

The effects of red surrounds on visual magnocellular and parvocellular cortical processing and perception

Laila Hugrass

Center for Human Psychopharmacology,
Swinburne University of Technology,
Melbourne, Victoria, Australia



Thomas Verhellen

Center for Human Psychopharmacology,
Swinburne University of Technology,
Melbourne, Victoria, Australia



Eleanore Morrall-Earney

Center for Human Psychopharmacology,
Swinburne University of Technology,
Melbourne, Victoria, Australia



Caitlin Mallon

Center for Human Psychopharmacology,
Swinburne University of Technology,
Melbourne, Victoria, Australia



David Philip Crewther

Center for Human Psychopharmacology,
Swinburne University of Technology,
Melbourne, Victoria, Australia



More than 50 years ago, Hubel and Wiesel identified a subpopulation of geniculate magnocellular (M) neurons that are suppressed by diffuse red light. Since then, many human psychophysical studies have used red and green backgrounds to study the effects of M suppression on visual task performance, as a means to better understand neurodevelopmental disorders such as dyslexia and schizophrenia. Few of these studies have explicitly assessed the relative effects of red backgrounds on the M and P (parvocellular) pathways. Here we compared the effects of red and green diffuse background illumination on well-accepted cortical M and P signatures, both physiologically through nonlinear analysis of visual evoked potentials (VEPs; $N = 15$), and psychophysically through pulsed and steady pedestal perceptual thresholds ($N = 9$ with gray pedestals and $N = 8$ with colored pedestals). Red surrounds reduced P-generated temporal nonlinearity in the VEPs, but they did not influence M-generated VEP signatures. The steady and pulsed pedestal results suggest that red surrounds can have different effects on M and P contrast sensitivities, depending on whether the target is colored gray or red, presented centrally or peripherally, or whether it is brighter or dimmer than the surround. Our results highlight difficulties in interpreting the effects of

red backgrounds on human VEPs or perception in terms of M specific suppression.

Introduction

Multiple parallel pathways transmit visual information from the retina to the cortex, leading to perception of form, color and motion. The parvocellular (P) pathway is highly sensitive to (red/green) color, but it is less sensitive to luminance contrast, and has a preference for high spatial frequency/low temporal frequency stimulation. The magnocellular (M) pathway is highly sensitive to luminance contrast but not color, and has a preference for low spatial frequency, high temporal frequency stimulation (Derrington & Lennie, 1984; Kaplan & Shapley, 1986; Livingstone & Hubel, 1988). The koniocellular (K) pathways are made up of an amalgam of cells with different properties and presumably different functions, including the transmission of input from short-wavelength (blue) cones to the visual cortex (Casagrande, 1994; Ghodrati, Kha-

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ligh-Razavi, & Lehky, 2017; Hendry & Reid, 2000; Martin, White, Goodchild, Wilder, & Sefton, 1997).

There are several reasons why psychologists and cognitive neuroscientists have studied M function. Firstly, M input reaches the primary visual cortex (V1) faster than P input, playing an important role in foreground-background segmentation of the visual scene (Bullier, 2001; Hupé, James, Payne, & Lomber, 1998), a primary stage of object recognition. Secondly, the dorsal “vision for action” stream receives predominantly M input (Maunsell, Nealey, & DePriest, 1990). Furthermore, the M system is implicated in rapid threat detection because it feeds into the colliculo-pulvinar route to the amygdala (Schiller, Malpeli, & Schein, 1979). Finally, there is evidence of M dysfunction across various clinical populations including dyslexia (Lovegrove, 1996; Stein & Walsh, 1997), schizophrenia (Butler et al., 2006) and autism (Laycock, Crewther, & Crewther, 2007). Therefore, it is important for scientists to develop noninvasive techniques to investigate how M function influences perception and behavior.

Over 50 years ago, primate single cell studies identified a subpopulation of M neurons that are suppressed by diffuse red light (Wiesel & Hubel, 1966). These “Type IV” cells respond transiently to light presented in their receptive field (RF) centers, and exhibit tonic suppression when long wavelength (red) light is presented in the RF surround (de Monasterio, 1978; Wiesel & Hubel, 1966). Type IV RF characteristics have been observed in M (parasol) retinal ganglion cells (RGCs; de Monasterio, 1978), the ventral layers of LGN (Wiesel & Hubel, 1966), and within the cytochrome oxidase blobs in V1 layers 2 and 3 (Livingstone & Hubel, 1984). In the retina, there is a clear distinction between Type IV and Type III M RGCs, which have spatially opponent, but not spectrally opponent RFs (de Monasterio, 1978). Unlike Type III cells, Type IV cells tend to have a central retinal distribution, they frequently receive input from short-wavelength cones, and they do not project to the superior colliculus, as verified by the absence of antidromic stimulation of Type IV RGCs from electrodes placed in the superior colliculus (de Monasterio, 1978). At the level of the LGN, the distinction between Type III and IV cells is less clear, with almost all M cells showing some degree of chromatic and spatial opponency (Derrington, Krauskopf, & Lennie, 1984).

Based on these physiological studies, many cognitive neuroscientists have presented tasks on a red background to suppress processing contributions from the M pathway (Awasthi, Williams, & Friedman, 2016; Bedwell, Brown, & Orem, 2008; Breitmeyer & Williams, 1990; Chapman, Hoag, & Giaschi, 2004; Edwards, Hogben, Clark, & Pratt, 1996; West, Anderson, Bedwell, & Pratt, 2010; Williams, Breit-

meyer, Lovegrove, & Gutierrez, 1991). For instance, West et al. (2010) found that with a green background, fearful faces are perceived more rapidly than neutral faces, whereas with a red background, this temporal precedence is diminished. The authors suggested that the red surround could have suppressed M input to the colliculus-pulvinar route to the amygdala (Schiller et al., 1979). However, this interpretation seems unlikely because Type IV M cells do not project to the superior colliculus (de Monasterio, 1978).

Despite physiological evidence that most P receptive fields are spatially and chromatically opponent (Derrington et al., 1984), the psychological studies discussed above did not adequately consider the effects of a red background on the P pathway. Skottun (2004) calculated the effects of red and green filters on long, medium, and short-wavelength cone pigments, and on the four broad classes of chromatically opponent receptive fields (De Valois, Abramov, & Jacobs, 1966). Skottun’s calculations showed that a red filter would have large effects on red-green and blue-yellow color opponent neurons, whereas the green filter had relatively little effect on the modelled responses. Due to the heterogeneity of K receptive field properties (Hendry & Reid, 2000; White, Solomon, & Martin, 2001), it is unclear how K cells might contribute to the effects of red backgrounds on visual processing. Yet, to our knowledge, no behavioral or neuroimaging experiments have been conducted to measure the effects of a red surround on the central M and P pathways.

In order to investigate the effects of red surrounds on M and P processing, we used well-validated electrophysiological (Experiment 1) and psychophysical (Experiment 2) paradigms. Temporal processing in the M and P pathways can be inferred using nonlinear VEP (Baseler & Sutter, 1997; Jackson et al., 2013; Klistorner, Crewther, & Crewther, 1997) and nonlinear MEG (Crewther, Brown, & Hugrass, 2016). In multifocal VEP experiments, multiple patches of light are flashed in pseudorandom binary sequences, each de-correlated from the others. This not only allows for simultaneous recordings across the visual field, but also for the analysis of higher order temporal nonlinearities through Wiener kernel decomposition (Sutter, 1992; Sutter & Tran, 1992). For a temporally linear system, the first order kernel is the impulse response function of the system (Benardete & Victor, 1994). The first and second slices of the second order kernel (K2.1 and K2.2) are measures of nonlinearity over one and two video frames respectively. K2.1 responses (and the early components of K2.2 responses) have high contrast gain and a saturating contrast response function, consistent with an M pathway generator (Jackson et al., 2013; Klistorner et al., 1997). The later component (N100-P140) of the K2.2 waveform has low contrast gain and a nonsaturating contrast response function, consistent

with a P pathway generator (Klistorner et al., 1997). A highly efficient system (i.e., one that recovers rapidly from stimulation) would produce large K1 responses, with no nonlinear responses. Higher amplitude K2.1 and K2.2 responses are associated with lower temporal efficiency in the M and P pathways respectively (Bauer et al., 2011; Thompson et al., 2015). Hence, if a red background decreases M temporal efficiency, we would expect it to increase the K2.1 amplitude; whereas if it decreases P temporal efficiency, we would expect it to increase the K2.2 amplitude (Experiment 1).

M and P responses can also be measured psychophysically using pulsed and steady pedestal paradigms (Pokorny, 2011; Pokorny & Smith, 1997). In both paradigms, observers are required to detect a brief luminance increment in one of four pedestal stimuli. When the pedestals are lighter or darker than the background, neural responses are mediated by “on” or “off”-centered cells respectively (Schiller, 1992; Zemon & Gordon, 2006), such that the spike rate of cells with the preferred polarity increases along the contrast response function (Pokorny, 2011). When observers adapt to steady pedestals in between target presentations, thresholds are interpreted as steady-state M sensitivity, which tends to increase with pedestal luminance, regardless of the surround luminance (Pokorny & Smith, 1997). When the pedestals and target are pulsed simultaneously, M responses are saturated and detection thresholds are interpreted in terms of P contrast sensitivity (Pokorny & Smith, 1997). Hence, when pulsed-pedestal detection thresholds are plotted against pedestal contrast, they form a “V” shape around the point of equiluminance (Pokorny, 2011). If a red surround suppresses the M pathway, we would expect it to decrease sensitivity to steady pedestals, whereas if it suppresses the P pathway, we would expect it to decrease sensitivity to pulsed pedestals (Experiment 2).

Experiment 1: Method

Participants

Fifteen participants (Three male, 12 female; $M = 21.8$ years, $SD = 2.5$ years) gave written informed consent for the experiment, which was conducted with the approval of the Swinburne Human Research Ethics Committee and in accordance with the code of ethics of the Declaration of Helsinki. The first four authors were included in the sample. All participants had normal, or corrected-to-normal, visual acuity as measured with a Snellen chart, and normal color vision, as tested with Ishihara color plates.

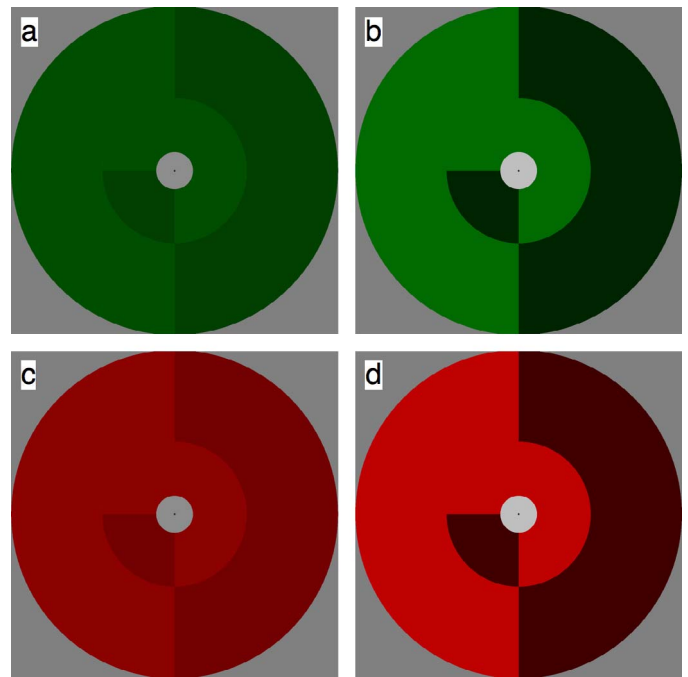


Figure 1. Dartboard stimulus configuration for the green low contrast (a), green high contrast (b), red low contrast (c), and red high contrast (d) conditions. We compared VEP kernel responses to the central patch for the conditions with red and green surrounds.

Stimuli

The stimuli were presented on a 60 Hz LCD monitor (ViewSonic, 80% rise latency = 3 ms, 20% fall latency = 2 ms, resolution $1,024 \times 768$) with linearized color output (measured with a ColorCal II), at a viewing distance of 70 cm. The 9-patch multifocal dartboard was created using VPixx software (version 3.2, <http://www.VPixx.com>), with a 5.4° diameter central patch and two outer rings of four patches (21.2° and 48°). The luminance for each patch was modulated at the video frame rate (60 Hz) in a pseudorandom binary M-sequence ($M = 14$), at either low (10% Michelson) or high (70% Michelson) temporal contrast. The M-sequences for each patch were maximally offset, so we could record independent responses across the visual field (Figure 1). The stimuli are specified in CIE1931 color space. For the purpose of this experiment, we only analyzed responses to the central, achromatic patch, (42 cd/m^2 , CIE $x = 0.32$, CIE $y = 0.33$). Separate recordings were made with red (42 cd/m^2 , CIE $x = 0.65$, CIE $y = 0.34$) and green (42 cd/m^2 , CIE $x = 0.33$, CIE $y = 0.60$) surrounds. For each experimental condition, the m-sequences were split into four approximately one-minute recording segments, with the recordings lasting 16 minutes in total for the four conditions. Participants were instructed to maintain strict fixation

during the recordings and to rest their eyes between recordings.

EEG recording and analysis

EEG was recorded using a 64-channel cap (Neuroscan, Compumedics). The data were sampled at 1 KHz and band-pass filtered from 0.1–200 Hz. Electrode site AFz served as ground and linked mastoid electrodes were used as a reference. EOG was monitored using electrodes attached above and below one eye. Data were processed using Brainstorm (Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011), which is documented and freely available for download online under the GNU general public license (<http://neuroimage.usc.edu/brainstorm>). EEG data were band-pass filtered (1–40 Hz) and signal space projection was applied to remove eye-blink artefact. Custom Matlab/Brainstorm scripts were written for the mfVEP analyses in order to extract K1, K2.1, and K2.2 kernel responses for the central patch. K1 is the difference between responses to the light and dark patches (S_1 and S_2), i.e., $K1 = 0.5(S_1 - S_2)$. K2.1 measures neural recovery over one frame (16.67 ms) by comparing responses when a transition did or did not occur, i.e., $K2.1 = 0.25(S_{11} + S_{22} - S_{12} - S_{21})$. K2.2 measures neural recovery over two frames (33 ms), it is similar to K2.1, but includes an interleaving frame of either polarity.

For each participant, the electrode with the highest amplitude responses was selected for group-level averages. The highest amplitude responses were recorded at Oz for 12 participants, POz for two participants and O2 for one participant. Peak and trough amplitudes and latencies for the kernel waveforms were identified in Labview, and exported to SPSS for linear mixed-effects modelling.

Experiment 1: Results and discussion

Grand averages for the K1, K2.1, and K2.2 responses were calculated for all experimental conditions (red and green surrounds, high and low contrast). As illustrated in Figure 2, there were some individual differences in the waveforms, yet the averaged traces for K1 and K2.1 recorded with red and green surrounds overlap almost perfectly (Figure 2a and b), and the K2.2 traces diverge. Separate linear mixed effects models were computed (using the case ID codes to account for random effects for participants), to investigate the effects of background color (red vs. green) and temporal contrast (10% vs. 70%) on

the peak amplitudes of the K1, K2.1, and K2.2 responses.

K1 amplitude

The results of Klistorner et al. (1997) suggest that the first order response (K1) is produced by complex interactions between the M and P pathways. Running paired-samples *t* tests (Figure 2a and d) showed no significant effect of surround color on VEP amplitude, except in the 70% contrast condition at approximately 30 ms latency; however, this difference was very small. More detailed analyses of the effects of surround color and luminance contrast were performed with linear mixed-effects models of the main peak-trough amplitudes ($K1_{N60 - P90}$ and $K1_{N120 - P150}$). For both the early and late peak-trough complexes, there were no significant main effects of surround color on K1 peak amplitudes, $K1_{N60 - P90}$: $F(1, 56) = 0.02$, $p = 0.91$; $K1_{N120 - P150}$: $F(1, 56) = 0.03$, $p = 0.87$; nor were there any significant surround by contrast interactions, $K1_{N60 - P90}$: $F(1, 56) = 0.04$, $p = 0.84$; $K1_{N120 - P150}$: $F(1, 56) = 0.05$, $p = 0.83$. As expected, there were significant main effects of contrast on K1 amplitudes, with greater responses at 70% than 10% temporal contrast, $K1_{N60 - P90}$: $F(1, 56) = 46.58$, $p < 0.001$; $K1_{N120 - P150}$: $F(1, 56) = 58.19$, $p < 0.001$. In summary, K1 amplitudes are greater when the central patch is high contrast, but they are not affected greatly by the surround color.

K2.1 amplitude

Previous results suggest that the $K2.1_{N60 - P90}$ amplitude is of M pathway origin (Jackson et al., 2013; Klistorner et al., 1997). Running paired-samples *t* test comparisons (below Figure 2b and e) showed no significant effect of surround color on VEP amplitude within the N60–P90 latency range, yet there were some differences for the later potentials. Linear mixed-effects models were computed to compare the effects of surround color and luminance contrast on the N60–P90 and N115–P140 and peak-to-trough amplitudes.

There was no significant main effect of surround color on amplitude, $K2.1_{N60 - P90}$: $F(1, 56) = 0.04$, $p = 0.85$; $K2.1_{N115 - P140}$: $F(1, 56) = 0.14$, $p = 0.72$. As expected, there was a significant main effect of contrast on amplitude, with greater responses at 70% than 10% temporal contrast, $K2.1_{N60 - P90}$: $F(1, 56) = 21.49$, $p < 0.001$; $K2.1_{N115 - P140}$: $F(1, 56) = 4.85$, $p = 0.03$. The mean contrast ratio (70%/10%) for the major $K2.1_{N60 - P90}$ peak was similar with the red ($M = 1.98$, $SD = 0.80$) and green ($M = 1.97$, $SD = 0.80$) surrounds, and there was no surround color by contrast interaction, $F(1, 56) =$

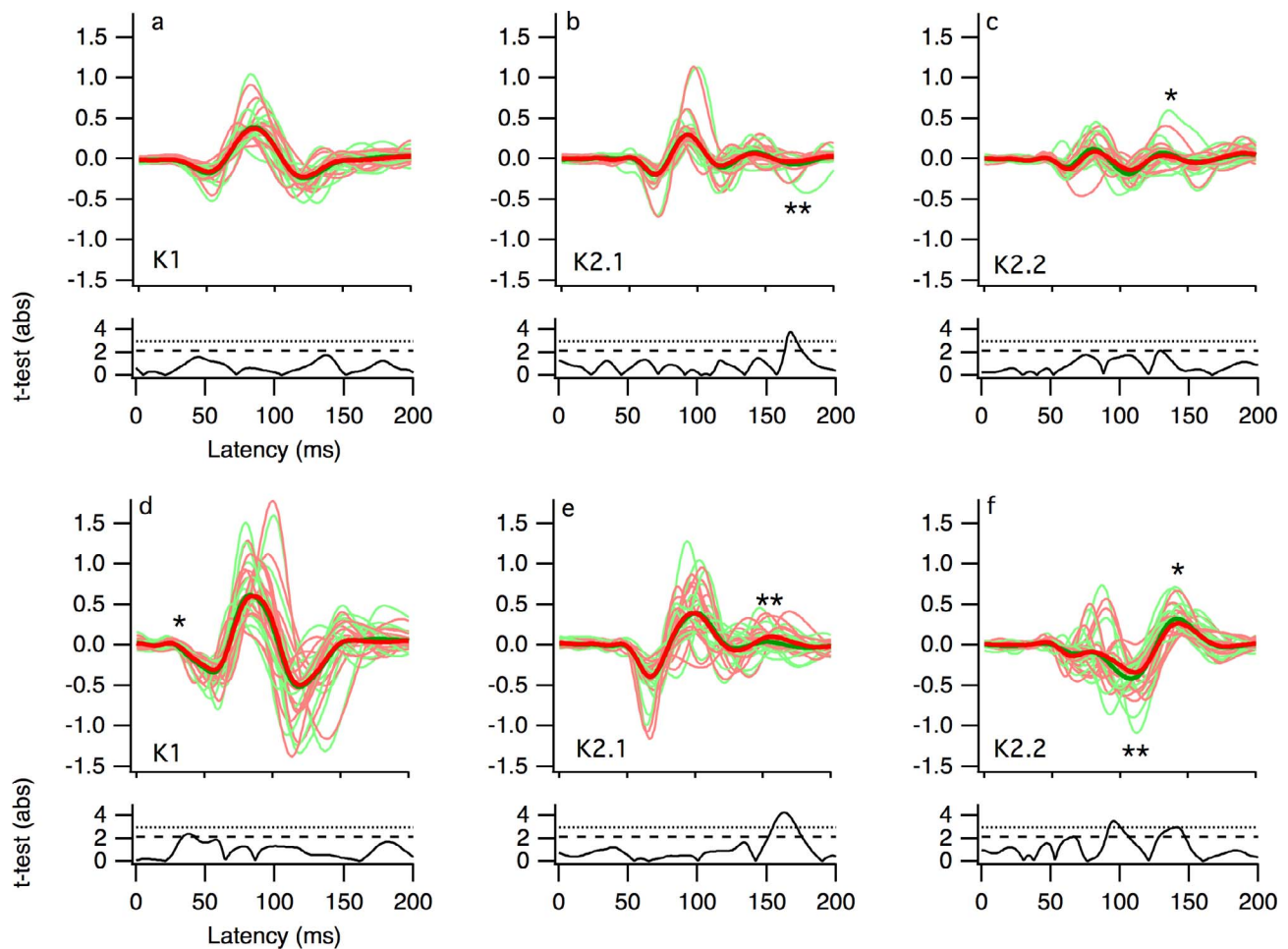


Figure 2. K1, K2.1, and K2.2 responses to the central patch at 10% (a, b, c) and at 70% (d, e, f) temporal contrast. The bold red and green lines correspond to the averaged waveforms for the conditions with red and green backgrounds respectively. Responses from each participant are illustrated in the faint red and green traces. VEP amplitudes for the red and green surrounds were compared using running paired samples t tests ($df = 14$). The absolute t values are shown in the black traces at the bottom of each panel, with the dashed and dotted horizontal lines signifying the $p < 0.05$ and $p < 0.01$ two-tailed significance thresholds respectively. Times when the VEP traces differed significantly are flagged with * ($p < 0.05$) and ** ($p < 0.01$).

0.04 $p = 0.85$. These results suggest that, as expected, K2.1 response amplitudes increase with contrast; yet contrary to expectation, K2.1 amplitudes are not greatly affected by the background color. Therefore, our results suggest that a red surround does not influence temporal nonlinearity generated by the M pathway.

K2.2 amplitude

Previous studies indicate that the short latency K2.2_{N60 – P80} waveform is also of M origin (Jackson et al., 2013). As illustrated in the running t test comparisons (Figure 2c and f), differences between the red and green traces did not reach significance at these latencies. The linear mixed effects model of the K2.2_{N60 – P80} amplitude showed there were no

significant main effects of surround color, $F(1, 56) = 0.14$, $p = 0.71$, or contrast, $F(1, 56) = 3.11$, $p = 0.08$, and there was no color by contrast interaction, $F(1, 56) = 0.03$, $p = 0.88$. Hence, consistent with our findings for the K2.1 amplitudes, a red surround does not appear to affect temporal nonlinearity in the M pathway.

Previous studies indicate that the K2.2_{N100 – P140} waveform is of P origin (Jackson et al., 2013; Klistorner et al., 1997). As illustrated in the running t test comparisons (Figure 2c and f), peak amplitudes were significantly lower with the red surround in both the 10% and 70% contrast conditions. A linear mixed effects model showed a significant main effect of surround color, $F(1, 56) = 4.91$, $p = 0.03$, on average responses to the central patch were smaller with the red surround than with the green surround. There was also a main effect of contrast, with greater K2.2 responses at 70% than at 10% contrast, $F(1, 56) = 86.07$, $p < 0.001$.

The mean contrast ratio was similar with red ($M = 2.85$, $SD = 1.14$) and green surrounds ($M = 2.92$, $SD = 1.01$), and the mixed effects model showed there was no significant surround color by contrast interaction, $F(1, 56) = 0.28$, $p = 0.60$. These results indicate that red surrounds reduce temporal nonlinearity in the P pathway, but they do not appear to affect the contrast response function.

Summary

As expected based on the contrast response functions for nonlinear VEPs (Jackson et al., 2013; Klistorner et al., 1997), the effect of temporal contrast on response amplitude was greater for the P-driven $K2.2_{N100 - P140}$ waveform than for the M-driven $K2.1_{N60 - P90}$ and $K2.2_{N60 - P80}$ waveforms. This is consistent with the $K2.1$ response showing higher contrast gain and saturation than the $K2.2$ response.

Contrary to expectation, the M-driven responses were unaffected by surround color, but the P-driven nonlinear responses were significantly smaller with the red surround than with the green surround. This result was surprising, and could be interpreted either in terms of the red surround reducing P output, or increasing P temporal sensitivity. The former interpretation seems unlikely given that color did not affect the amplitude or contrast response for the linear (K1) kernel. The latter interpretation seems plausible, given that a system with less efficient recovery from stimulation would show increased power in the nonlinear VEP response kernels (Jackson et al., 2013). In summary, our results do not support the hypothesis that red surrounds suppress the M pathway at the level of the cortical evoked response. On the contrary, our results indicate that red surrounds increase temporal efficiency in the P pathway.

Experiment 2: Method

Participants

There were nine participants (six female, three male; $M = 24.0$ years, $SD = 4.5$ years) for the experiment with gray pedestals on colored backgrounds. The first two authors participated in the experiment, but no other participants from this sample participated in Experiment 1. There were eight participants (seven female, one male; $M = 28.5$ years, $SD = 5.8$ years) for the experiment with all red and all green stimuli (the first author and two others participated in both psychophysics experiments). Participants gave written informed consent for the experiment, which was conducted with the approval of Swinburne Human

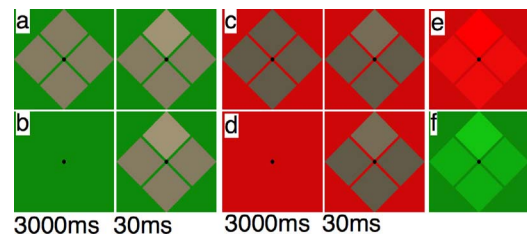


Figure 3. Illustration of the steady (a and c) and pulsed (b and d) pedestal paradigms on green and red backgrounds. An additional experiment was performed with pedestals and targets that were all red (e) or all green (f). In the steady paradigms, observers adapted to the pedestals for 3 s prior to a 30 ms test stimulus. They were required to identify the location of the luminance increment (the top square, in this case). The pulsed paradigms were the same except observers adapted to the background, rather than to the pedestals.

Research Ethics Committee and in accordance with the code of ethics of the Declaration of Helsinki. All participants had normal, or corrected-to-normal, visual acuity and normal color vision.

Stimuli

We used a gamma-corrected PROPixx data projector (120 Hz, VPixx.com) to rear-project the images to a screen at a viewing distance of 70 cm. The contrast discrimination tasks were created using VPixx, and our stimulus design was based on previous studies (McKendrick, Badcock, & Morgan, 2004; Pokorny & Smith, 1997). The steady and pulsed contrast discrimination stimuli are illustrated in Figure 3a and b, respectively. The stimuli are specified in CIE1931 color space. The background color was set to either red (30 cd/m^2 , CIE $x = 0.66$, CIE $y = 0.33$) or green (30 cd/m^2 , CIE $x = 0.13$, CIE $y = 0.73$). In both the steady and pulsed paradigms, the 30 ms test stimulus was a luminance increment in one of the four gray pedestals (squares with 1° edges, CIE $x = 0.33$ CIE $y = 0.39$). Observers used a RESPONSEPixx button pad (vpixx.com) to report which of the pedestals contained the luminance increment (4AFC). For the steady conditions, observers adapted to the pedestals for 3 s between each test presentation, whereas for the pulsed conditions, observers adapted to the background in between test presentations. The pedestal luminance levels were varied from decrements through to increments (-15 , -6 , 0 , 8 , 30 , or 45 cd/m^2) relative to the colored background (30 cd/m^2). In the peripheral condition, the same stimuli were presented in the upper right of the screen, 3.5° away from fixation.

As illustrated in Figure 3a through d, the borders between the gray pedestals and colored backgrounds

are defined by both color and luminance, which may influence the effects of pedestal luminance contrast on detection thresholds. In order to ensure our results could be interpreted in terms of previous findings (Pokorny, 2011), we conducted an additional experiment with versions of the stimuli that were all red (Figure 3e; CIE $x = 0.64$ CIE $y = 0.33$) or all green (Figure 3f; CIE $x = 0.15$ CIE $y = 0.70$).

Increment/Decrement detection thresholds were measured using separate 30 to 40-trial VPESTs (the PEST inbuilt in VPixx) for each of the 48 stimulus conditions. To allow time to adapt to the background, two fixed-value repetitions were completed with high contrast test stimuli prior to the onset of the PEST. The experiment was split into eight blocks, 2 (central vs. peripheral) \times 2 (red vs. green background) \times 2 (steady vs. pulsed pedestal) of 6 PESTs (one at each pedestal luminance). The order of the pedestal-luminance PESTs was randomized within blocks, and the order of the blocks was counterbalanced across participants. To reduce fatigue and allow for recovery from adaptation, observers took breaks between blocks (~10 minutes), and completed no more than three blocks per lab visit.

For any given condition, most observers' thresholds fell within narrow ranges. When outliers were detected (>3 SD from the mean), thresholds for the same observer in different conditions tended to fall within the 2 SD of group mean. Furthermore, roughly equal numbers of outliers were identified across the red and green surround conditions. Therefore, we assumed that any outliers reflected a measurement error, such that the PEST failed to converge on the observer's true threshold. Based on this logic, we replaced outliers for a condition with the group mean for that condition.

Experiment 2: Results and discussion

Before discussing the effects of red backgrounds on the steady and pulsed pedestal tasks, we begin by comparing our results against previous studies that used achromatic stimuli. Previous studies showed that steady pedestal thresholds increase monotonically with pedestal luminance, whereas pulsed pedestal thresholds form a "V" shape around the point of equiluminance (McKendrick et al., 2004; Pokorny, 2011; Pokorny & Smith, 1997). In our experiment with gray pedestals (Figures 4a and 4b), steady pedestal thresholds dropped substantially when the pedestals were equiluminant with the background, and pulsed pedestal thresholds departed from the classic "V" shape. These discrepancies could be because our

pedestals were not the same color as the background, so they remained visible at equiluminance. Hence, we repeated the experiment with pedestal stimuli that were the same color as the backgrounds (Figure 3e and f). Under these conditions, the averaged linear fits for the red and green steady pedestal tasks (Figure 4c and d, solid yellow traces) are similar to those reported in previous studies that used achromatic stimuli, and the pulsed pedestal thresholds formed the classic "V" shape (McKendrick et al., 2004; Pokorny, 2011; Pokorny & Smith, 1997).

Gray steady pedestal tasks

For the gray versions of the steady pedestal tasks, thresholds measured with the red and green backgrounds were almost perfectly overlapping (solid red and green traces, Figure 4a and b), except for the peripherally presented, increment pedestals (Figure 4b), where thresholds were higher with the red background. There were no significant effects of background color on mean thresholds for pedestals that were equiluminant with central: $t(8) = 0.78$, $p = 0.50$; peripheral, $t(8) = 0.04$, $p = 0.97$; or dimmer than the background: central, $F(1, 8) = 0.52$, $p = 0.49$; peripheral, $F(1, 8) = 0.30$, $p = 0.87$. For increment pedestals, there was no effect of surround color on thresholds when the stimuli were presented centrally, $F(1, 8) = 1.39$, $p = 0.27$. When the stimuli were presented peripherally, steady increment thresholds were significantly higher with the red background, $F(1, 8) = 11.19$, $p = 0.03$, $\eta_p^2 = 0.47$; but there was no significant interaction between the effects of background color and pedestal luminance, $F(2, 16) = 1.77$, $p = 0.20$. Overall, these results are only partially consistent with the prediction that red surrounds reduce psychophysical measures of M sensitivity.

Gray pulsed pedestal tasks

Results for the task with gray, pulsed pedestals are illustrated in Figure 4a and b (dashed lines). At equiluminance, pulsed pedestal thresholds were much lower with the green background than with the red background: central, $t(8) = 4.51$, $p = 0.002$; peripheral, $t(8) = 4.92$, $p = 0.001$. This suggests that M responses are swamped by the appearance of gray targets on red backgrounds, but can still contribute to contrast sensitivity when gray targets appear on green backgrounds. For the centrally presented task, there was a significant interaction between the effects of decrement pedestal luminance and surround color, $F(1, 8) = 7.16$, $p = 0.028$, $\eta_p^2 = 0.47$. Increment pulsed-pedestal thresholds were significantly higher with the red background,

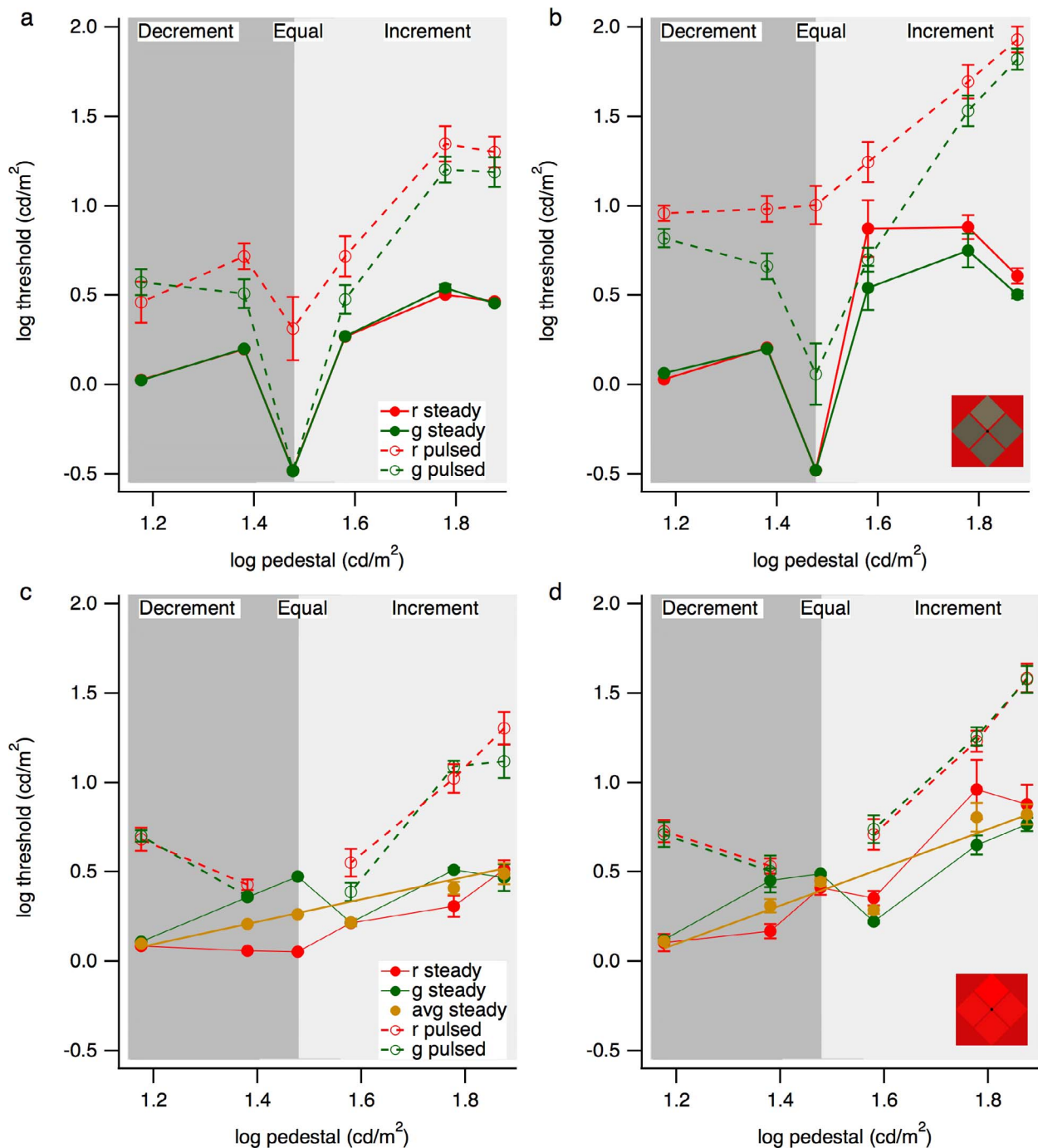


Figure 4. Plots of mean log luminance increment thresholds versus log pedestal luminance for the centrally (a) and peripherally (b) presented gray pedestal tasks ($N = 9$) and for the centrally (c) and peripherally (d) presented colored pedestal tasks ($N = 8$). Results for the red and green background conditions are shown in the red and green traces respectively. Results for the steady pedestal task are shown in the filled markers (solid lines), whereas results for the pulsed pedestal task are shown in the unfilled markers (dashed lines). For the colored pedestal tasks, the yellow markers are the average of thresholds obtained in the red and green steady pedestal conditions, and the yellow solid line illustrates the linear fit. The backgrounds have been shaded in dark and light grays to show when the pedestals were decrements and increments relative to the background luminance. The error bars denote ± 1 SEM.

$F(1, 8) = 8.74, p = 0.018, \eta_p^2 = 0.52$. For the peripherally presented task, thresholds were significantly higher with the red surround for the decrement, $F(1, 8) = 14.96, p = 0.005, \eta_p^2 = 0.65$, and increment-pulsed pedestals, $F(1, 8) = 14.96, p = 0.005, \eta_p^2 = 0.65$. There

was also a significant interaction for the peripheral increment pedestals, $F(2, 16) = 10.68, p = 0.001, \eta_p^2 = 0.57$, with shallower slopes for the red surround. These results indicate that red surrounds can reduce P sensitivity to gray target stimuli.

Colored steady pedestal tasks

In a subsequent experiment, we created all red and all green versions of the pedestal stimuli. This subtle difference in the stimuli substantially altered the effects of background color on steady pedestal thresholds (solid red and green markers, Figure 4c and d). When the thresholds are averaged across the red and green conditions, the linear fits (yellow traces, Figure 4c and d) are consistent with previous evidence of a monotonic increase in thresholds with pedestal luminance (Pokorny, 2011). Curiously, thresholds recorded with the $+8 \text{ cd/m}^2$ pedestals tended to fall below the linear fits.

For the steady decrement pedestal stimuli, a repeated measures ANOVA showed significant interactions between the effects of color and pedestal luminance on contrast detection for the centrally, $F(1, 7) = 1472.78$, $p < 0.001$, $\eta_p^2 = 0.995$, and peripherally presented stimuli, $F(1, 7) = 8.91$, $p = 0.02$, $\eta_p^2 = 0.56$. Thresholds tended to increase with pedestal luminance for the green stimuli and decrease with pedestal luminance for the red stimuli. At equiluminance, mean thresholds were significantly lower for the red stimuli when the target was centrally presented, $t(7) = 100.88$, $p < 0.001$, but not when it was in the periphery, $t(7) = 1.97$, $p = 0.09$. For the centrally presented steady increment pedestals, there was a significant color by luminance interaction, $F(1, 7) = 7.18$, $p = 0.007$, $\eta_p^2 = 0.51$, with reduced thresholds for red steady increment pedestals at $+30 \text{ cd/m}^2$, $t(7) = 4.17$, $p = 0.004$. For the peripherally presented steady increment pedestals, there was a main effect of surround color, $F(1, 7) = 9.16$, $p = 0.02$, $\eta_p^2 = 0.57$, with significantly elevated thresholds for the red stimuli at $+8 \text{ cd/m}^2$, $t(7) = 3.09$, $p = 0.002$. These results suggest that a red surround can improve or impair M sensitivity, depending on whether the target stimuli are presented centrally or peripherally, and whether they are brighter or dimmer than the background.

Colored pulsed pedestal tasks

For the all red and all green, pulsed pedestal stimuli (Figure 4c and d, dashed lines), there were no significant main effects of color on thresholds, nor were there any significant color by pedestal luminance interactions ($p > 0.05$). For the centrally presented task, thresholds for the $+8 \text{ cd/m}^2$ pulsed pedestals were slightly higher with the red background, and this difference was approaching significance, $t(7) = 2.08$, $p = 0.076$. This pattern of results is different from the experiment with gray, pulsed pedestals, and indicates that a red surround does not influence P sensitivity when there is no chromatic edge between the target and the surround.

Summary

Overall, the results we obtained with the colored pedestal stimuli (Figure 4c and d) align closely with the classic linear and “V” fits of steady and pulsed pedestal thresholds respectively. The results we obtained with the gray pedestals on colored backgrounds depart from these classic fits (Figure 4a and b). Therefore, we can be more confident in interpreting the colored pedestal results in terms of evidence that links steady and pulsed pedestal thresholds with M and P functions (McKendrick et al., 2004; Pokorny, 2011; Pokorny & Smith, 1997).

Our results for the steady pedestal experiments suggest that it would be an oversimplification to say that red surrounds suppress M sensitivity. We found that red surrounds can either improve or impair M sensitivity, depending on whether the target stimuli are presented centrally or peripherally and whether they are brighter or dimmer than the background. This could be due to the fact that L cones are more numerous than M cones (Pandey Vimal, Pokorny, Smith, & Shevell, 1989; Vos & Walraven, 1971) and M RGCs cells receive more input from L cones than M cones (Diller et al., 2004). In both the gray and colored versions of the experiment, thresholds for the peripherally presented, steady-increment pedestals tended to be higher with the red surround. Responses to increment and decrement pedestals are dominated by “on” and “off” centered neurons respectively (Pokorny, 2011; Schiller, 1992; Zemon & Gordon, 2006), so our findings are consistent with evidence that Type IV M ganglion cells tend to have “ON” centers (de Monasterio, 1978). However, these findings cannot easily be explained in terms of Type IV M RGCs, which tend to have a more central distribution than Type III M cells (de Monasterio, 1978). Given that the error bars for the peripheral increment thresholds were large, there might be some individual differences in the effects of surround color on M sensitivity.

Our results for the pulsed pedestal stimuli provide mixed evidence as to whether red surrounds affect P contrast sensitivity. For the gray, pulsed pedestal stimuli, we observed an overall elevation in thresholds with the red surround, both for the centrally presented and peripherally presented stimuli. This suggests that red surrounds decrease P contrast sensitivity. These results could be explained by the fact that we did not attempt to match color contrast levels between the gray pedestals and the red and green backgrounds (Pammer & Lovegrove, 2001). Hence, we repeated the experiment with all red and all green stimuli. Under these conditions, there was no effect of background color on pulsed pedestal thresholds. This suggests that when the effects of color contrast have been accounted for, P contrast sensitivity is unaffected by the color of the background.

General discussion

Taken together, our results from Experiments 1 and 2 show it is difficult to interpret the effects of red backgrounds on VEP amplitudes and psychophysics solely in terms of M pathway suppression. In the nonlinear VEP experiment, we observed almost identical K2.1 responses with the red and green backgrounds, and smaller K2.2 amplitudes with the red background. This indicates that a red background does not influence temporal nonlinearity in the M pathway, yet it does reduce P-driven temporal nonlinearity (Klistorner et al., 1997). Our results for Experiment 2 indicate that red backgrounds have different effects on putative M and P psychophysical measures, depending on whether the target stimuli are red or gray, central or peripheral, or brighter or dimmer than the background.

Previous studies have reported effects of red backgrounds on a range of tasks including metacontrast masking (Bedwell & Orem, 2008; Breitmeyer & Williams, 1990; Pammer & Lovegrove, 2001), motion processing (Bedwell, Miller, Brown, & Yanasak, 2006; Breitmeyer & Williams, 1990; but also see Pammer & Lovegrove, 2001) and face processing (Awasthi et al., 2016; Bedwell et al., 2013; West et al., 2010). The authors interpreted the effects of red surrounds on task performance in terms of M suppression. We showed that under some conditions, a red background has the expected suppressive effects on putative M psychophysics, but only when the pedestal stimuli are presented in the periphery and have higher luminance than the background. This indicates that the existing literature regarding the effects of red backgrounds on task performance should be reconsidered, depending on the color, eccentricity, and luminance contrast of the target stimuli.

Although a red background can almost completely suppress Type IV M cells, its effects on putative “M” psychophysics are more variable and subtle (Pammer & Lovegrove, 2001). We were surprised to find that the red background enhanced putative M psychophysics under some conditions. For instance, the red background lowered steady pedestal detection thresholds for the centrally presented, coloured pedestal stimuli, and for the peripherally presented coloured decrement pedestals. Although there are many processing stages in between LGN afferent responses and perception, these results imply that contrast sensitivity is enhanced when Type IV M cells are suppressed. It is worthwhile considering the different roles that Type III (i.e., broadband) and Type IV M cells might play in visual processing, particularly given their different retinal distributions, and the absence of Type IV M projections to the superior colliculus (de Monasterio, 1978).

We also found that red backgrounds can influence P signatures in nonlinear VEPs and psychophysics. In the

nonlinear VEP experiment, K2.2 responses were lower with the red surround than with the green surround. The more rapidly neurons recover from stimulation, the smaller their contributions to nonlinear VEP responses (Bauer et al., 2011; Sutter, 2000; Thompson et al., 2015). Based on this reasoning, our results suggest that red surrounds increase temporal sensitivity in the P pathway, with an immediate prediction of enhanced L-M color fusion frequencies. In Experiment 2, the red surround decreased contrast sensitivity for gray, pulsed pedestal stimuli. This may suggest a reduction in P sensitivity; however, Pammer and Lovegrove (2001) argued that confounds between the effects of color and luminance contrast make it difficult to interpret the effects of red backgrounds in terms of the M and P afferent streams. Consistent with this argument, there were no significant differences in pulsed pedestal thresholds for the colored pedestal versions of the experiment. This suggests that when color contrast has been taken into account, P sensitivity to achromatic contrast is unaffected by the surround color.

Although it is well known that red surrounds suppress Type IV M cells in the retina and LGN (de Monasterio, 1978; De Valois et al., 1966; Derrington et al., 1984; Wiesel & Hubel, 1966), we cannot rule out the possibility that the effects of chromatic surrounds on perception also reflect cortical interactions. Livingstone and Hubel (1984) identified cells with Type-IV receptive fields within the cytochrome oxidase blobs in V1 layers 2 and 3. Within cytochrome oxidase blobs, cells tend to prefer low spatial frequency red and blue stimulation, whereas between blobs, cells tend to prefer oriented edges and green-yellow colors (Dow & Vautin, 1987). Crewther and Crewther’s (2010) chromatic nonlinear VEP study showed that K2.1 responses to diffuse surface colors almost disappear for yellow-gray or green-gray stimuli, whereas K1 responses to oriented edges are robust for all colors. Hence, although previous studies have interpreted the effects of red surrounds on task performance in terms of the subcortical M and P pathways (Skottun, 2004), an alternative explanation could be that red surrounds influence “surface,” but not “edge” representations.

A limitation of studying human M and P responses with VEP and psychophysics is that we can only infer processing in the afferent pathways indirectly, based on what we know from primate physiology. The temporal characteristics and contrast response functions of the K2.1 and K2.2 VEP waveforms (Jackson et al., 2013; Klistorner et al., 1997) and steady and pulsed pedestal paradigms (reviewed in Pokorny, 2011) provide converging evidence of their origins in the M and P pathways respectively. Approximately 10% of LGN cells are koniocellular (Hendry & Reid, 2000), and K cells within ventral and dorsal LGN regions have contrast response functions similar to those of M and P

cells respectively (White et al. 2001). This complicates interpretations of “M” and “P” VEP and psychophysiological measures. Yet due to their relatively small population and heterogeneous receptive field properties, it seems unlikely that K cells would contribute substantially to steady and pulsed psychophysical thresholds or K2.1 and K2.2 nonlinear VEP amplitudes. Furthermore, due to sluggish K responses to temporal modulation (Irvin et al., 1986), one would expect K-driven nonlinear VEPs to exhibit different temporal structures to M and P driven nonlinear VEPs.

When making inferences about human visual processing based on primate single cell studies, it is important to consider potential differences between the primate and human visual systems. To our knowledge there have not been any direct recordings from Type-IV M cells in humans, but comparative studies suggest that excitatory inputs from the LGN to V1 layers 4Ca and 4Cb are highly similar in macaques and humans (Garcia-Marin, Ahmed, Afzal, & Hawken, 2013). Whereas midget (P) RGCs are highly similar in macaques and humans, parasol (M) RGCs tend to have larger dendritic field sizes in humans than in macaques (Dacey & Petersen, 1992). This may lead to some functional differences in the human and macaque M and P pathways.

In conclusion, we applied two different techniques to test claims that red backgrounds suppress human cortical measures of putative M responses while sparing cortical measures of putative P responses. Our results for the electrophysiology experiment did not provide any evidence that red surrounds suppress the M pathway; however, the K2.2 results imply that red surrounds affect temporal nonlinearity generated by the P pathway. Our results for the second experiment suggest that red surrounds can influence either M or P psychophysical signatures, depending on the color, eccentricity, and luminance of the target stimuli. We argue that it was an oversimplification for previous studies to have interpreted the effects of red backgrounds on behavioral performance solely in terms of M suppression. Our results highlight difficulties in predicting human perceptual effects based on subcortical M and P physiology.

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Corresponding author: Laila Hugrass.

Email: lhugrass@swin.edu.au.

Address: Center for Human Psychopharmacology, Swinburne University of Technology, Hawthorn, Victoria, Australia.

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