (see Murray and Plainis 2003).

In figure 2, the RT contrast sensitivities for the two physiological channels are plotted as a function of eccentricity for two spatial frequencies. Data from the left and right hemifields are shown either side of zero eccentricity. As expected, sensitivity for both P and M channels varies with eccentricity, reaching its peak at the fovea. The ratio in sensitivity between M and P is fairly constant (<5) across eccentricity for the lower spatial frequency (0.49 cycle deg^{-1}) and is maximal (~ 10) at 0 deg for the higher spatial frequency (5.57 cycles deg^{-1}).

4 Discussion

In this paper, we use a psychophysically derived measure of contrast gain, ie the RT contrast sensitivity, to investigate the relative contribution of neural mechanisms at suprathreshold contrasts. This metric, which is reciprocal to slopes of biphasic RT versus C^{-1} functions, has been shown to be similar to the physiological contrast gain used to model the contrast response characteristics of neurons in the primary visual pathway (Kaplan and Shapley 1986; Murray and Plainis 2003; Sclar et al 1990).

As highlighted in figure 1, the sensitivity of the M-dominated channel (derived from the low-contrast segment of the RT versus C^{-1} function) resembles the band-pass characteristics of the individual M cells, but also the shape of the luminance CSF. On the other hand, the P-dominated channel (derived from the high-contrast segment of the RT versus C^{-1} function) exhibits a low-pass function, which holds for chromatic modulation and the P cells. The other interesting observation is that the ratio in sensitivity between the two channels (M/P) varies with spatial frequency and stimulus presentation, in agreement with physiological findings.

Figure 1 indicates a maximal ratio (~ 10) for the middle (~ 2 to 5 cycles deg^{-1}) spatial frequencies, when a 500 ms presentation stimulus (encouraging sustained mechanisms) is used. This is not surprising, since it is known that human CSF peaks at the same frequencies. It is believed that, when the sensitivity of the system is high, classes of

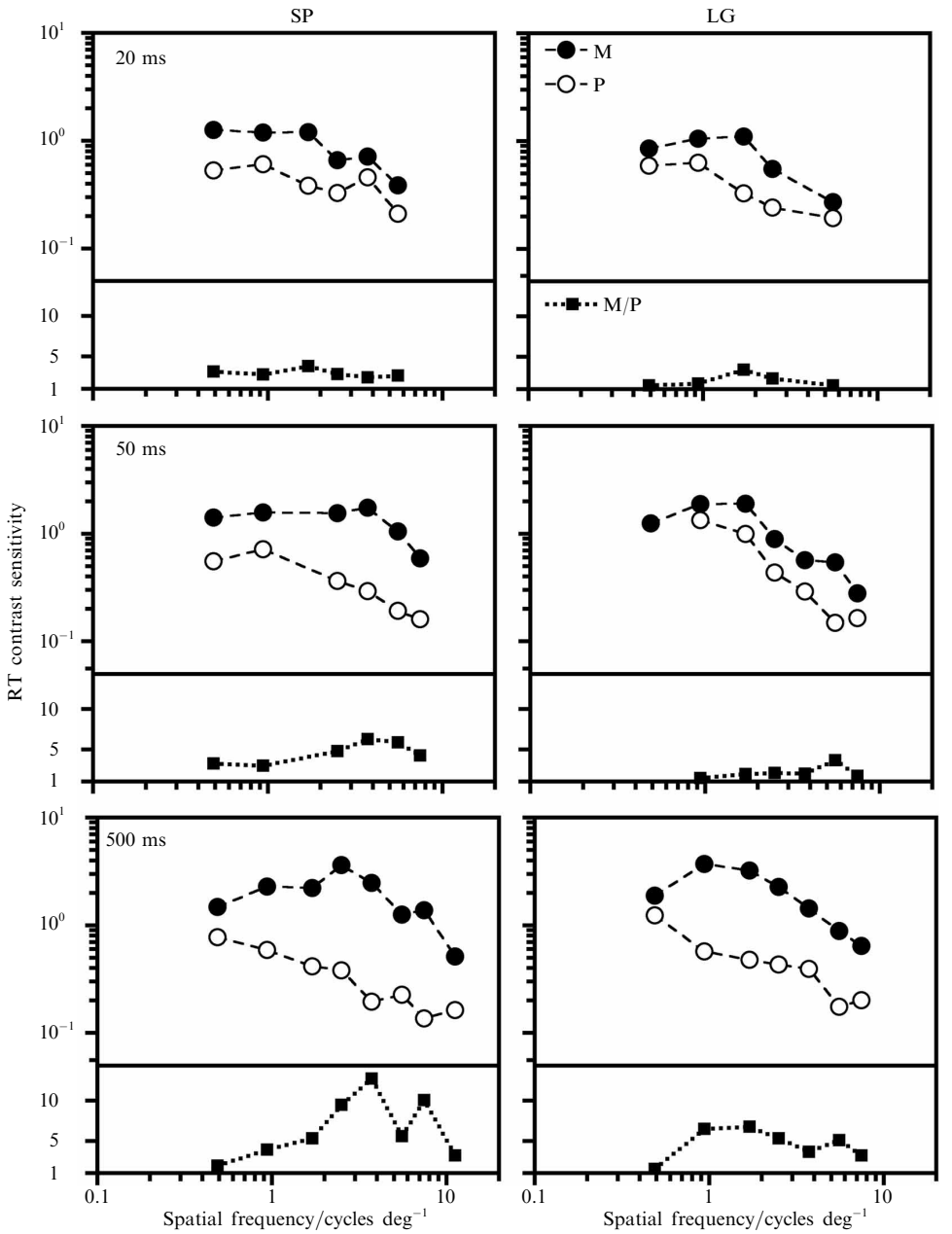

Figure 1. Plots of the RT contrast sensitivity for the M-mediated (filled circles) and P-mediated (open circles) channels as a function of spatial frequency, for a range of stimulus presentations (20, 50, and 500 ms). Data from two subjects are shown. The lower part of each figure shows the ratio M/P. Sensitivities were derived from the slopes of the low-contrast and high-contrast segments of the RT versus $1/C$ functions (see Murray and Plainis 2003).

neurons having pure M and P inputs are activated, with the segregation of their responses being very prominent. However, the use of a more transient stimulus (eg 20 ms duration) and/or low spatial frequencies, produces a less pronounced difference in contrast sensitivity between the high-contrast and the low-contrast systems. It is possible that low spatial frequencies activate a population of neurons that receive convergent inputs from both M and P channels, thus producing a functional gradient for contrast gain.

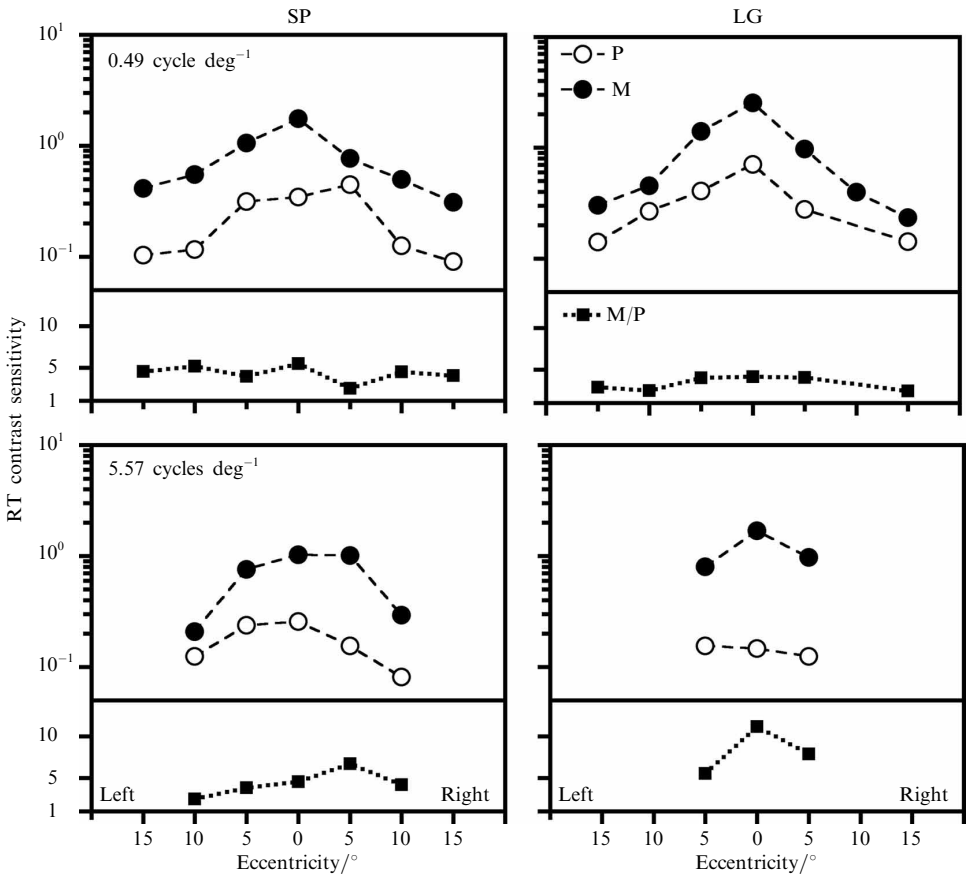

Figure 2. Plots of the RT contrast sensitivity of the M-mediated (filled circles) and P-mediated (open circles) channels as a function of eccentricity for two spatial frequencies (0.49 cycle deg^{-1}, upper panel; 5.57 cycles deg^{-1}, lower panel). Data from two subjects are shown. Stimulus presentation was 500 ms. Sensitivities were derived from the slopes of the low-contrast and high-contrast segments of the RT versus $1/C$ functions (see Murray and Plainis 2003).

This is consistent with recent anatomical physiological data which provide a substrate of functional convergence of P and M cells in layer 4C of cortical area V1 (Bauer et al 1999; Lund et al 1995; Vidyasagar et al 2002).

As noted in Murray and Plainis (2003), higher spatial frequencies produce monophasic suprathreshold functions. It has been postulated that high spatial-frequency processing (>10 cycles deg^{-1}) is probably subserved by a mechanism of higher spatial resolution (but lower sensitivity), which can be achieved by the summation of the more numerous P neurons (Kulikowski 1989). Probability summation may improve resolution, but physiological data do not support the notion that P cell convergence could effectively increase the sensitivity of the P system (Kaplan et al 1990). On the other hand, spatial resolution of the M system is limited by the large receptive fields and the sparse population of M neurons (Derrington and Lennie 1984). There is again a possibility that high-spatial-frequency patterns are mediated by neurons located in the overlap region of layer 4C, having both P-like and M-like spatiotemporal properties.

If we consider now the effect of eccentricity, we find that the reduction in RT contrast sensitivity agrees with CSF findings. Croner and Kaplan (1995) showed that the contrast gains of P and M cells are roughly constant across the macaque retina.

This constancy is not obvious in threshold-based human psychophysical measurements, which show decreased sensitivity in the peripheral retina (Mullen and Kingdom 2002; Rovamo et al 1978). This may be due to the attenuation of contrast on the retina, as more aberrations are introduced in the periphery by the optics of the eye (Atchison and Scott 2002; Navarro et al 1998). However, it is now believed (Lee 2004) that peripheral sensitivity is mainly affected by increased convergence of cones in peripheral primate retina (Goodchild et al 1996) and the increased amount of cortical area devoted to representing the periphery (Rovamo et al 1978). This means that the psychophysical loss of sensitivity must have a central origin. Finally, RT-based measurements are recorded at suprathreshold contrast levels, and may therefore be less susceptible to these effects.

Although there is no direct evidence about the spatial frequency resolution of the neural systems that support psychophysical tasks, such as reaction times to achromatic patterns, it is highly likely that there are several spatiotemporal mechanisms involved. The RT contrast sensitivity measure derived by reaction times is very helpful in understanding suprathreshold processing by linking psychophysical performance to neuronal physiological properties. There is a strong indication that the M system is responsible for close-to-threshold detection and probably forms the basis of the CSF, whereas the P system takes over at suprathreshold contrast levels. It seems likely that another mechanism with converging P and M inputs mediates detection when the sensitivity of the system is low.

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Appendix A: The derivation of contrast gain from RT data

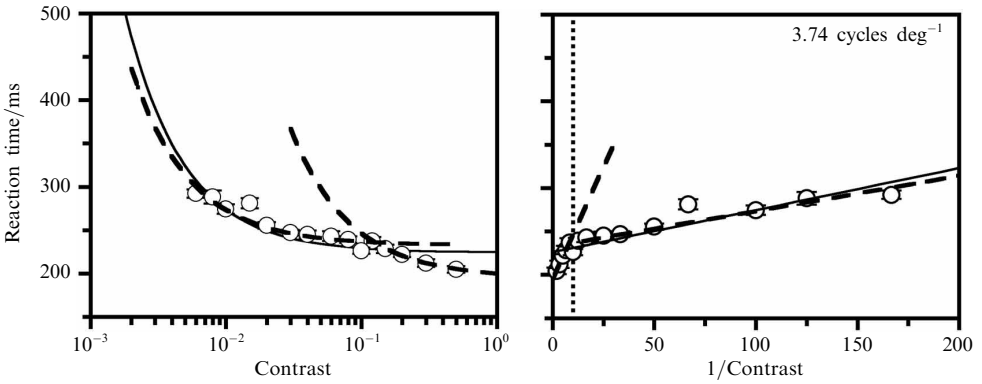

Figure A1. RTs versus contrast (a) and the reciprocal of contrast (b) for spatial frequency 3.74 cycles deg^{-1}. For these conditions (500 ms duration and 20 cd m^{-2}) a biphasic function is revealed. The dashed lines in (a) are the best fits for equation (1) and in (b) the least-square-regression fits for the low (0.1 to threshold) and high (0.5 to 0.1) contrast segments of the curves. Solid lines are the best fits for all data points. The vertical solid line indicates $C = 0.1$. Modified from Murray and Plainis (2003).

Appendix B: Derivation of RT contrast gain from the Naka – Rushton equation

Gain control in terms of the Naka – Rushton equation is typically expressed as:

$$R_{\mathrm{C}} = R_{\max} \frac{C^n}{C^n + C_{50}^n}$$

where R_{C} = response, $R_{\max}$ = maximum (saturated) response, n = the exponent controlling the steepness of the contrast function, and C_{50} = the semisaturating response.

If we take the reciprocal of reaction time (τ) as a function of contrast and allow this to be the response, then we can write:

$$\tau^{-1} = \frac{1}{(\tau_0 + kC^{-1})} = \frac{\tau_0^{-1} C}{(C + k\tau_0^{-1})}\,, \tag{B1}$$

which is the same form as equation (1). The slope of the Naka – Rushton function (2) at contrast C is:

$$\tau^{-1}(C) = \frac{\tau_0^{-1}}{C + k\tau_0^{-1}} - \frac{\tau_0^{-1} C}{C + k\tau_0^{-1}}\,,$$

and the slope at $C = 0$ is

$$\tau^{-1}(0) = \frac{\tau_0^{-1}}{k\tau_0^{-1}} = k^{-1}\,.$$

Thus, k^{-1} is an index of sensitivity (the gain) of the underlying detecting mechanism; steep slopes indicate low gain and consequently low sensitivity, shallow slopes indicate high gain (ie high sensitivity). Values of k^{-1} are plotted in figures 1 and 2 as RT contrast sensitivity.

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