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Visual evoked potentials elicited by chromatic motion onset

D.J. McKeefry *

Vision Science Research Group, School of Biomedical Sciences, University of Ulster, Coleraine, Northern Ireland BT52 1SA, UK

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Abstract

Visually Evoked Potentials (VEPs) were recorded in response to the onset of chromatic and luminance motion gratings of 1 cpd and luminance 40 cd m^{-2} subtending a 7° field. At slow speeds (≤ 2 cycles s^{-1}) the motion onset response exhibits a clear amplitude minimum at isoluminance. Over the Michelson contrast range tested (0.05–0.75) the chromatic response at 2 cycles s^{-1} possesses a linear response function compared to the saturating function of the luminance response and the contrast dependency of the former is a factor of 5–6 times greater than for the latter. These differences are suggestive of different neural substrates for the chromatic and luminance motion VEPs at slow speeds. At 10 cycles s^{-1} the chromatic motion onset VEP exhibits no amplitude minimum at isoluminance and becomes more like its luminance counterpart in terms of its saturating contrast response function. Furthermore, the contrast dependency of the chromatic and luminance responses differs by only a factor of 1.6 at this faster rate. These findings are consistent with the idea of separate motion mechanisms that operate at fast and slow speeds, the latter having separate channels for colour and luminance motion.

Keywords: Colour; Motion; Visual evoked potentials

1. Introduction

The discovery that colour and motion are processed by separate cortical areas in the macaque monkey brain provided the initial inspiration for the theory of functional specialisation and segregation within the visual system (Zeki, 1978). Subsequent psychophysical and anatomical studies (Ramachandran & Gregory, 1978; Livingstone & Hubel, 1987) appeared to substantiate the idea that colour and motion are processed by separate pathways within the visual system. In apparent support of this view are reports that motion perception is somehow impaired or impoverished at isoluminance (e.g. Ramachandran & Gregory; Cavanagh, Tyler, & Favreau, 1984; Troscianko & Fahle, 1988; Mullen & Boulton, 1992). But it would be erroneous to consider the motion system as being simply 'colour blind' as numerous studies have shown that colour can give unambiguous cues about motion (Derrington & Henning, 1993; Cropper & Derrington, 1996; Willis & Anderson, 1998). What is less clear is the extent of independence or interaction between the chromatic and luminance inputs to the motion system. Some studies have suggested independence (Krauskopf & Farrell, 1990; Metha, Vingrys, & Badcock, 1994; Cropper, Mullen, & Badcock, 1996), with recent reports raising the possibility that chromatic motion is processed solely by a 'third-order' motion mechanism (Lu, Lesmes, & Sperling, 1999). Other studies demonstrate that there are strong interactions between colour and motion pathways (Cavanagh & Favreau, 1985; Derrington & Badcock, 1985; Kooi & DeValois, 1992; Chichilnisky, Heeger, & Wandell, 1993; Papathomas, Gorea, & Julesz, 1993; Ffytche, Skidmore, & Zeki, 1995; Edwards & Badcock, 1996). A recent model (Gegenfurtner & Hawken, 1996), may provide a limited degree of reconciliation between some of these conflicting ideas and proposes the existence of two motion processing pathways that differ mainly in their temporal properties. One mechanism operates at low temporal rates and has different channels for luminance and chromatic motion. The other operates at higher temporal rates possessing a single motion channel with both chromatic and luminance inputs. The fast and slow mechanisms are both sensitive to colour, but they respond in different ways.

* Present address: Dept. Optometry, University of Bradford, Bradford BD7 1DP, UK. Tel.: +44-1274-236240; fax: +44-1274-235570.
E-mail address: d.mckeefry@bradford.ac.uk (D.J. McKeefry).

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The latter encodes colour veridically, but not velocity; the former velocity veridically, but not colour (however see Gorea, Papathomas, & Kovacs, 1993; Metha & Mullen, 1997; for alternative views).

Visually Evoked Potentials (VEPs) are a measure of cortical activity in response to a visual stimulus, which when suitably chosen, they can selectively reflect the operation of specific neural processes (Kulikowski, Robson, & McKeefry, 1996; Kulikowski, McKeefry, & Robson, 1997). Like reaction times, VEPs offer the advantage of allowing the examination of suprathreshold visual performance. Many studies have reported the existence of VEPs that reflect motion related processing in the visual system (Clarke, 1972, 1973, 1974; Tyler & Kaitz, 1977; Müller & Göpfert, 1988; Müller, Göpfert, Schlykowa, & Anke, 1990; Göpfert, Müller, & Simon, 1990; Kuba & Kubova, 1992; Bach & Ullrich, 1994; Snowden, Ullrich, & Bach, 1995; Kubova, Kuba, Spekreijse, & Blakemore, 1995; Bach & Ullrich, 1997; Odom, DeSmedt, Van Malderen, & Spileers, 1999). The consensus appears to be that the response is motion specific if the VEP fulfils the following criteria: (i) possesses high contrast sensitivity; (ii) exhibits a saturating contrast response characteristic; (iii) is susceptible to motion adaptation. These criteria are met by the N200 component of the motion onset VEP (Kuba & Kubova, 1992; Bach & Ullrich, 1994, 1997; Kubova et al., 1995) and by steady-state VEPs elicited by directional changes in motion (Snowden et al., 1995).

The criteria for motion-specificity have been derived from VEPs generated by luminance motion stimuli. Fewer studies in comparison have examined VEPs elicited by chromatically defined motion (Morrone, Fiorentini, & Burr, 1996). This study will attempt to address the basic question of whether motion specific VEPs can be produced by an isoluminant chromatic motion stimulus. Motion specificity will be tested in terms of the adherence of the chromatic motion VEP to criteria (i) and (ii) listed above [adherence to criterion (iii) will be dealt with in a subsequent study].

In addition to the examination of the motion specificity of the chromatic motion VEP, I will also test whether motion VEPs show any sign of the segregation, suggested by the Gegenfurtner & Hawken (1996) model of motion processing. The rationale is that if separate channels do exist for luminance and colour at slow speeds, presumably with separate neural substrates, then this would be revealed by different response properties of the potentials generated by the two types of motion. Furthermore, if, as the model also proposes, the mechanisms signalling slow and fast chromatic information are different, one would expect the properties of the fast and slow chromatic motion VEPs to exhibit signs of this segregation.

2. Methods

2.1. VEP recording

VEPs were recorded using silver–silver chloride electrodes. An active electrode was placed at O_z and referenced to linked ear electrodes with a ground electrode placed on the forehead. The VEPs were averaged using a CED 1401 'micro' and accompanying Signal software (version 1.72). Amplifier (CED 1902) bandwidth was 0.5–30 Hz and signals were sampled at a rate of 250 Hz over 1.496 s.

Simultaneous electro-oculogram recordings performed on one experienced VEP subject and two naive subjects, demonstrated that motion VEPs were not contaminated by eye movement artefacts when subjects were instructed to maintain fixation on a centrally placed cross.

2.2. Subjects

A total of 15 undergraduate and postgraduate students aged between 22 and 35 years were used as subjects during the course of these series of VEP and psychophysical experiments (though not all of them took part in every experiment). All subjects had 6/6 (or better) unaided vision or corrected acuity and were classified as colour normal according to the Farnsworth–Munsell 100 Hue test.

2.3. Stimuli

Vertically oriented sinusoidal gratings of 1 cpd were generated on an Eizo T562-T colour monitor with a frame rate of 120 Hz, under the control of a VSG2/3 graphics card (version 5, Cambridge Research Systems). The stimulus subtended a circular field of 7° with a constant mean luminance of 40 cd m^{-2} and was surrounded by a neutral background (CIE 1931 chromaticity co-ordinates $x = 0.310$, $y = 0.316$) of the same luminance.

The luminance contrast content of the stimulus could be systematically varied by manipulation of the relative mean luminance of the red and green phosphors, expressed as the $G/(G+R)$ ratio. $G/(G+R)$ ratios $= 1$ and 0 produce green-dark green and red-dark red luminance modulated (achromatic) grating stimuli, respectively. At $G/(G+R) = 0.5$ the stimulus takes on the appearance of a bichromatic red–green grating (chromaticity co-ordinates $R_x = 0.366$, $R_y = 0.248$ and $G_x = 0.390$, $G_y = 0.517$). Calibrations and measurements were performed using a PR650 Spectrascan SpectraColorimeter. Theoretically, a $G/(G+R)$ ratio $= 0.5$ should constitute a purely isoluminant (chromatic) stimulus. However, the isoluminant ratio can vary between subjects and chromatic aberration can introduce luminance

contrast modulation in an erstwhile isoluminance pattern (Charman, 1991). Therefore, prior to the start of each recording session, subjects set their own individual isoluminant points using a minimum motion method (Anstis & Cavanagh, 1983) for each of the experimental conditions employed. The average setting across all subjects for isoluminance was $G/(G+R) = 0.45$ (S.D. = 1.38).

The use of a 7° stimulus was necessary in order to minimise the effects of luminance intrusions which have been shown to compromise the selectivity and specificity of chromatic VEPs in response to isoluminant stimuli (Kulikowski et al., 1996). These intrusions arise from changes in the isoluminant point as a function of retinal eccentricity and also as a result of chromatic aberrations (both longitudinal and transverse). Empirical evidence suggests that isoluminant red/green gratings should contain less than eight cycles in order to minimise such intrusions (Kulikowski et al., 1996).

VEPs were elicited by the motion onset of the vertically orientated gratings, the speed of which could be varied (1–10 cycles s^{-1}). Response averaging was triggered by the onset of horizontal motion that lasted 350 ms, followed by a stationary grating phase lasting 1170 ms (Fig. 1A) giving a duty cycle of approximately 23%. A typical response generated by this stimulus is shown in Fig. 1B, which indicates the major components of the motion onset response, and how intra-response amplitudes and latencies were measured.

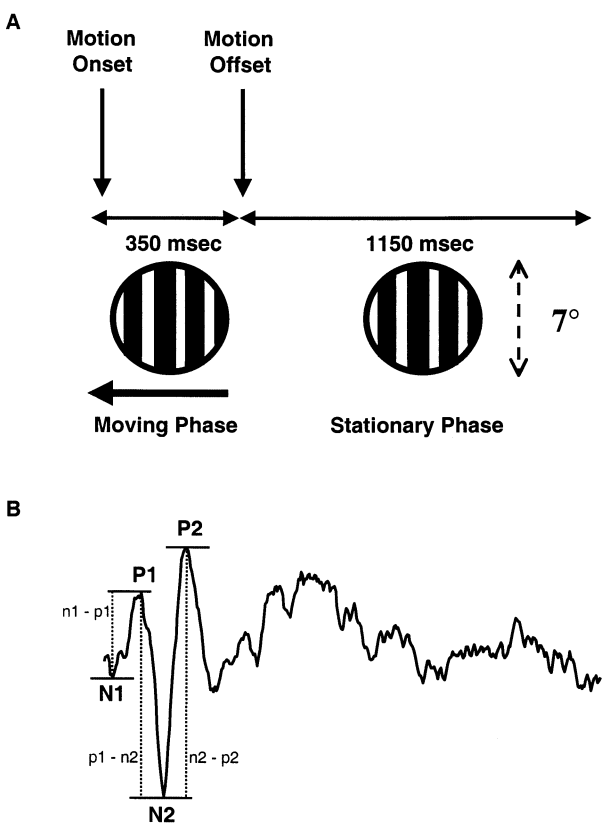


Fig. 1. (A). The spatial and temporal configuration of the stimulus used to elicit motion onset VEPs, the leftward pointing arrow indicates the direction of motion. Subjects were instructed to fixate on a centrally placed target (not shown). (B). A typical motion onset (luminance) VEP indicating the position, in terms of latency to peak measurements, of the main components examined as well as how the amplitudes of the various components were measured.

2.4. Luminance and chromatic contrast

When comparing chromatic and luminance visual function the problem of how to express chromatic modulation arises (see Lennie & D'Zmura, 1988; Derrington & Henning, 1993). Achromatic contrast can be simply expressed in terms of the Michelson contrast $(L_{max} - L_{min}/L_{max} + L_{min})$. But for the expression of chromatic contrast two different approaches have been adopted. In the majority of instances chromatic contrast is assigned as being equal to the luminance contrast of the grating at $G/(G+R) = 0$ or 1. In cases where a direct comparison of contrast sensitivity between luminance and chromatic motion was required, chromatic contrast was calculated in terms of L and M cone modulations. This was done using the luminance and CIE chromaticity co-ordinates of the red–green stimulus (x, y, Y) which are then converted to Judd modified CIE 1931 values (x', y', Y'). Calculated X', Y' and Z' values can be then be used in conjunction with cone fundamentals (e.g. Walraven, 1974; Smith & Pokorny, 1975; Vos, 1978) to obtain a value for cone excitation by each colour from which modulation can be calculated. This allows the expression of cone contrast as a percentage of luminance modulation. For the isoluminant chromatic stimulus, M cone contrast was calculated as 27% of luminance modulation and L cone contrast as 8%. A mean value of L and M cone contrast was then employed as a measure of chromatic contrast and used as a scaling factor to adjust chromatic response data, enabling a more appropriate comparison to be made with the luminance data.

3. Results

3.1. Motion onset responses as a function of $G/(G+R)$ ratio

The use of gratings of varying $G/(G+R)$ ratio offers the advantage of allowing a gradual and systematic transformation of the stimulus from achromatic to chromatic. Furthermore, the intermediate $G/(G+R)$ ratios generate stimuli containing a mixture of both chromatic and luminance contrast. Thus we can observe the effects of such transformations on the motion onset VEP.

Fig. 2A shows motion onset VEPs elicited by a 2 cycles s^{-1} stimulus as a function of $G/(G+R)$ ratio for six subjects. As has been described elsewhere (Gallichio & Andreassi, 1982; Göpfert et al., 1990; Kubova et al., 1995; Kuba & Kubova, 1992), the motion onset VEP for luminance motion ($G/(G+R)=0$ or 1) exhibits a triphasic positive–negative–positive (P1–N2–P2) complex with a prominent negativity occurring at around 200 ms (the N200 or N2 component). Fig. 2 (B–D) plots the latency variations of the P1, N2 and P2 components as a function of $G/(G+R)$ ratio. It can be seen that as the stimulus tends towards isoluminance ($G/(G+R)=0.45$), there is an increase in latency for the P1, N2 and P2 components of the motion onset VEP, which is highly significant $P<0.0001$ for all three components (repeated measures ANOVA). In addition to this increase in latency, the motion onset response also exhibits a reduction in amplitude at isoluminance (Fig. 2 E–G) which is only just significant for the n1–p1 ($P<0.05$) component, but highly significant for the p1–n2 and n2–p2 ($P<0.0001$) components. Consistent with the findings of Kubova et al. (1995); Spileers, Mangelschots, Maes, and Orban (1996) the earliest n1–p1 component was of small amplitude at this slow speed.

The notion that different mechanisms may subserve chromatic motion perception at fast and slow speeds raises the question as to whether the VEP exhibits any sign of this segregation. Fig. 3 shows the response variations as a function of $G/(G+R)$ for a 10 cycles s^{-1} stimulus. The most obvious difference between the VEPs generated by the faster and slower motion is that for the former a robust motion onset VEP is maintained at isoluminance. This is indicated in Fig. 3

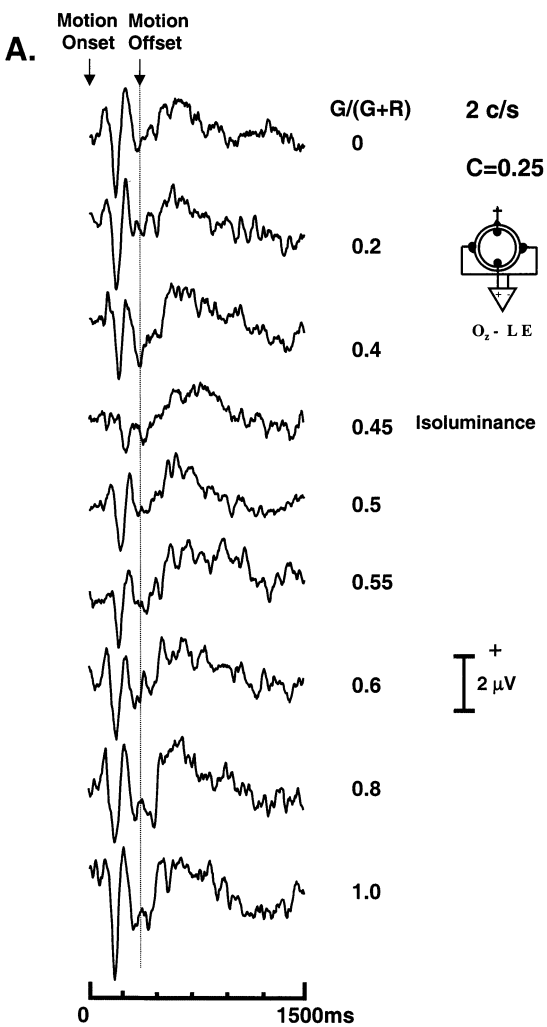
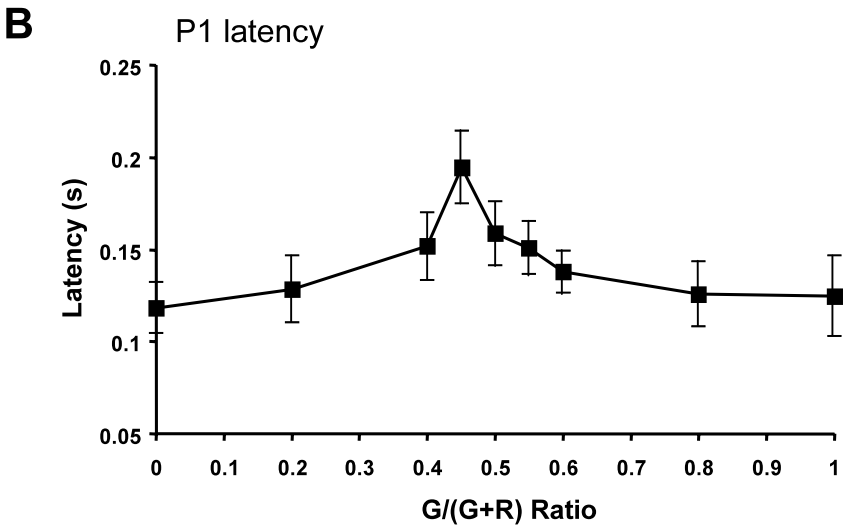
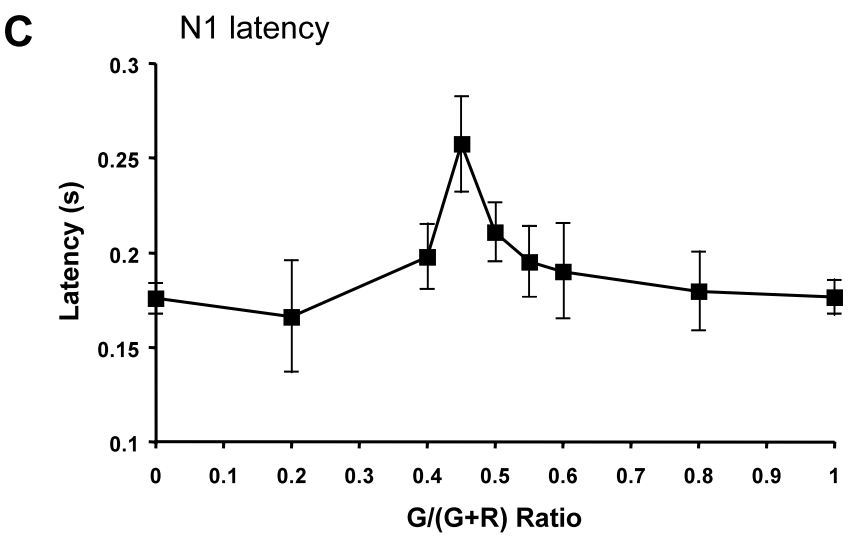
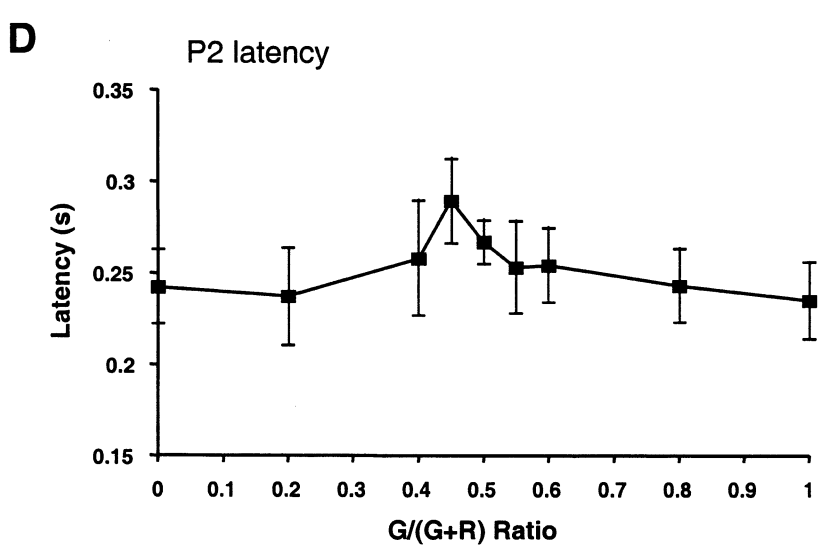


Fig. 2. (A) Group averaged ($n=6$) motion onset VEPs elicited as a function of $G/(G+R)$ ratio for a 2 cycles s^{-1} stimulus. Each trace is the average of at least 126 repetitions for each subject. At $G/(G+R)=0.45$ the stimulus is an isoluminant red/green grating, at values of 0 and 1 the stimulus contains only luminance modulation. The stimulus had a Michelson contrast of 0.25 and mean luminance = 40 cd m^{-2}. The responses were recorded from electrode position O_z referenced to linked ears. (B–D). Latency variation of the P1, N2 and P2 components as a function of $G/(G+R)$ ratio. (E–G). Amplitude variation of n1–p1, p1–n2 and n2–p2 components as a function of $G/(G+R)$ ratio. The data points represent the mean across subjects and the bars = ± 1 S.D.







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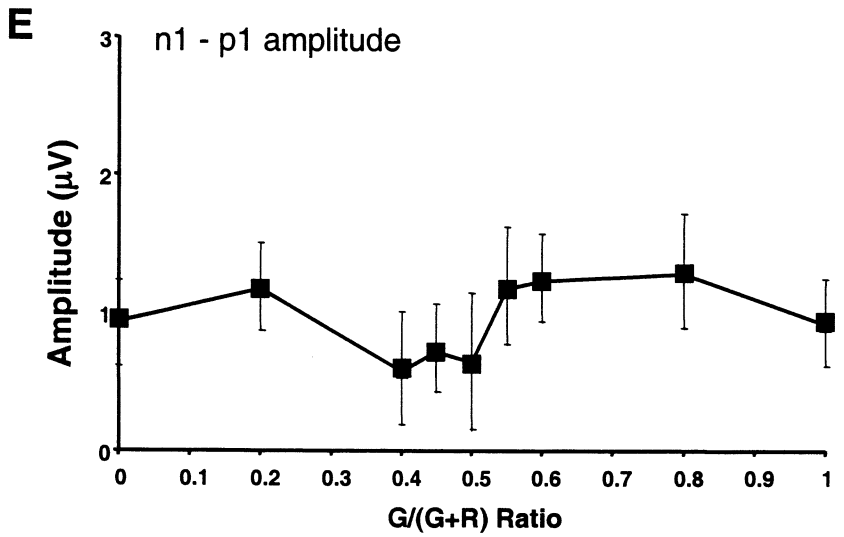
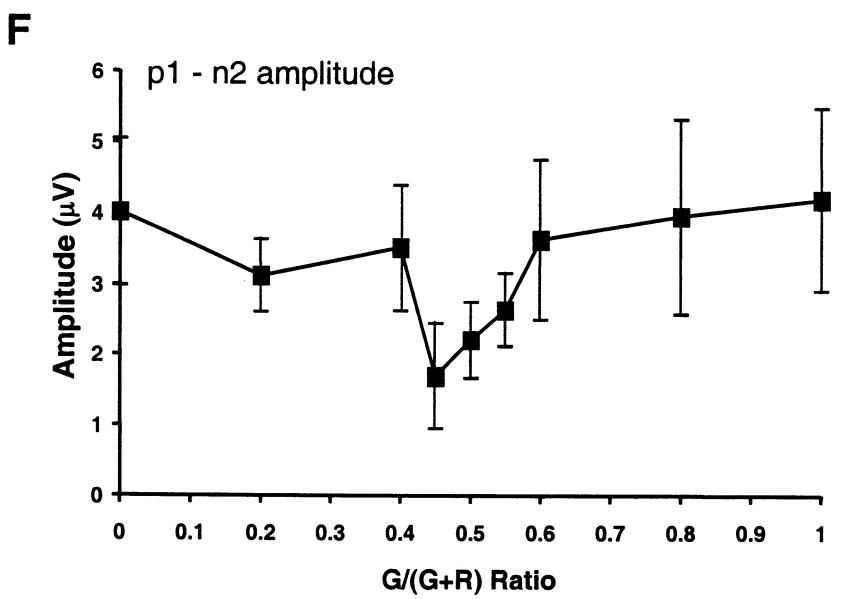




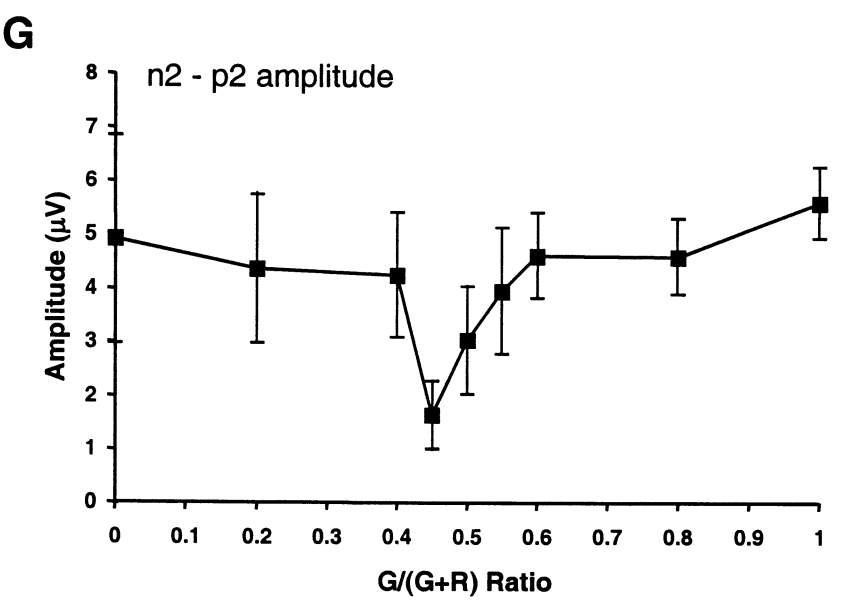


Fig. 2. (*Continued*)

(E–G) where the amplitude of the motion onset components are plotted as a function of $G/(G+R)$ ratio at this faster speed. Unlike for the 2 cycles s^{-1} data, there is no statistically significant amplitude minimum at isoluminance for the 10 cycles s^{-1} stimulus for the n1–p1, p1–n2 or n2–p2 components. However, response latency at this faster rate, as shown in Fig. 3(B–D), does increase significantly for all three components (P1, $P < 0.005$; N2, $P < 0.001$; P2, $P < 0.05$).

3.2. Contrast response functions of chromatic and luminance motion onset VEPs

The dependence of the luminance motion onset VEP upon contrast has been previously examined (Müller & Göpfert, 1988; Snowden et al., 1995; Kubova et al., 1995; Bach & Ullrich, 1997) and has been significant in the ascription of motion specificity to this response. In the next experiment the contrast dependence of the chromatic motion onset VEP was compared to that of the luminance response.

The group averaged ($n = 6$) motion onset VEPs for luminance and chromatic stimuli are plotted in Fig. 4 A–B, respectively. Fig. 5 plots the amplitude variation of the p1–n2 component as a function of contrast (n2–p2 was found to behave in a similar fashion and is not shown). Chromatic contrast in this instance is defined as equivalent to the Michelson contrast of the grating at $G/(G+R) = 0$ or 1. Consistent with earlier studies, the luminance motion VEP exhibits a saturating response function that reaches saturation around 10% contrast and can be fitted by a Naka–Rushton equation:

$$A = A_{\max} \frac{c^n}{c^n + c_{50}^n} \quad (1)$$

where: $A_{\max}$ = maximum VEP amplitude, c = contrast, c_{50} = contrast at which VEP amplitude reaches half maximum (Bach & Ullrich, 1997).

The behaviour of the chromatic motion onset response is different. Rather than being described by a saturating function, like its luminance counterpart, the

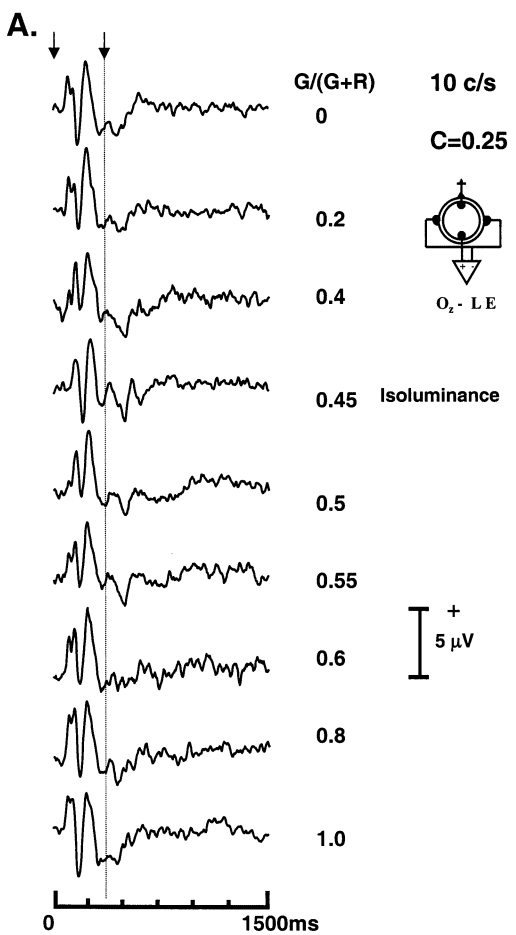
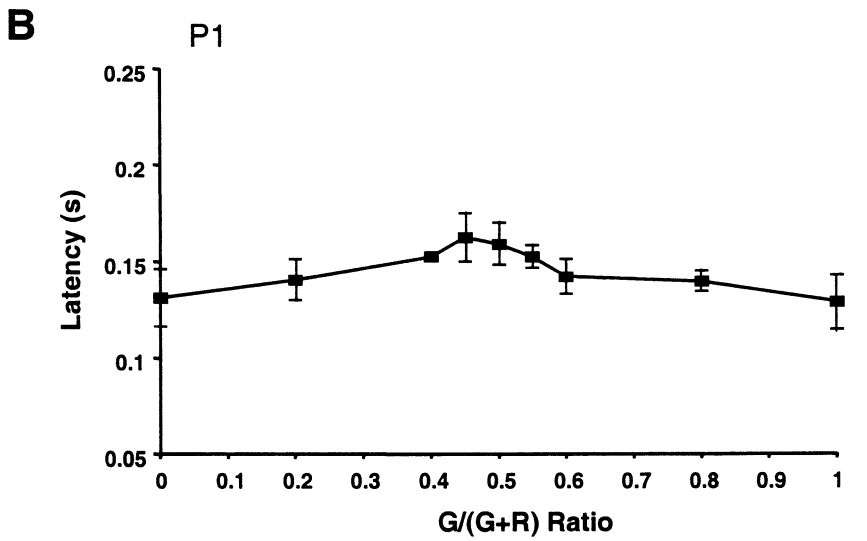
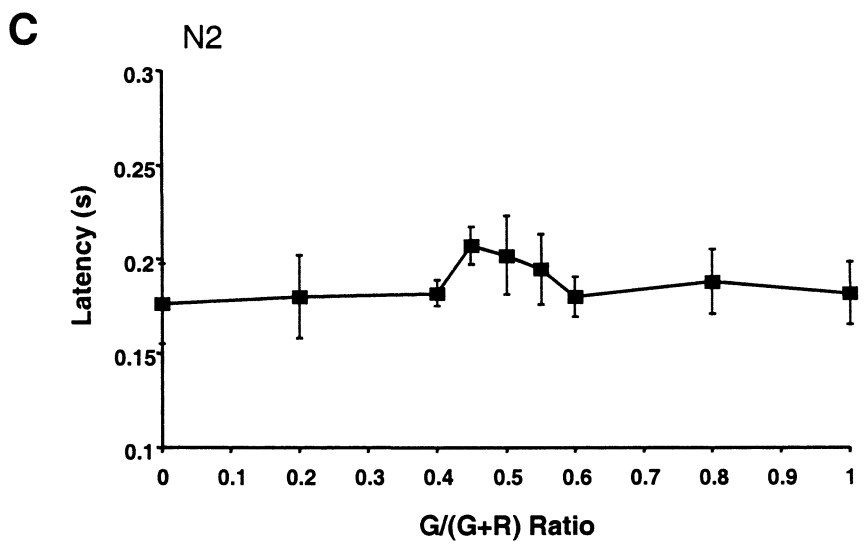
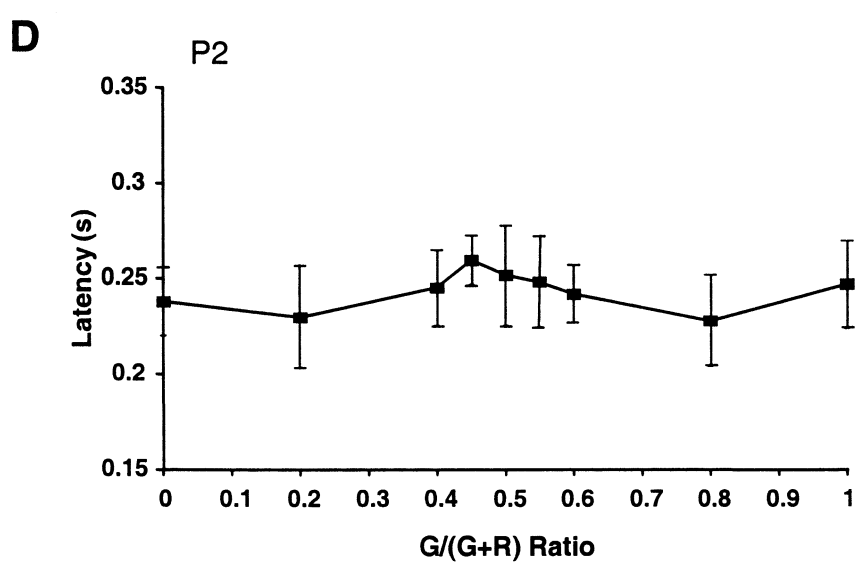


Fig. 3. (A) Group averaged ($n = 6$) motion onset VEPs elicited as a function of $G/(G+R)$ ratio for a 10 cycles s^{-1} stimulus. Stimulus and recording protocols are otherwise as for Fig. 2. (B–D) Latency of the P1, N2 and P2 components plotted as a function of $G/(G+R)$ ratio. (E–G) n1–p1, p1–n2 and n2–p2 amplitude plotted in a similar manner. Note that the vertical scale is different from that in Fig. 2A.







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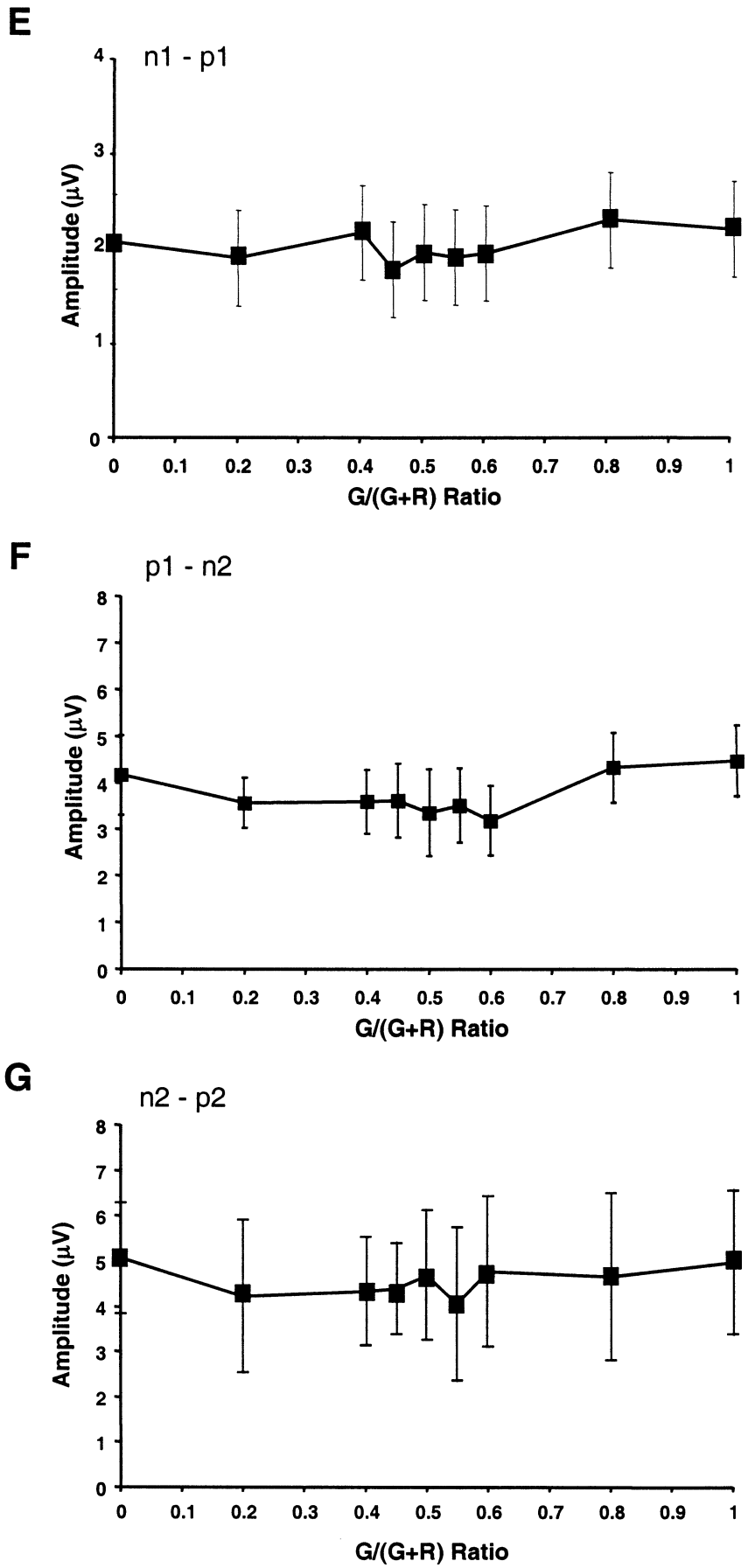

Fig. 3. (*Continued*)

chromatic motion VEP is well described by a linear function ($r = 0.89$; $P < 0.001$) when contrast is plotted on a logarithmic scale. Attempts to fit the achromatic data with a similar linear function produces a correlation co-efficient that is not significant ($r = 0.599$, $P > 0.05$).

Differences between the response behaviour of the fast (10 cycles s^{-1}) and slower (2 cycles s^{-1}) motion onset responses in the first experiment, prompted further examination of the contrast response characteristics at this faster speed. Fig. 6A–B) shows the luminance and chromatic VEP waveforms and Fig. 7A plots the p1–n2 amplitude variation as a function of contrast. The luminance motion onset VEP, like its counterpart at slower speed, exhibits a saturating contrast response function. The chromatic motion VEP however, unlike the slower chromatic response, can no longer be adequately described by a simple linear function (correlation analysis indicating a weaker and non-significant association ($r = 0.38$, $P = 0.31$)). In fact the chromatic response function now appears to be described better by a saturating Naka–Rushton function.

Fig. 7B shows the variation of n1–p1 amplitude as a function of contrast for the chromatic and luminance stimuli. This component appears to be more prominent at faster speeds, as has been noted in other studies (Kubova et al., 1995; Spileers et al., 1996), and the behaviour of the n1–p1 is quite different from the later p1–n2 component in the luminance motion VEP. Whilst the later component reaches saturation around contrast levels of 10%, the earlier n1–p1 amplitude exhibits little evidence of saturation below 70% contrast. This behaviour would appear to be consistent with the findings of Spileers et al. (1996) and the non-saturating nature of n1–p1 also appears similar to the prominent positive component recorded by Bach and Ullrich (1997) using an electrode at O_z referenced to a frontal electrode (Fpz). As a result of this less prominent saturation the luminance n1–p1 amplitude data, like the chromatic data, can be fitted with a linear function ($r = 0.92$; $P < 0.01$).

Fig. 8 shows the latency variations as a function of contrast for two of the components in the luminance and chromatic motion onset VEP. In order to obtain an estimate of contrast dependency of the components elicited by luminance and chromatic motion the approach of Burr, Fiorentini, and Morrone (1998), in their study of reaction times (RTs), was adopted. They

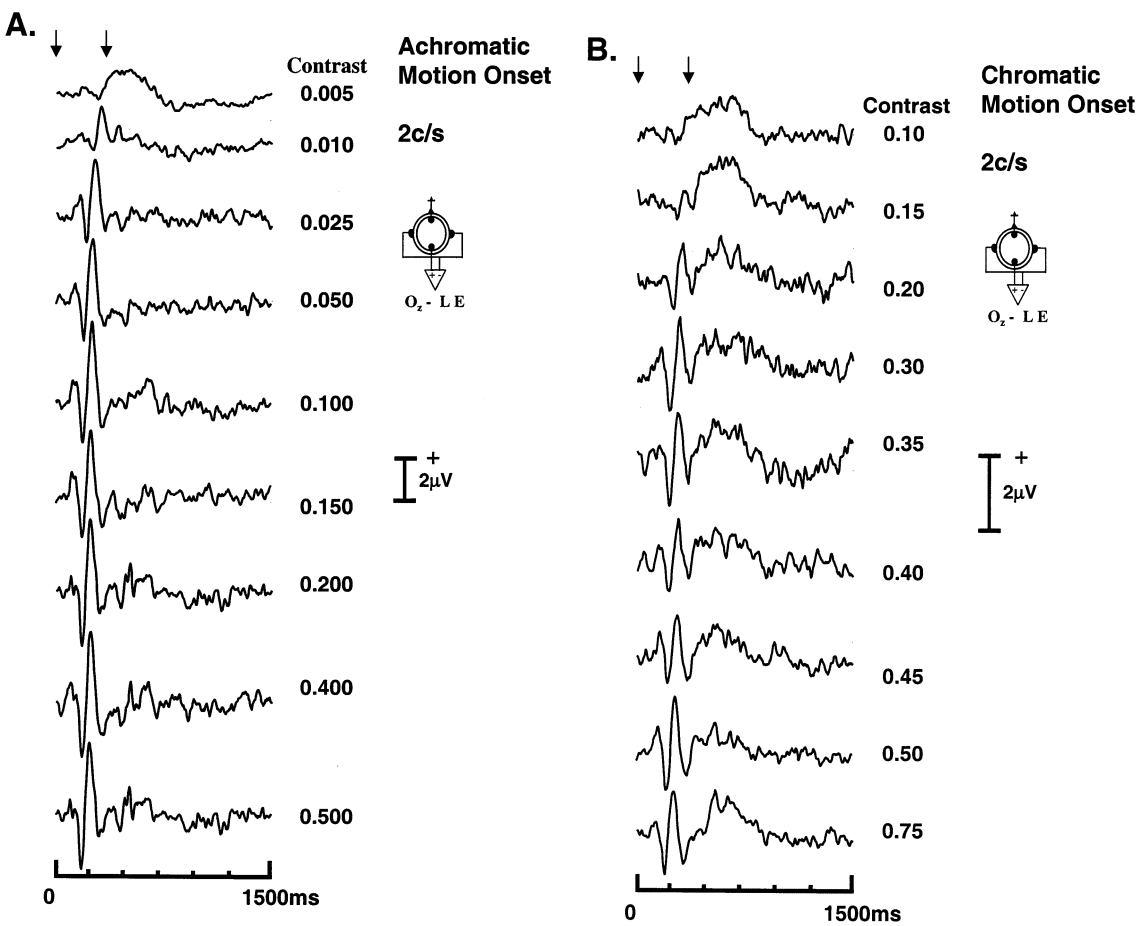

Fig. 4. Group averaged ($n = 6$) motion onset VEPs elicited by stimuli of increasing contrast at a speed of 2 cycles s^{-1}. Achromatic responses are shown in A) and chromatic in B). Contrast in this case is defined as Michelson contrast and mean luminance = 40 cd m^{-2}. Note that there are differences in vertical scale for the achromatic and chromatic reponses.

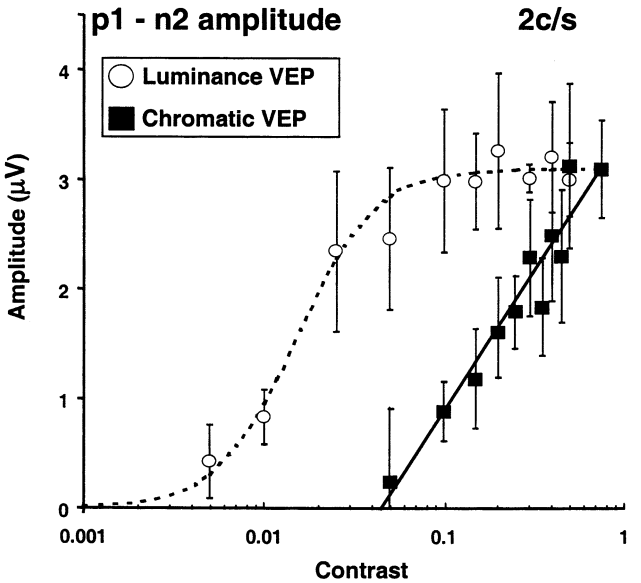

Fig. 5. Amplitude of the p1–n2 motion onset VEP component plotted as a function of contrast for a 2 cycles s^{-1} stimulus. The achromatic data (circles) have been fitted by a Naka–Rushton equation ($A = A_{max}\, c^n/(c^n + c_{50}^n)$) and the chromatic data (filled squares) by a linear regression line. The data points represent the mean across subjects and the bars = ± 1 S.D.

employed a modification of Piéron's equation to describe the effects of contrast on reaction times. This modification has the advantage of possessing only one parameter that determines slope, rather than two in the more traditional form of the Piéron equation, furthermore, it asymptotes to infinity at threshold (Burr et al., 1998). Obviously, in this instance the relationship to be examined is between VEP response latency and contrast rather than reaction time and the equation is given as:

$$L = \frac{\alpha}{\log(x/\tau)} + L_{\infty} \quad (2)$$

where: L = VEP latency, α = constant determining slope of curve (i.e. contrast dependency), x = contrast, τ = detection threshold, L_{∞} = latency asymptote. The data in Fig. 8 have been fitted with this type of equation and it can be seen that, similar to the RT data (Burr et al., 1998), it provides a good description of both the luminance and chromatic data at fast and slow presentation speeds for the components shown.

Fig. 9 plots the values for α, the contrast dependency, as a function of stimulus speed for the N2, P1 and P2 components of the chromatic and luminance motion onset VEPs. The general trend appears to be the same across all of these components. At 2 cycles s^{-1} there is considerable difference between the contrast dependency of the chromatic and luminance responses, $\alpha = 250$–300 ms log unit for colour but with lower values of between 50 and 60 ms log unit for luminance motion. However, at 10 cycles s^{-1} the differences between luminance and chromatic responses are less marked, with $\alpha = 40$–50 ms log unit for luminance and $\alpha = 60$–100 ms log unit for chromatic motion.

One of the key characteristics of the (luminance) motion onset VEP is that it exhibits high contrast sensitivity (Müller & Göpfert, 1988; Snowden et al., 1995; Kubova et al., 1995; Bach & Ullrich, 1997). The basic question is whether the chromatic motion onset VEP exhibits similar high contrast sensitivity. The answer is complicated by the fact that it depends upon how one chooses to define chromatic contrast. When chromatic contrast is defined simply in terms of the Michelson contrast of the constituent gratings which are added in antiphase, sensitivity to luminance motion is higher than for chromatic motion (Cavanagh & Anstis, 1991). However, when expressed in terms of a more physiologically meaningful metric, i.e. the modulation of cone excitation, it has been shown that the converse is true (Stromeyer, Cole, & Kronauer, 1987). Subsequent studies using the same metric have confirmed that chromatic motion sensitivity is higher for low temporal frequencies, but at high temporal frequencies sensitivity to luminance motion is greater (Derrington & Henning, 1993; Stromeyer, Kronauer, Ryu, Chaparro, & Eskew, 1995). Cone modulation has become a widely applied metric of chromatic contrast (see for example: Lennie & D'Zmura, 1988; Chaparro, Stromeyer, Huang, Kronauer, & Eskew, 1993). Therefore in Fig. 10A contrast response functions for motion onset VEPs show the chromatic response data now plotted in terms of chromatic contrast rather than Michelson contrast. The effect is that the chromatic data have undergone a simple linear transformation that shifts the function leftwards along the x-axis, thus equating cone with luminance modulation. The contrast response functions in Fig. 10 differ further from earlier figures in that the luminance data contains only points that occur before response saturation (contrast < 0.1). This is to enable the data to be fitted with regression lines which when extrapolated to zero amplitude give an estimate of contrast threshold. This technique would seem to be justifiable as Fig. 10 indicates that the threshold estimates obtained by VEP extrapolation agree closely with the psychophysically measured luminance and chromatic motion detection thresholds. The results (Fig. 10A) show that at slow speeds there is no significant difference between the VEP threshold estimates of contrast sensitivity for chromatic and luminance motion. However, when the results for 10 cycles s^{-1} are plotted in the same fashion (Fig. 10B), chromatic contrast sensitivity is shown to be lower than for luminance, consistent with psychophysical findings (Derrington & Henning, 1993).

4. Discussion

The basic aims of this study were twofold: firstly, to examine VEPs generated by chromatic isoluminant motion stimuli and then determine whether or not they could be classified as being motion specific, like their luminance counterparts. Secondly, to examine if there was any evidence for the type of segregation of motion processing proposed by Gegenfurtner and Hawken (1996). Support for this model would be revealed by differences in the response properties of luminance and chromatic motion VEPs at slow speeds, and by differences in response properties of slow and fast chromatic VEPs.

The major findings of this study are that at relatively slow speeds (≤ 2 cycles s^{-1}) chromatic, isoluminant motion generates VEPs of reduced amplitude and longer latency compared to those elicited by luminance motion. Furthermore, at slow speeds the amplitude of chromatic motion VEP shows a high degree of linearity as a function of log contrast, once above threshold. This differs from the saturating contrast response function exhibited by the luminance response. Measures of contrast dependency also indicate a difference between chromatic and luminance motion onset VEPs at slow speeds, with contrast dependency of the chromatic response being a factor of 5–6 times greater than that for luminance. At 10 cycles s^{-1} the response properties of the chromatic VEP differ from the chromatic response at slow speeds. The fast response is more robust at isoluminance and tends to have properties that are similar to its luminance motion counterpart. In particular it exhibits a saturating, rather than a linear, contrast response characteristic and has a contrast dependency that is only 1.6 times greater than the luminance motion onset VEP.

4.1. The motion-onset VEP and contrast

Two of the criteria for determining whether or not VEPs are generated by motion mechanisms rely upon the variation of the responses with contrast. Previous studies have demonstrated that luminance motion specific VEPs: (i) possess high contrast sensitivity; and (ii) exhibit a saturating response function (Snowden et al., 1995; Kubova et al., 1995; Bach & Ullrich, 1997). This study further confirms that the luminance motion onset VEP meets these criteria at both slow and fast speeds.

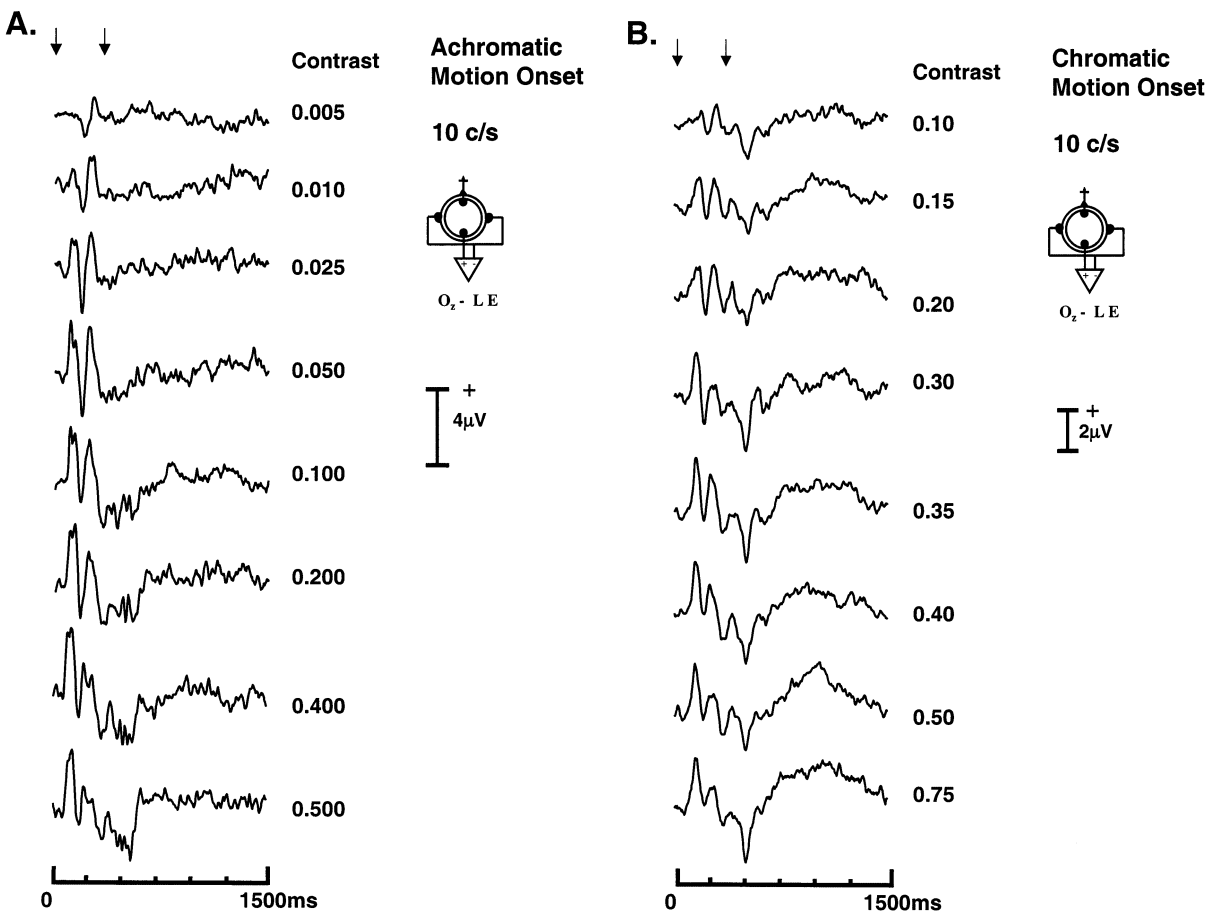

Fig. 6. Group averaged ($n = 5$) motion onset VEPs elicited by stimuli of increasing contrast at a speed of 10 cycles s^{-1}. Achromatic responses are shown in A) and chromatic in B). Mean luminance = 40 cd m^{-2}.

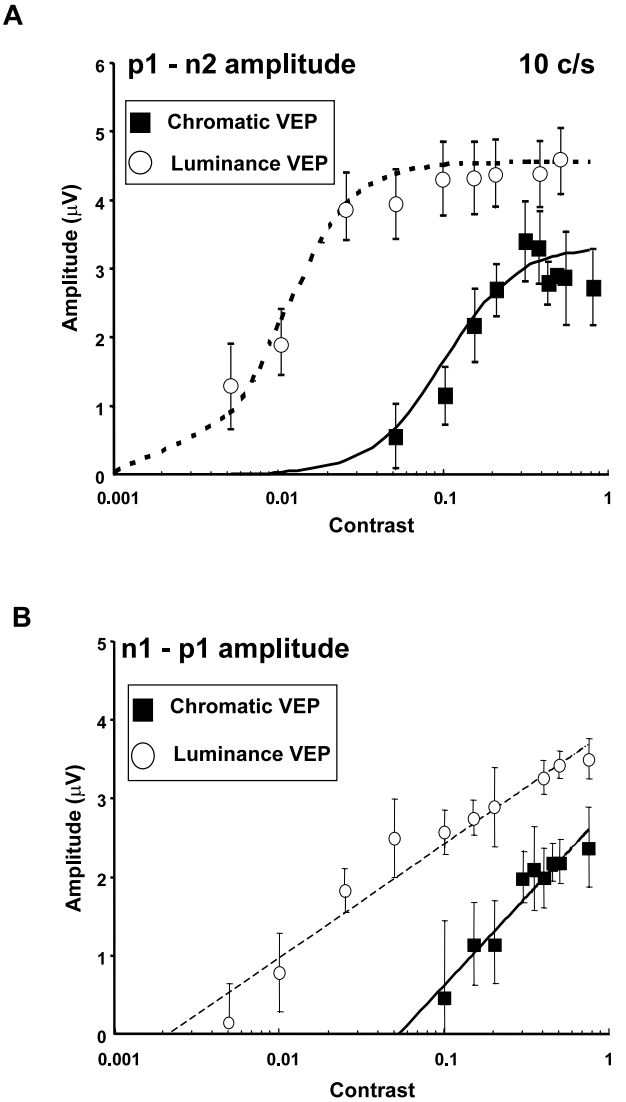

Fig. 7. (A). Amplitude of the p1–n2 motion onset VEP component plotted as a function of contrast for a 10 cycles s^{-1} stimulus. Both the achromatic (circles) and chromatic (filled squares) data have been fitted by Naka–Rushton functions. The data points represent the mean across subjects and the bars = ± 1 S.D. (B) Amplitude of the n1–p1 motion onset VEP component plotted as a function of contrast for the same stimulus. In this case the achromatic (circles) and chromatic (filled squares) data have been fitted by linear functions.

Such properties are in keeping with single-unit (Derrington & Lennie, 1984; Hawken & Parker, 1984; Blasdel & Fitzpatrick, 1984; Kaplan & Shapley, 1986; Sclar, Maunsell, & Lennie, 1990), fMRI (Tootell et al., 1995) and certain psychophysical studies (Nakayama & Silverman, 1985; McKee, Silverman, & Nakayama, 1986; Derrington & Goddard, 1989; Cropper, 1994). All these investigations confirm the idea of a motion system that is dominated by input from the magnocellular system, and as a result, possesses high contrast sensitivity and saturates with increasing contrast. This accounts for the suggestion that it is the neurons of the magnocellular system that form the physiological substrate of the luminance motion onset VEP (Kubova et al., 1995).

The main question is whether the chromatic motion onset VEP meets the criteria for motion specificity. In the case of contrast sensitivity, whether or not it can be described as higher or lower than achromatic contrast sensitivity, depends crucially upon how chromatic contrast is defined. In this instance, in order for a meaningful comparison to be made with luminance, chromatic contrast has been expressed in terms of cone modulation. Not surprisingly, as a result of this definition, the findings are consistent with those psychophysical studies that have used a similar metric (Derrington & Henning, 1993), in that chromatic motion sensitivity is as high as luminance sensitivity at low speeds, but is lower at faster temporal rates. This presumably is a result of the low pass nature of chromatic temporal processing and the band-pass nature of achromatic processing (De Lange, 1958; Regan & Tyler, 1971; Kelly, 1974). Comparisons of absolute sensitivity to luminance and chromatic stimuli are always going to be subject to how one chooses to define chromatic contrast. But the dichotomy that exists between luminance and chromatic responses, based upon differences in the their respective contrast dependencies and gain functions, is unaffected by the metric chosen to quantify chromatic contrast.

It could be argued that the reduced motion-onset VEP amplitude observed at isoluminance for slow speeds, is simply the result of reduced chromatic contrast. The visual system could, in effect, be treating an isoluminant chromatic grating in the same way as a low contrast luminance grating, rather than as an intrinsically different kind of stimulus (Troscianko & Fahle, 1988). However, other evidence tends to suggest that chromatic motion processing is not as straightforward as this. Cavanagh et al. (1984), for example, have shown that the addition of chromatic contrast to a luminance motion stimulus can reduce its perceived speed, as well as its ability to generate a motion aftereffect (Cavanagh & Favreau, 1985). Reductions in VEP amplitude have also been reported at isoluminance for S-cone isolating stimuli that have much higher chromatic contrast ($\approx 70\%$) than the stimuli employed in this study (McKeefry, 2001). Even if the effects upon the motion onset VEP at isoluminance for slow speeds could be explained purely in terms of a reduction in chromatic contrast, it fails to explain why there is not a similar diminution in the response for chromatic motion at fast speeds. One would need to resort to explaining these differences in terms of separate motion mechanisms operating at slow and fast speeds, the former in which chromatic contrast is an important means of coding and the latter in which it is not (see below).

A second criterion for motion specificity dictates that the chromatic motion VEP should exhibit a saturating response characteristic. However, the results from this study indicate a deviation away from this behaviour. At low speed the most obvious difference between the chromatic and luminance motion responses is that rather than exhibiting a saturating function, the amplitude of the chromatic VEP varies linearly with log contrast. Non-saturation, however, does not necessarily preclude contributions from motion mechanisms. Some motion tasks, such as induced motion effects (Raymond & Darcangelo, 1990) and the detection of coher-

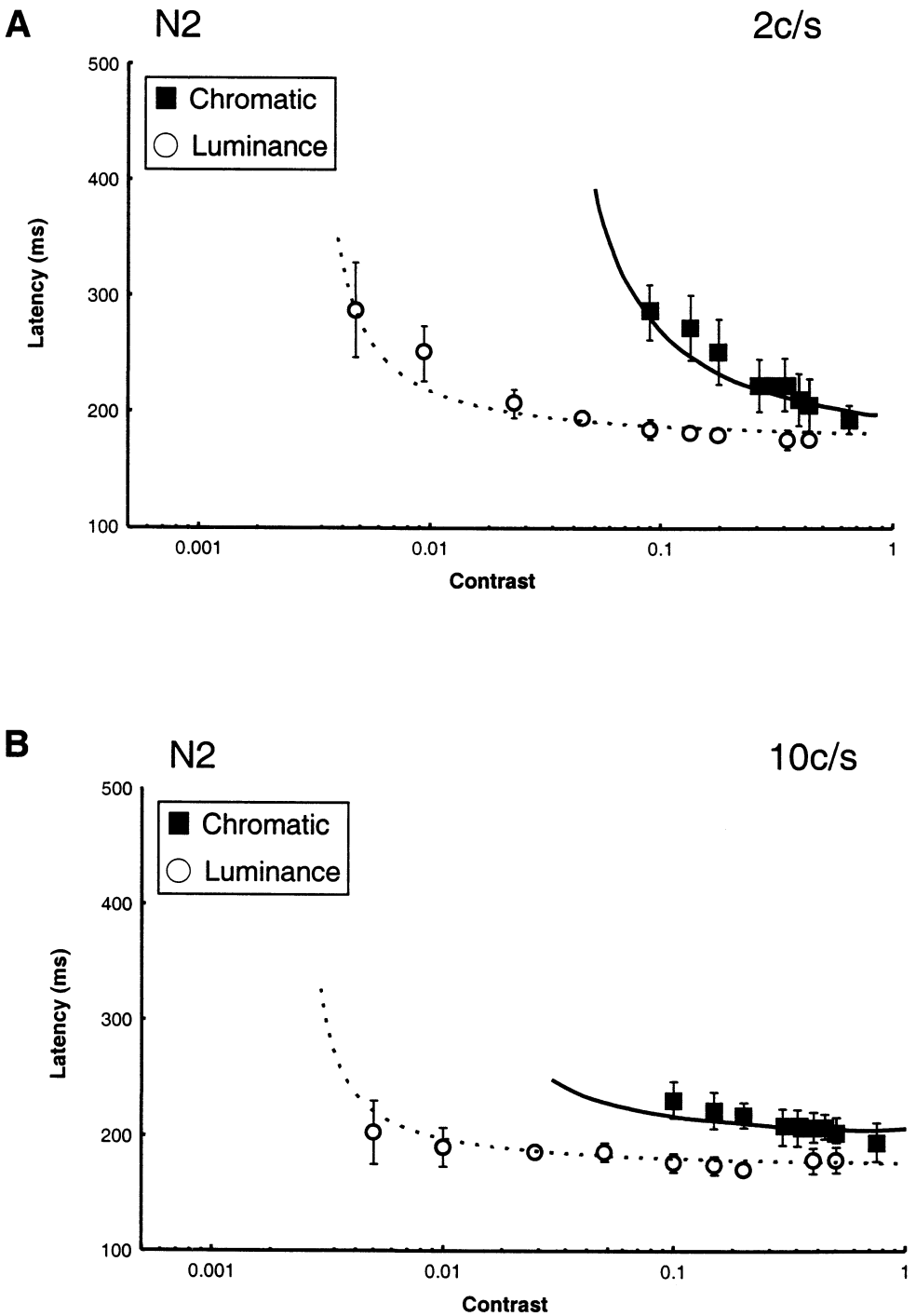

Fig. 8. Variation in latency as a function of contrast for motion onset VEP components N2 (A and B) and P1 (C and D) elicited by chromatic and luminance stimuli at speeds of 2 and 10 cycles s^{-1}. The data have been fitted by a modified Piéron equation: $L = \alpha/\log(x/\tau) + L_{\infty}$ (see text). The data points represent the mean across subjects and the bars = ± 1 S.D.

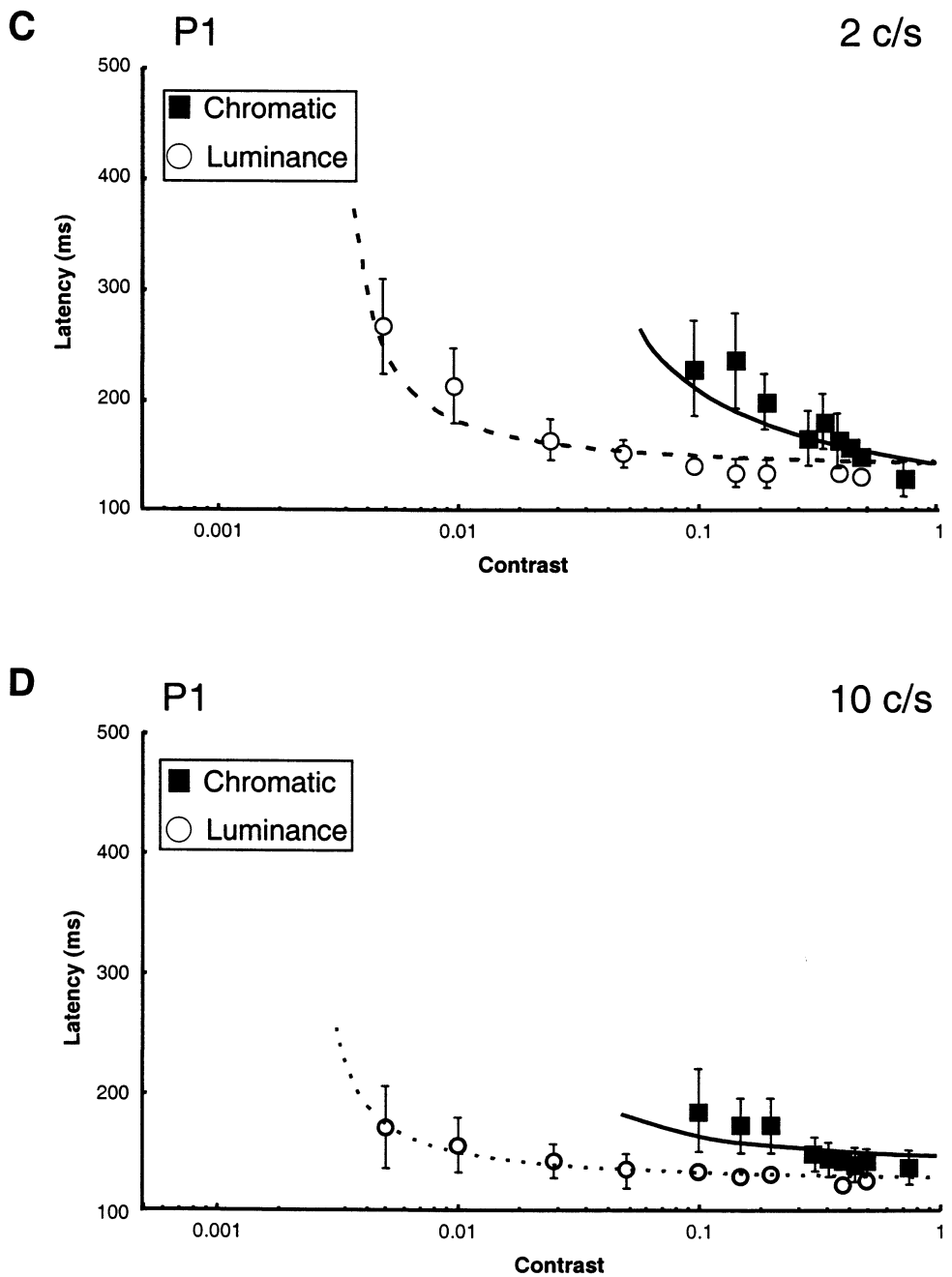

Fig. 8. (*Continued*)

ent motion (van de Grind, Koenderink, & van Doorn, 1987), for example, do not exhibit performance saturation. This led Raymond and Darcangelo (1990) to suggest that the parvocellular system was the likely physiological substrate for those tasks that did not exhibit saturation. Although Edwards, Badcock, and Nishida (1996) present an alternative view suggesting that, rather than being a property of any cells that perform local motion detection, saturation or non-saturation is actually a property of global motion detection. Nevertheless, the high degree of response linearity of the chromatic motion VEP over the contrast range tested is certainly reminiscent of that displayed by the parvocellular neurons recorded from the monkey retina by Kaplan and Shapley (1986). In the light of this similarity, and the known propensity of the parvocellular system to signal changes in colour (Schiller, Logothetis, & Charles, 1990), it is likely that the parvocellular system forms the neural substrate for the chromatic motion onset VEP at slow speeds. The traditional approach has been to explain chromatic motion detection in terms of the response properties of V5

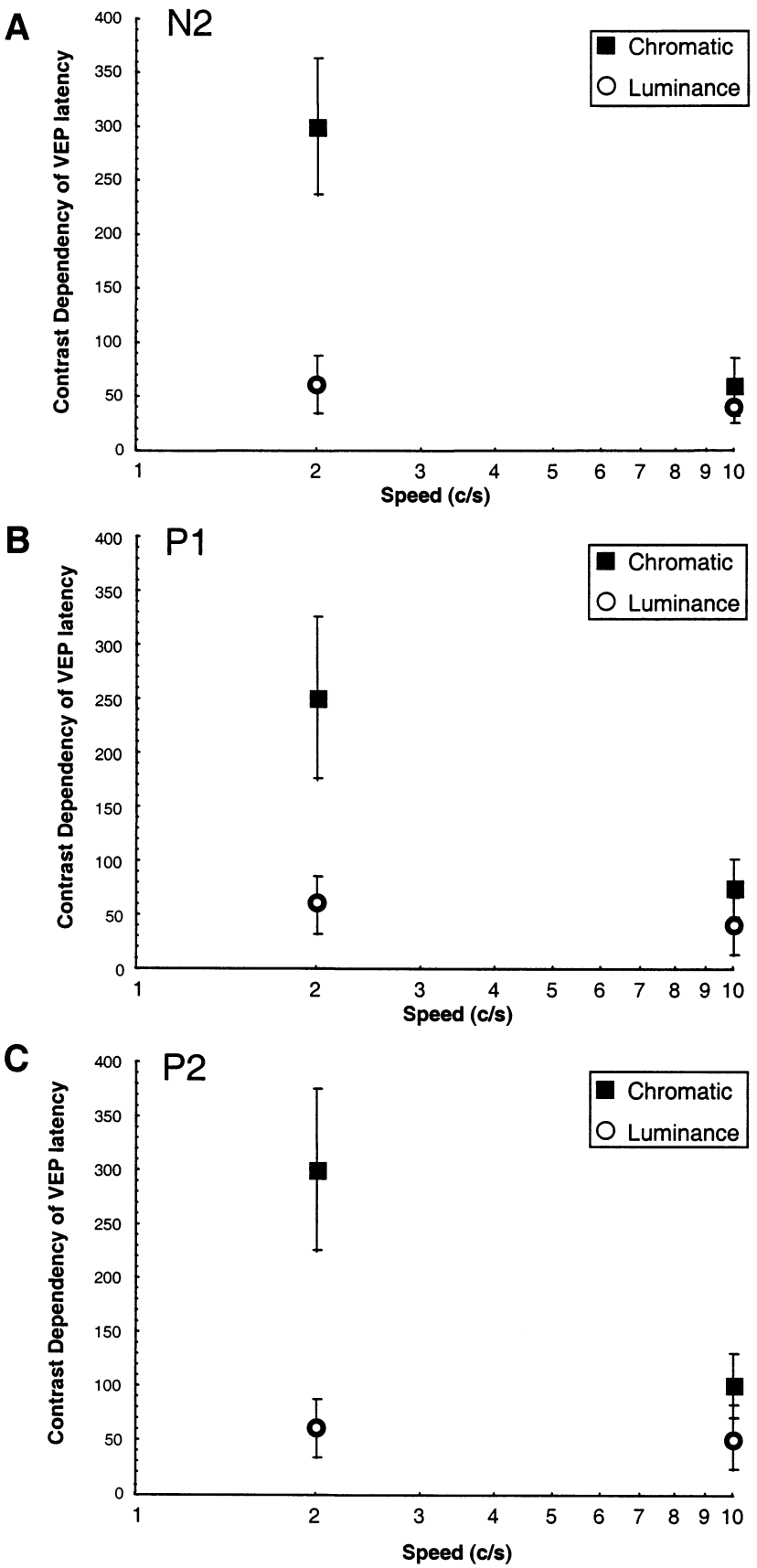

Fig. 9. Values of contrast dependency, α, for P1, N2 and P2 components as a function of speed for chromatic and luminance motion onset VEPs. The data points represent the mean across subjects and the bars = ± 1 S.D.

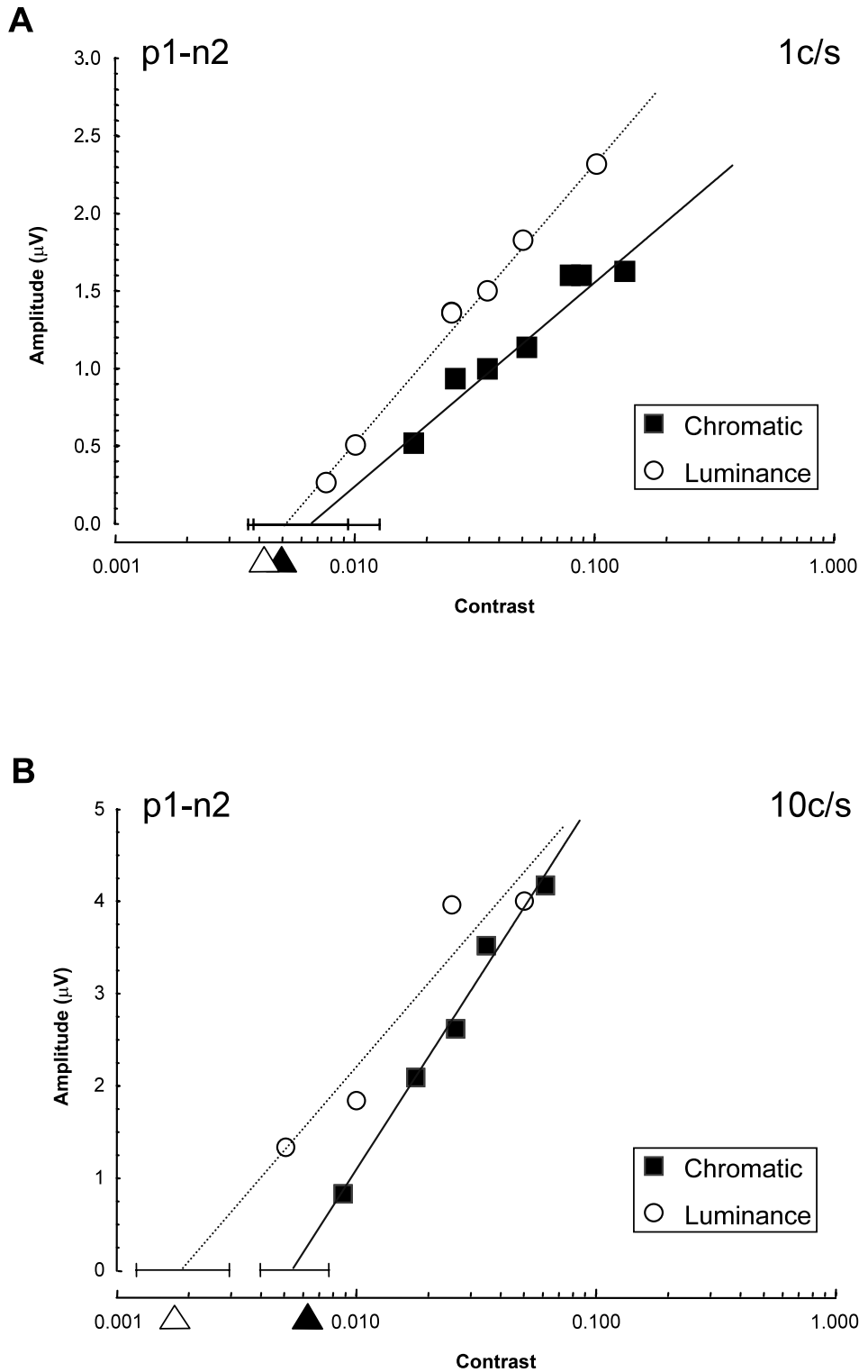

Fig. 10. Contrast response functions of the p1–n2 component for luminance and chromatic motion onset VEPs elicited by a stimulus of speed 1 cycles s^{-1} (A) and 10 cycles s^{-1} (B). Chromatic contrast in this instance has been calculated in terms of cone modulation (see text). Regression lines were fitted to the chromatic data (A: $r = 0.89$, $P = 0.006$; B: $r = 0.94$, $P = 0.016$) and to the pre-saturation luminance data points (A: $r = 0.89$, $P = 0.04$; B: $r = 0.86$, $P = 0.13$). These lines were extrapolated to zero amplitude in order to give an estimate thresholds (horizontal lines indicate 95% confidence intervals). Psychophysical measures of thresholds for chromatic (filled triangle) and luminance (empty triangle) motion detection are also shown.

(MT) neurons which have been shown to be responsive to moving isoluminant stimuli (Saito, Tanaka, Isono, Yasuda, & Mikami, 1989; Gegenfurtner, Kiper, Beusmans, Cardandini, & Zaidi, 1994; Dobkins & Albright, 1994). But the parvocellular system must play some part in signalling chromatic motion (Cropper & Derrington, 1996). Selective lesioning of the magnocellular pathway (Merigan, Byrne, & Maunsell, 1991) has shown that although motion detection thresholds may be raised, the perception of motion is not otherwise affected, implying that the parvocellular system must be able to support some form of motion analysis. In addition, Ferrera, Rudolph, and Maunsell (1994) have demonstrated that neurons in the parvocellular dominated infero-temporal visual pathway are capable of responding to motion, when it is important in object identification.

At high velocity the linear contrast response function of the chromatic motion VEP is replaced by a saturating function, which is similar to that observed for the luminance response. This change in response behaviour may be indicative of a shift in the underlying nature of the cellular substrate from linear parvocellular to non-linear magnocellular mechanisms. It is well known that the magnocellular system is quite capable of responding to isoluminant stimuli modulated at high temporal rates (Lee, Martin, & Valberg, 1989a,b) but that encoding of chromatic contrast occurs in an 'unsigned' (Dobkins & Albright, 1993) manner. This proposed change in the nature of the cellular substrate of the VEP is consistent with the idea (see Gegenfurtner & Hawken, 1996) of a veridical colour sensitive (i.e. signed) channel that operates at low stimulus speeds and a non-veridical colour insensitive (i.e. unsigned) channel that operates at high speeds. Furthermore, it also consistent with the more general hypothesis that the mediation of particular visual functions, by either parvo- or magno- cellular pathways, is dictated primarily by the spatio-temporal characteristics of the stimulus (Merigan, 1990).

4.2. Consistency with reaction times

VEPs, like the study of reaction times (RTs), allow the assessment of supra-threshold visual performance. Combined RT and VEP studies have been used in the past to compare chromatic and luminance spatial vision which have been shown to exhibit different contrast dependencies (Parry, Kulikowski, Murray, Kranda, & Ott, 1988). The properties of the luminance and chromatic motion, as revealed in this study by VEP latency variation, show similar differences and are highly consistent with the RT data of Burr et al. (1998). The main area of consistency lies in the fact that there is a stronger contrast dependency for VEPs and RTs to chromatic stimuli than for VEPs and RTs to luminance stimuli, especially at slow speeds. In addition, the differences between luminance and chromatic VEPs and RTs become less marked under conditions of high contrast and high speed. This divergence in the response properties of the chromatic and luminance motion VEPs at low speed and convergence at high, and the consistency with RTs, further validates the notion that different mechanisms operate for the perception of chromatic motion at fast and slow speeds (Gegenfurtner & Hawken, 1996).

4.3. Comparisons with other motion VEP studies

A key objective of this study has been to elicit motion onset VEPs from a branch of the motion system that supposedly possesses chromatic sensitivity. In order to do this, stimulus parameters have been adopted from spatio-chromatic VEP studies which have shown that chromatically selective responses, with minimum involvement from luminance mechanisms, can be obtained as long as stimulus parameters are carefully chosen (Kulikowski et al., 1996, 1997). Based upon this empirical evidence isoluminant grating stimuli have to be limited in their spatial extent in order to minimise luminance intrusions caused by changes in isoluminance with retinal eccentricity and by chromatic aberrations. In the motion domain, however, certain studies have advocated the use of large (35°) stimuli (Kubova et al., 1995) as being optimal for motion onset VEPs. But to ensure isoluminance across such an extensive stimulus would be difficult. Thus, it would appear that at first glance the demands of optimising both colour and motion responses are mutually exclusive; maximising the response from one modality would lead to a reduction in the selectivity of the responses from the other. So there has to be some form of compromise in balancing the requirements of the two modalities. Smaller motion stimuli have been used in other studies (e.g. Clarke, 1973), indeed stimuli as small as 4.2° have been used successfully in motion VEP experiments (Müller et al., 1990). It is also worth noting that Göpfert et al. (1990) have shown that the size of the stimulating field may not be critical for eliciting motion VEPs beyond 1° in central vision. Therefore, in the light of these findings, the use of a 7° stimulus in this study should not compromise the motion response to a severe degree, whilst maintaining optimum conditions for colour.

As well as different field sizes, previously published motion VEP studies have utilised a wide variety of stimuli ranging from noise patterns (Clarke, 1973; Spileers et al., 1996;Odom et al., 1999), random dot patterns (Snowden et al., 1995; Hoffmann et al., 1999), checkerboards (Tyler & Kaitz, 1977; Kubova et al., 1995) to square and sinusoidally modulated gratings (Müller et al., 1990; Bach & Ullrich, 1994, 1997). In spite of this varied array of stimuli the elicited re-

sponses exhibit a remarkable degree of consistency, with a characteristic P1–N2–P2 triphasic response being obtained in most cases. However, the relative predominance of the constituent components tend to vary, for example, as a function of stimulus speed as well as electrode placement. In the case of the latter, the N2 component in particular appears to be most prominent when the electrodes are placed over the lateral occipital cortex, rather than the more centrally placed O_z electrode (Kubova et al., 1995; Bach & Ullrich). This presumably is the result of the closer proximity of the lateral electrodes to the motion processing area of the human brain, V5, which is found nearby (Watson, Myers, Frackowiak, Hajnal, Woods, Mazziotta, Shipp, & Zeki, 1993). Further experimentation will be required in order to ascertain whether the N2 component of the chromatic motion onset VEP follows a similar pattern to its luminance counterpart. The fact that the processing of colour information takes place along the ventral occipito-temporal cortex in the human cortex (McKeefry & Zeki, 1997), would lead to the prediction that there may be a difference in behaviour between the chromatic and luminance N2 component as a function of lateral electrode placement. On the other hand, recent experiments have revealed that human V5 is capable of processing information about moving isoluminant colour stimuli (Dougherty, Press, & Wandell, 1999; Wandell, Poirson, Newsome, Baseler, Boynton, Huk, Gandhi, & Sharpe, 1999). This would imply that chromatic and luminance N2 should behave in a similar fashion as a function of lateral placement.

5. Conclusions

This study has established that motion specific VEPs can be elicited by moving isoluminant red/green stimuli. VEPs elicited by luminance and chromatic motion stimuli at low speeds have different response characteristics. Luminance motion VEPs saturate at low contrasts, whilst chromatic motion VEPs increase in a linear fashion, chromatic responses also have a higher contrast dependency. These differences imply that there are separate channels for the mediation of colour and luminance motion, with the parvocellular and magnocellular systems, respectively, being the likely physiological substrates. At faster speeds the nature of the chromatic motion VEP changes and becomes more like the luminance response, it exhibits a saturating contrast response characteristic and its contrast dependency is not very different from that for luminance. These shifts in response properties represent changes in the properties of the neural substrate of the VEP and may be indicative of a shift away from parvocellular to magnocellular involvement, the neurons of which are known to be responsive to rapidly changing isoluminant stimuli.

The differences in the properties of VEPs elicited by luminance and chromatic motion stimuli at fast and slow rates are consistent with ideas about the motion system comprising of two systems: one for fast motion that is responsive to both colour and luminance, but which does not encode chromaticity. The other for slow motion that has separate luminance and colour inputs.

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