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Is the S-opponent chromatic sub-system sluggish?

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Abstract

The S-opponent pathway has a reputation for being sluggish relative to the L/M-opponent pathway. Cottaris and De Valois [Nature 395 (1998) 896] claim that S-opponent signals are available in Macaque V1 only after 96–135 ms whereas L/M-opponent signals are available after 68–95 ms. Our experiments tested whether this large latency difference could be observed psychophysically. We measured reaction times to S/(L + M) and L/(L + M) increments. Both the equiluminant plane and the tritan line were empirically determined and we used spatio-temporal luminance noise to mask luminance cues. An adaptive staircase progressed according to observers' performance on a 'go, no-go' task and provided concomitant estimates of threshold and of reaction time. When brief stimuli are confined to chromatic channels and presented at equivalent (threshold) levels and when latency is estimated from visually triggered reaction times, we find that the difference between the L/M-opponent and S-opponent sub-systems is, at most, 20–30 ms.

1. Introduction

To make discriminations based on colour, the outputs of different classes of cone must be compared. Early in the human visual system the signals from the three cone-classes are thought to be re-coded into post-receptoral channels that make these comparisons explicit. One chromatic channel compares signals from long-wavelength sensitive (L-) cones with signals from middle-wavelength sensitive (M-) cones, and the other compares signals from short-wavelength sensitive (S-) cones with some combination of signals from M- and L-cones. The two chromatic channels are thought to have evolved at different times and for different purposes and their substrates remain anatomically, morphologically and immunologically distinct (see Mollon, 2002 for review). It has often been suggested that the phylogenetically ancient S-opponent system has a long response latency compared to the L/M-opponent system. For example, Cottaris and De Valois (1998), recording from cortical area V1 in the Macaque, found that S-opponent signals were available only after 96–135 ms, whereas L/M-opponent signals were available after 68–95 ms. Here we test whether this large difference can be observed in visually triggered reaction times.

There certainly are asymmetries between the S-cones and the L- and M-cones. The S-cones are much rarer, fewer than 10% of all cones (Dartnall, Bowmaker, & Mollon, 1983), and are absent from the central foveola where our acuity is highest (Bumsted & Hendrickson, 1999; Williams, MacLeod, & Hayhoe, 1981). The S-cone signal is thought to be carried initially by a special class of bipolar cell that connects exclusively to two or three S-cones. Recently Dacey and colleagues have presented evidence that this S-cone bipolar supplies a whole family of chromatically opponent S-cone pathways that

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project in parallel to the LGN. In addition to the small bistratified ganglion cell-type (Dacey & Lee, 1994), a sparse monostratified ganglion cell-type is thought to carry an S-OFF signal (sign-inverted from the S-cone bipolar), and a large field bistratified cell-type gives a blue-ON type light response (Dacey, Peterson, & Robinson, 2002; Dacey, Peterson, Robinson, & Gamlin, 2003). Beyond the retina, the S-cone pathway is thought to remain morphologically distinct. The exact projections of the large field bistratified and the sparse monostratified ganglion cells are as yet unknown, but the small bistratified ganglion cells project not to the main parvocellular layers (as traditionally thought) but to the so-called interlaminar or koniocellular zones, K3 and K4 (see Hendry & Reid, 2000 for review). Parvocellular layers project to layer 4Cβ of primary visual cortex, and from there to the 'blobs' in layers 2 and 3. In contrast, koniocellular zones K3 and K4 exhibit a direct projection to layers 2 and 3 (Hendry & Yoshioka, 1994). The blobs contain cells that are selective for colour but not for orientation. Moreover, Ts'O and Gilbert (1988) report that a subset of blobs, about 1 in 4 of them, are selective for colours defined only by a change in the ratio of S to (L + M), at constant ratios of L to M.

So where in the visual pathways might the alleged sluggishness of the S-opponent system arise? The first candidates are the receptors themselves. Schnapf, Nunn, Meister, and Baylor (1990) made direct measurements of the membrane-current of outer segments projecting from small pieces of Macaque retina. Only three S-cones were studied in detail, but their kinetics and sensitivity were roughly comparable to those of the L- and M-cones.

Using silent substitution, Yeh, Lee, and Kremers (1995) measured the temporal characteristics of signals from the three cone-types at the ganglion cell level. They found similar temporal modulation transfer functions for +L − M, +M − L, and +S−(L + M) cells, for both excitatory and inhibitory cone inputs. Recording from S-opponent ganglion cells, Chichilnisky and Baylor (1999) found that the time-courses of blue-ON and yellow-OFF signals were similar, but that the time-to-peak of the blue component of the response was approximately 10–20 ms shorter than that of the red and green components. They argue that the poor temporal resolution of the S-cone system (Brindley, Du Croz, & Rushton, 1966; Wisowaty & Boynton, 1980) does not reflect sluggish responses of S-cones, or differential retinal filtering of S-cone signals, but that the yellow-OFF signals in S-opponent cells are delayed relative to blue-ON signals.

There is some controversy over the temporal response of the koniocellular division of the retinogeniculate pathway. Solomon, White, and Martin (1999), though unable to rule out the presence of sluggish, poorly responsive cells within the koniocellular population (see also Irvin, Norton, Sesma, & Casagrande, 1986), show that the temporal contrast sensitivity characteristics of cells in the koniocellular layers of the LGN are intermediate between those of magnocellular and parvocellular cells. However, conduction velocity is proportional to axon diameter and, in so far as axon diameter reflects soma size, transmission from the koniocellular layers might provide a modern explanation for the delay that Cottaris and De Valois (1998) report in the arrival of the S-cone signal at the cortex.

Psychophysical correlates of the sluggishness of the S-cone pathway have a long established history. Stromeyer (1887) states "our perception of colour is slower for the blue and violet rays than for the green, yellow and red ones". But how does this difference relate to the underlying physiological mechanisms mediating our perception of these lights? Our understanding of human colour vision has evolved significantly since Stromeyer's statement, and so have studies concerning the influence of colour on reaction time. McKeefry, Parry, and Murray (2003b) provide a useful review of this parallel evolution.

In the current study, we used measurements of simple reaction time to test for a latency difference between psychophysical correlates of the two chromatic pathways. We have paid particular attention to the exclusion of magnocellular or luminance signals that may accompany transient stimuli, and to the isolation of an individual observer's tritan line (the line in colour space that modulates only the S-opponent system). Our method also provides concomitant estimates of reaction time and threshold, so that a direct comparison can be made between reaction times to equivalent (threshold) stimuli in the two sub-systems of colour vision.

1.1. Eliminating luminance cues

It is not straightforward to create brief stimuli that are visible only to chromatic channels, and indeed the determination of the latency of chromatic pathways has been plagued by luminance signals accompanying the chromatic target (McKeefry et al., 2003b; Mollon, 1980).

Physical luminance artefacts may occur when a temporal transition is made from one chromaticity to another. For example, Vingrys and King-Smith (1986) have described how differences between the time constants of phosphors of a CRT display may lead to a detectable change in luminance when a temporal substitution is made between nominally equiluminant stimuli. Moreover, Lee, Martin, and Valberg (1989) have shown that equiluminant modulation can generate a frequency-doubled response in phasic ganglion cells in the Macaque retina, although the response is absent if the modulation is along a tritan line. McKeefry, Murray, and Kulikowski (2001) claim that this asymmetry is the basis of the L/M advantage in psychophysical meas-

ures of temporal and spatial sensitivity, and by compensating for transient contributions to L/M sensitivity they show that the two chromatic sub-systems are equally sensitive.

While L- and M-cone signals have access to a variety of post-receptoral channels, S-cone signals are commonly thought to be intrinsically confined to chromatic pathways (see Martin, 1998 for review). However, recent electrophysiological evidence suggests a small (10%) but consistent S-cone input to magnocellular neurons in Macaque LGN (Chatterjee & Callaway, 2002, though see Dacey & Lee, 1994 for a counter view). Stockman, MacLeod, and Lebrun (1993) have shown that, under extreme L- and M-cone adaptation, rapid S-cone flicker can produce visible beats if superimposed on L- or M-cone flicker. Under these conditions, they suggest that the S-cone signal is transmitted by a "luminance" pathway and the magnocellular pathway is a possible, though controversial, candidate.

In the present study we wished to compare the transmission of signals within chromatic pathways. Subjects made settings of subjective equiluminance using the minimum-motion technique (Cavanagh, MacLeod, & Anstis, 1987), but rather than trying to eliminate all luminance signals we used spatial (Regan, Reffin, & Mollon, 1994; Stilling, 1877) and temporal (Birch, Barbur, & Harlow, 1992; Mollon, 1982) luminance noise to render luminance an unreliable cue.

1.2. Separating chromatic sub-systems

If we are to demonstrate a difference between the two opponent channels, we must ensure that they are isolated by our stimuli: any L/M-opponent contamination of our S-opponent stimuli would dilute any differences we might be able to measure. However, the physical lights required to isolate one of the colour-opponent mechanisms depend not only on the spectral sensitivity of the photoreceptors, but also on spectrally selective prereceptoral filtering. Spectral transmission properties of the lens vary with age (Pokorny, Smith, & Lutze, 1987) and there are large variations in the normal population in the amount and distribution of macular pigment (Hammond, Wooten, & Snodderly, 1997; Moreland & Bhatt, 1984). A pair of physical lights distinguishable only by the S-opponent channel of one observer may offer detectable modulation to the L/M-opponent channel of a second observer. Moreover, the amount of macular pigment varies with eccentricity, peaking at the fovea and falling off towards 3° eccentricity. So, no stimulus can be perfectly tritan across the whole retina. In the experiments reported here, we chose to present our chromatic stimuli beyond 3° eccentricity in order to use an area of retina that is relatively homogeneous for short-wave cones and for macular pigment. As a preliminary to gathering reaction time measurements we used transient tritanopia to locate the tritan line for each observer (Smithson, Sumner, & Mollon, 2003). The spatial configuration of the stimuli was identical for the transient tritanopia measurements and for the reaction time measurements.

1.3. Equating stimuli across different sub-systems

A further challenge in studies of this kind is to equate stimuli in different channels. The approach adopted here is that taken by Mollon and Krauskopf (1973). A physically punctate stimulus will elicit a response in the visual system that is temporally and spatially dispersed. So, when using psychophysical measures to compare sensory latencies, it is important to fix the element of neural response that is to be compared. Mollon and Krauskopf suggest that a brief stimulus of liminal intensity generates a slow, graded response at an early stage in the visual system and that, if and when a threshold amplitude is reached, subsequent neural events are triggered ballistically. A psychophysical difference in reaction times to liminal stimuli could reflect a difference in time constants at receptoral or post-receptoral stages, or a difference in transmission time of the pathway that carries the chromatic signal. We explicitly assume that central and motor response stages are equivalent for different stimuli. We used a staircase procedure that gave concurrent estimates of threshold and reaction time.

In the experiments reported here, we compare reaction time distributions obtained in response to liminal S-opponent increments with those obtained in response to liminal L/M-opponent increments. We use spatio-temporal luminance noise to ensure that our L/M-opponent stimuli are not detected via magnocellular pathways. In control conditions we set the luminance noise contrast to zero. We additionally measure reaction times to luminance increments with and without luminance noise.

2. Methods

2.1. Apparatus and calibration

Stimuli were presented on a Sony Multiscan colour monitor (17se II), running at a frame rate of 100 Hz and controlled from the host PC via a Cambridge Research Systems (CRS) graphics board (VSG 2/3). The monitor was gamma corrected using the CRS OptiCAL system. The MacLeod–Boynton chromaticity coordinates of each of the phosphors were derived from spectral radiance measurements of the phosphor (obtained with a Photo Research PR-650 SpectraScan spectroradiometer) multiplied by the Smith and Pokorny cone fundamentals (Smith & Pokorny, 1975). Gun weightings for chromaticities defined in MacLeod–Boynton space were then calculated via the rules of colour mixture.

The final calibration was checked with the PR-650 spectroradiometer.

2.2. Stimuli

Our chromatic stimuli were embedded in spatial luminance noise. As in pseudoisochromatic plates, the stimulus area was broken down into many small circular discs and we varied the luminance of the individual discs: each disc was randomly assigned a luminance between ±7 cd/m^2 (for tritan line estimation) or ±3 cd/m^2 (for reaction time measurements) of the average luminance of 22.5 cd/m^2. The initial chromaticity of the individual discs of the array was that of equal energy white, and they were set within a uniform field of the same chromaticity. For the target stimulus, a subset of discs was changed to the required chromaticity. The target Gestalt was defined as a subset of elements falling within one quarter of an annulus, and could appear in one of four quadrants (see the central frame of Fig. 1). By presenting the target in one of four possible locations arranged symmetrically around a central fixation marker, we discourage the observer from altering fixation and forcing the probe stimuli off the tritan line. At the viewing distance of 1 m, the width of the chromatic arc was 1.55° of visual angle and the inner radius of the arc was 3°.

2.3. Stage one: finding the tritan line

Before running the main reaction time experiment, we determined the tritan line for each observer. The aim here was to identify the chromaticity vector that exhibits the largest loss of sensitivity under conditions of transient tritanopia (Smithson et al., 2003). Ten test vectors were chosen spanning a range that covered both sides of the theoretical tritan axis, from 312° to 54° in MacLeod–Boynton space. Observers were first required to view a spatially uniform yellow adapting field ($r = 0.67$, $b = 0.0028$, 60 cd/m^2) for 2 min, and then the trial sequence began. After each top-up adaptation period, the display changed abruptly to equal energy white (22.5 cd/m^2), and after 400 ms the chromatic probe stimulus was presented, for 4 frames only (at a frame rate of 100 Hz). In order to maintain the observer's adaptive state, the duty cycle was fixed, with 7.25 s adaptation every 8 s. The observer's task was to locate the coloured target by pressing one of four buttons, and the

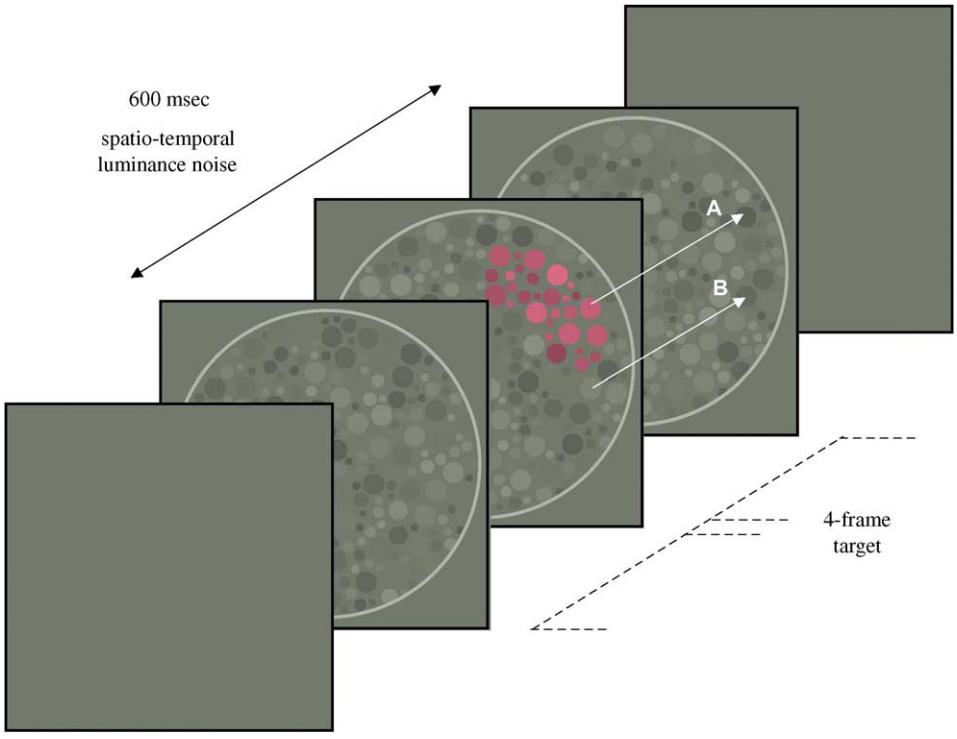

Fig. 1. A schematic representation of the sequence of events in a reaction time trial. After a sequence of three warning-tones, each separated by 100 ms, the uniform field is replaced by a train of spatio-temporal luminance noise. The spatial arrangement mimics the Ishihara plates, since the field is composed of many small discs of varying luminance. The luminance of each disc can change from frame to frame (see arrow B) and the chromaticity can be modulated independently of luminance (see arrow A). 280 ms after the start of the noise-train, a chromatic target that forms a 90° arc is presented, for 4 frames only, in any one of 4 quadrants chosen at random. The observer's task is to release a button as quickly as possible if he sees a target, and otherwise to withhold his response. The next trial is initiated by depressing the response button. The test stimulus used in stage one (finding a tritan line) is spatially identical to the target used in the reaction time experiment. The target is introduced between periods of adaptation to a bright yellow field, and the observer's task is to identify the target quadrant.

chromatic contrast of the test vector was modified adaptively (Robbins & Monroe accelerated stochastic approximation, as described by Treutwein, 1995) until a threshold was found. Baseline thresholds were also measured for each of the probe stimuli. For the latter measurements, there was an initial 2-min adaptation to equal energy white, but trial timings were under the subject's control.

2.4. Stage two: determining subjective equiluminance

We determined phenomenological equiluminance with a version of the Cavanagh et al. (1987) minimum-motion technique. A repeating four-frame sequence, consisting of a 0° phase luminance grating, a 90° phase chromatic grating, a 180° phase luminance grating and a 270° chromatic grating, produces apparent motion if the components of the chromatic grating differ in luminance. The direction of motion is determined by the phase of the luminance difference. Our minimum-motion stimulus formed a complete annulus at the same eccentricity as the reaction time targets. Gratings varied maximally along concentric circular contours, and minimally along radial contours. The observer's task was to indicate whether this stimulus appeared to rotate clockwise or anticlockwise. Our chromatic gratings were modulated either along the observer's tritan line, or along the theoretical L/M axis. The relative luminances of the chromatic components were adjusted according to the progression of two interleaved staircases, and the point of subjective equivalence was estimated from the reversal points.

2.5. Stage three: concurrently estimating threshold and reaction time

We measured reaction times to brief positive excursions in the S-opponent, L/M-opponent or luminance direction (see above for a description of the spatial and chromatic properties of the stimuli). To prevent the magnocellular pathway from mediating detection of our brief chromatic modulations, we embedded them in a flickering train of temporal luminance noise: the luminance of each disc changed from frame to frame (at a frame rate of 100 Hz) and the chromaticity of each disc could be modulated independently of luminance changes. The onset of the four-frame target was fixed at 280 ms after the onset of the 600-ms stimulus train (see Fig. 1).

We ran control conditions in which the luminance contrast was set to zero. The pseudoisochromatic plates were outlined by a thin white ring, so the onset of the stimulus train provided a strong temporal cue, even when luminance contrast was set to zero. Immediately before presentation of the stimulus train, the subject was primed by a sequence of three auditory tones, each separated by 100 ms.

The primary comparisons in this study are between reaction time distributions obtained in response to liminal stimuli. An adaptive staircase progressed according to the observer's performance on a 'go, no-go' task and provided concomitant estimates of threshold and reaction time. On each trial there was a 25% chance that no target was presented. The observer was required to depress a button to initiate each trial, and to release the button as quickly as possible (whilst avoiding false positives) whenever a target was seen in any one of the four possible quadrants. If no target appeared the observer was required to keep the button depressed until an auditory tone, presented 1 s after the target, signalled the end of the trial.

On the basis of the observer's responses, the chromatic or luminance contrast of the target stimulus was modified adaptively (Robbins & Monroe accelerated stochastic approximation, as described by Treutwein, 1995). Staircase parameters were chosen to converge on 75% 'go' responses. Final step sizes were between 0.01 and 0.02 threshold units (approximately equal to the standard deviation of threshold measurements). Four interleaved staircases continued until all had reached the 10th reversal.

Responses less than 150 ms after the presentation of the target were counted as anticipations, and were excluded from the staircase. Immediate auditory feedback was given for false positives and anticipations. At the end of each session the false positive rate was displayed on the screen. Subjects were asked to keep their false positive rate below 5%.

In a 45-min session, we ran one unmixed block (four interleaved staircases) for each of the six stimulus-types (two chromatic directions plus luminance, with and without luminance noise). The order of stimulus-type was counter-balanced across six repetitions. Data from observers RES and JDM were obtained over 24 repetitions; data from observer MST were obtained over six repetitions.

3. Results

All observers have normal colour vision, and are experienced in psychophysical tasks. RES and MST were naïve to the purposes of the study; JDM is one of the authors.

Fig. 2 shows data from stage one of the experiment, in which we used the transient tritanopia method to locate the tritan line for each individual and for a specific location in the visual field. Since the scaling of the S-opponent axis of MacLeod–Boynton space is arbitrary, we describe the data in a scaled version of MacLeod–Boynton space $(S/(L + M) \times 4.0)$, chosen such that baseline sensitivity, considered in the scaled space, is approximately equal across all vectors. Values

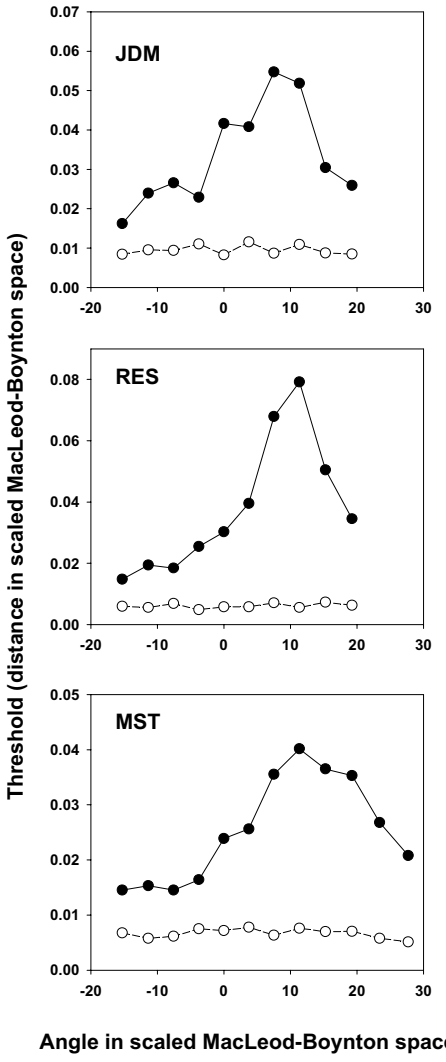

Fig. 2. Data from stage one: finding a tritan line with transient tritanopia, for observers JDM, RES and MST. Thresholds are expressed in a scaled version of MacLeod–Boynton space (S/(L + M) × 4.0) such that baseline performance, considered in the scaled space, is approximately equal over all test angles. Values along the abscissa are probe chromaticities, defined as clockwise angular rotation from the theoretical tritan line in scaled MacLeod–Boynton space. Values on the ordinate are thresholds for the baseline condition (open circles), or following offset of the yellow adapting field (filled circles). The maximum locates the tritan line.

along the abscissa are probe chromaticities, defined as clockwise angular rotation from the theoretical tritan line in scaled MacLeod–Boynton space. Thresholds for the baseline condition (open circles) plot as a horizontal line after scaling, and thresholds following offset of the adapting field (filled circles) show elevations from baseline, indicating a transient tritanopia effect. Smithson et al. (2003) suggest that the maximum elevation locates the tritan line, and we have used their procedure to locate the tritan line for each observer. With test stimuli between 3° and 4.5° eccentricity, we locate the tritan line for JDM at 29° in MacLeod–Boynton space (7.8° in the scaled space), for RES at 34° in MacLeod–Boynton space (9.5° in the scaled space), and for MST at 42° in MacLeod–Boynton space (13° in the scaled space).

Fig. 3 shows histogram plots of a subset of reaction times, for each observer and for each of the three conditions with luminance noise. The histograms were constructed by pooling all reaction times from all sessions of a particular type and selecting all reaction times to stimuli with contrasts ±0.02 log units from the final threshold estimate. Histograms are normalised to unit area, and the total number of responses (n) is specified on each panel. Vertical, dashed lines show the time below which responses were counted as anticipations. The upper cut-off value was 1000 ms. Each bin represents a range of 25 ms. Reaction time is plotted on a linear scale, and all distributions are positively skewed ($p < 0.01$, Lilliefors test), as is typical for reaction time data. Before using parametric statistics on these data, we transformed them to a $\log_{10}$RT scale, which improved normality. A little positive skew remained in some cases but our conclusions remain the same if non-parametric tests are used. Columns x and σ in Table 1(Panel A) show mean and standard deviation derived from the log-transformed values and converted back to a linear scale. We show the upper estimate for the standard deviation, which is symmetric on a log scale but asymmetric when converted back to a linear scale. It is clear that there are no substantial differences in reaction time between the three types of test stimuli: +(L + M), +L/(L + M) and +S/(L + M). Observer MST shows larger variance in reaction time to +(L + M) stimuli than to +L/(L + M) or to +S/(L + M).

The histograms in Fig. 3 include data from more than one session, and as such combine within-session and between-session variance. An alternative way to analyse the data is to select reaction times to all stimuli presented within a single session that have chromatic contrasts within ±0.02 log units of the threshold estimate for that session. In this way we obtain 24 equally independent estimates of reaction time for each condition for RES and for JDM, and six for each condition for MST. Means and standard errors for these measurements are shown in Table 1(Panel A) in the column labelled RT. Again, calculations have been performed on log-transformed data, although values are quoted on a linear scale. The Sig column indicates significant differences between means ($p < 0.05$, ANOVA combined post-hoc with Tukey's honestly significant difference criterion). For observers RES and MST there are no significant differences between reaction times to the three types of test stimuli when presented in spatio-temporal luminance noise. For observer JDM reaction times to tritan stimuli are significantly slower than reaction times to +L/(L + M) and to +(L + M) stimuli, though reaction times to +L/(L + M) stimuli are not significantly different from reaction times to +(L + M) stimuli.

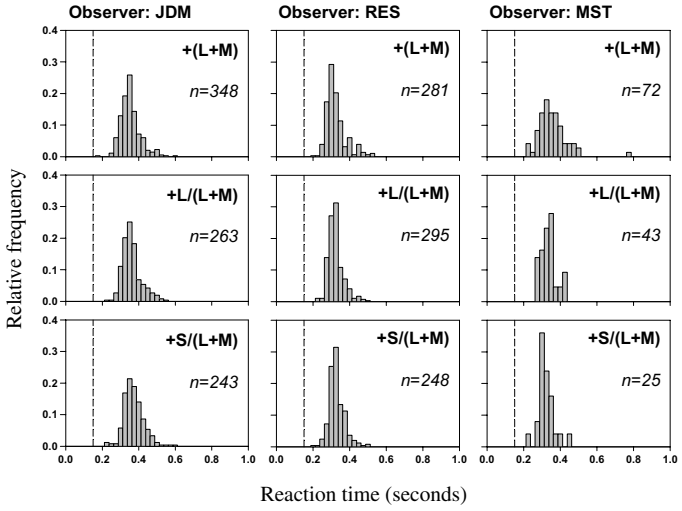

Fig. 3. Histogram plots of a subset of reaction times from conditions with luminance noise. The three columns refer to the three observers (JDM, RES and MST), and the three rows refer to the three stimulus conditions (+(L + M), +L/(L + M), +S/(L + M)). Histograms were constructed by pooling all reaction times from all sessions of a particular type and selecting all reaction times to stimuli with contrasts ±0.02 log units from the final threshold estimates. Histograms are normalised to unit area, and the total number of responses (n) is specified on each panel. Vertical, dashed lines show the time below which responses were counted as anticipations. The upper cut-off value was 1000 ms. Each bin represents a range of 25 ms.

A power analysis reveals that with the data collected for JDM and for RES ($N = 24$, $\sigma^2 = 300$, $\alpha = 0.05$), we have a >99% chance of detecting a latency difference of 20 ms between S/(L + M) and L/(L + M) or (L + M), and an 88% chance of detecting a latency difference of 15 ms, if such a difference exists. For MST we have fewer measurements ($N = 6$, $\sigma^2 = 300$, $\alpha = 0.05$), and only a 50% chance of detecting a difference of 20 ms, and an 88% chance of detecting a difference of 30 ms.

False positive rate (i.e. the percentage of blank trials to which subjects responded) is also quoted in Table 1(Panel A). For JDM and RES there were approximately 750 blank trials in total for each condition, so the confidence limit on false positive rate is ±1.5% ($p < 0.05$) based on an expected rate of 5%. For MST there were approximately 180 blank trials for each condition, so the confidence limit on false positive rate is ±3.2% ($p < 0.05$) based on an expected rate of 5%. For both JDM and RES, there is an increase in false positive rate from the +(L + M) condition to the +L/(L + M) condition, and the +S/(L + M) condition. None of the subjects gave anticipatory responses (RT < 150 ms) to stimuli falling within ±0.02 log units of threshold, and fewer than 1% of all responses were anticipatory.

Table 1(Panel B) shows summary data for the three conditions without spatio-temporal luminance noise. All observers have reaction times to tritan stimuli that are significantly longer than their reaction times to +(L + M) stimuli. In addition, observers JDM and RES show significant differences between reaction times to tritan and +L/(L + M) stimuli, and JDM shows a significant difference between reaction times to +L/(L + M) and +(L + M) stimuli. False positive rate is lower on average in the absence of spatio-temporal luminance noise.

Fig. 4 shows plots of reaction time versus stimulus contrast for the three conditions with luminance noise (Fig. 4a) and for the three conditions without luminance noise (Fig. 4b). Each data point in these plots is derived from reaction times to stimuli with contrasts falling within 0.1 threshold units of its location on the abscissa, and is therefore a smoothed representation of the data. Mean reaction times were calculated for log-transformed data though values are plotted on a linear scale. Vertical dashed lines indicate the range of data included in the histograms of Fig. 3, and in the summary statistics in Table 1.

4. Discussion

4.1. Is the S-opponent pathway sluggish?

In conditions without spatio-temporal luminance noise, when we would expect the magnocellular pathway to contribute to detection, all observers show significantly faster reaction times to +(L + M) stimuli than to tritan stimuli. And for JDM and RES, +L/(L + M) reaction times are significantly faster than tritan reaction times.

In the presence of spatio-temporal luminance noise, which was intended to saturate the magnocellular pathway, neither RES nor MST show significantly different reaction times to liminal signals in the two chromatic sub-systems. For JDM, reaction times to tritan stimuli are significantly longer than reaction times to +L/(L + M) stimuli, by 13 ± 7 ms (estimated from

Table 1
Summary statistics for three observers comparing three conditions (+(L + M), +L/(L + M), +S/(L + M)) with (Panel A) and without (Panel B) spatio-temporal noise

	x	σ	RT	Sig	FP rate
Panel A: with luminance noise					
JDM					
+(L + M)	349.9	56.1	347.8 ± 3.5	– × ✓	2.1
+L/(L + M)	357.0	53.4	353.5 ± 2.5	× – ✓	4.0
+S/(L + M)	370.1	57.2	372.1 ± 3.7	✓ ✓ –	6.0
RES					
+(L + M)	321.9	54.4	321.7 ± 3.1	– ××	3.4
+L/(L + M)	320.9	42.2	320.5 ± 3.1	× – ×	4.7
+S/(L + M)	326.8	44.4	328.7 ± 3.8	×× –	7.6
MST					
+(L + M)	348.8	77.3	335.5 ± 5.6	– ××	2.7
+L/(L + M)	332.1	45.7	337.7 ± 5.9	× – ×	5.0
+S/(L + M)	319.9	44.8	317.0 ± 12.6	×× –	1.1
Panel B: without luminance noise					
JDM					
+(L + M)	334.9	73.8	333.0 ± 3.8	– ✓ ✓	5.8
+L/(L + M)	354.4	52.1	355.5 ± 4.1	✓ – ✓	2.5
+S/(L + M)	369.0	44.2	373.3 ± 3.2	✓ ✓ –	2.8
RES					
+(L + M)	313.7	36.1	319.9 ± 2.9	– × ✓	1.9
+L/(L + M)	324.2	40.3	326.7 ± 3.4	× – ✓	1.5
+S/(L + M)	344.1	47.8	344.7 ± 4.3	✓ ✓ –	4.0
MST					
+(L + M)	291.9	36.7	284.7 ± 11.5	– × ✓	1.7
+L/(L + M)	312.3	44.7	313.1 ± 6.3	× – ×	1.6
+S/(L + M)	330.5	37.7	333.9 ± 5.3	✓ × –	1.3

The x column gives mean reaction time, and is derived from pooled data for all stimulus presentations within ±0.02 log units of the final threshold estimates. The σ column shows the standard deviation of the same data. The RT column shows mean and standard error derived from session by session estimates. The Sig column indicates significant differences between mean reaction times ($p < 0.05$, ANOVA combined post-hoc with Tukey's honestly significant difference criterion). For each row, the three symbols, from left to right, refer to a comparison with +(L + M), +L/(L + M) and +S/(L + M) conditions respectively. Ticks indicate a significant difference, dashes indicate no comparison, and crosses indicate no significant difference. All calculations were performed on log-transformed data. The FP rate column shows false positive rate, i.e. percentage of blank trials on which observers responded.

pooled data), or by 19 ± 7 ms (estimated from session by session estimates). A power analysis confirmed that for RES and JDM our data are precise enough (power > 0.80) to detect a difference of 15 ms, if such a difference exists. For MST our data are precise enough (power > 0.80) to detect a difference of 30 ms, if such a difference exists. We conclude that signals in the S-opponent sub-system can be delayed relative to signals in the L/M-opponent sub-system, but that the delay varies between individuals and does not exceed 20–30 ms.

Clearly, since time constants depend unquestionably on adaptive state (Mollon & Krauskopf, 1973), it would be possible to exaggerate or attenuate differences in time constants by choosing background colours that adapted one channel much more than the other. In the present experiment we used a background adaptation that was metameric to equal energy white. This is a neutral stimulus, often considered as the equilibrium point of opponent mechanisms. However, assuming all cone classes have equal quantal efficiency at their peak, this stimulus would produce greater quantal catch in the L- and M-cones than in the S-cones. An adapting stimulus chosen to produce equivalent quantal catch in the three cone types would be expected to reduce S-cone latencies relative to M- and L-cone latencies measured under adaptation to equal energy white (CIE $x = 0.333$, $y = 0.333$).

So why do McKeefry, Parry, and Murray (2003a, 2003b) find that, under adaptation to Illuminant C (CIE $x = 0.310$, $y = 0.316$), their observers take approximately 40 ms longer to respond to tritan stimuli than to L/M-opponent stimuli, when the two are equated in threshold units? There are several differences between our study and theirs. Perhaps the most significant is that we used temporal luminance noise to mask magnocellular activation by L/M-opponent targets. Even with a ramped equiluminant exchange, it is difficult to avoid some magnocellular activation by modulation along the L/M opponent axis. Previous psychophysical studies that have found little difference between the temporal responses of the two chromatic channels either estimated

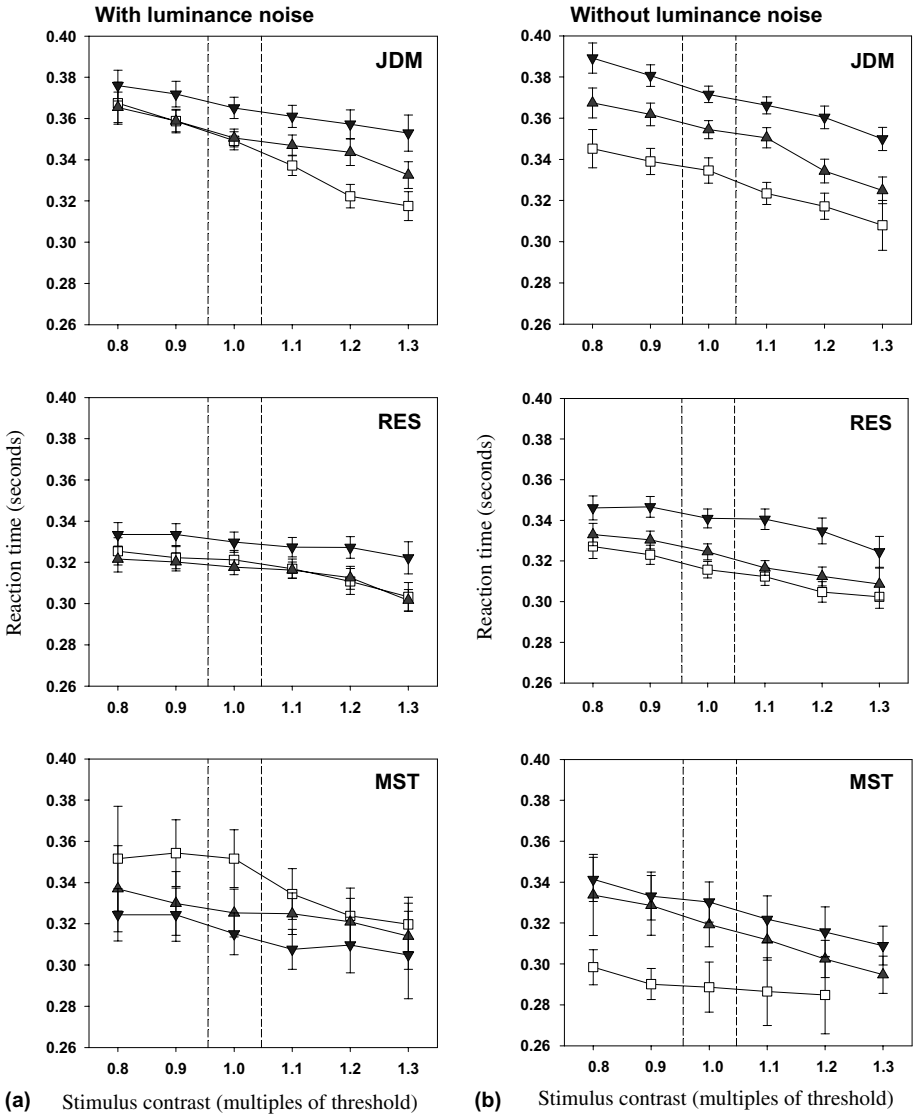

Fig. 4. Plots of reaction time versus stimulus contrast. Data in (a) were obtained with spatio-temporal luminance noise; data in (b) were obtained without spatio-temporal luminance noise. The three curves in each plot represent the three conditions: squares +(L + M), apex-up-triangles +L/(L + M), apex-down-triangles +S/(L + M). Each data point is derived from reaction times to stimuli with contrasts falling within 0.1 threshold units of its location on the abscissa, and is therefore a smoothed representation of the data. Mean reaction times were calculated for log-transformed data though values are plotted on a linear scale. Error bars show 95% confidence intervals. Vertical dashed lines indicate the range of data included in the histograms of Fig. 3, and in the summary statistics in Table 1.

and eliminated the contribution of the magnocellular pathway (McKeefry et al., 2001), or embedded the chromatic stimuli in temporal luminance noise (Smithson & Mollon, 2001). Our data for RES support the hypothesis that magnocellular signals can confer a reaction time advantage for L/M-opponent stimuli. In the presence of luminance noise (when the magnocellular signal associated with an L/M-opponent stimulus was unavailable), RES showed no L/M-opponent advantage, but in the absence of luminance noise (when the magnocellular signal associated with an L/M-opponent stimulus was available) RES gave faster responses to L/M-opponent stimuli than to tritan stimuli.

A further possible reason for the discrepancy between our findings and those of McKeefry et al. (2003a, 2003b) is that they used very small test stimuli (Gaussian profile, SD=0.2°=12′ visual angle). With exact fixation, the central 49% of this stimulus would fall within the nominally tritanopic region of foveola (estimated diameter 25′ visual angle, Williams et al., 1981). Fixation is not discussed in their paper, and it is unclear how observers would have behaved under these conditions. We might guess that a slight, chance eye-movement during the long (>190 ms) stimulus presentation would be necessary to position the stimulus on a region of retina containing S-cones. Thus, on average, the tiny tritan

stimulus would be available to the observer later than an L/M-opponent stimulus of the same size. Blocked presentation of test stimuli at different contrasts may also have allowed subjects to modify their response criterion under different levels of stimulus uncertainty.

4.2. Lightness signalled by the parvocellular system?

In the presence of spatio-temporal luminance noise, none of our observers show a significant difference between reaction times to +(L + M) stimuli and those to +L/(L + M) stimuli. In these conditions, subjects report that the +(L + M) targets appear as changes in lightness or whiteness rather than as the disturbances of the field that have traditionally been associated with the magnocellular system. Our reaction time data suggest that, when the magnocellular pathway is saturated by spatio-temporal luminance noise, liminal +(L + M) stimuli are detected by the parvocellular pathway, and thus can support reaction times only as rapid as those for +L/(L + M) stimuli. We are making a distinction here between lightness and luminance. The former is a property of surfaces in the natural world. To distinguish fine gradations in greyscale we require a channel that gives a near-linear response over the full range of stimuli: the classical measurements of Kaplan and Shapley (1986) suggest that the parvocellular pathway would be better adapted to this task than the magnocellular pathway. Morevoer, the two surface properties of chromaticity and lightness are strongly correlated in natural scenes and it would be appropriate for them to be analysed by the same pathway.

5. Conclusions

We draw two conclusions from our results: (i) when brief visual stimuli are confined to chromatic channels and presented at equivalent (threshold) levels and when latency is estimated from visually triggered reaction times, the difference between the L/M-opponent and S-opponent sub-systems does not exceed 20–30 ms. (ii) Spatio-temporal luminance noise may offer a way to distinguish psychophysically a lightness signal carried by the parvocellular system and a luminance or transient signal carried by the magnocellular system.

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