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Foveal motion standstill

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ABSTRACT

Visual analyses of movement are disproportionately reliant on luminance contrast, as opposed to colour differences. One consequence is that if a moving pattern is defined solely by changes in colour (is equiluminant), people can report having no sensation of movement, despite still being able to 'see' the pattern. This is called motion standstill. To date there have been no formal reports of foveal motion standstill. Here we investigate whether this is because the conditions necessary for inducing motion standstill are particular to peripheral vision and therefore absent at the fovea. We used pre-adaptation to luminance-defined motion to encourage motion standstill of equiluminant inputs (see Willis & Anderson, 1998). We found that this could be successful for both peripheral and foveal inputs. Our data thus show that the sensation of colour-defined movement can be similarly degraded by pre-adaptation to luminance-defined motion at both the fovea and in peripheral vision.

1. Introduction

A number of factors are challenging when studying equiluminant motion. Matching the physical luminance of colours does not necessarily equate *subjective* brightness, which is important for motion perception (Anstis & Cavanagh, 1983). So stimuli need to be carefully calibrated. Moreover, distributions of different classes of cones differ on an individual basis, and across the surface of an individuals' retina (Bilodeau & Faubert, 1997; Dobkins, Thiele, & Albright, 2000; Sumner, Nachev, Vora, Husain, & Kennard, 2004), and so stimuli have to be individually calibrated at each location, when projected to different retinal locations (Anstis & Cavanagh, 1983).

Ensuring there is absolutely no encoded brightness difference anywhere within the visual system, when a stimulus contains different wavelengths of light, might be *impossible* for a stimulus that covers the receptive fields of a large population of neurones. Individual neurons that are unresponsive to equiluminant inputs can have different equiluminant points – which refers to the relative physical intensity at which the two wavelengths of light are balanced, such that they excite no response from the neuron (Schiller & Colby, 1983). Thus, within a population of neurons there might be no single relative physical intensity for different wavelengths of light that elicits no response from neurons thought to be involved in signaling brightness differences. Accordingly, the probability that the visual system will signal a brightness difference for a given putatively 'equiluminant' input should scale with stimulus size, as this will determine the size of the population of neurons that is responsive to an input, and the probability that a subset of these neurons will have different equiluminant points (Schiller & Colby, 1983).

Despite the inherent difficulties, when equiluminance is approximated, by calibrating stimuli to minimize brightness contrast, some perceptually striking effects can be induced. The movement of a putatively equiluminant stimulus can, for instance, appear jerky rather than smooth (Cropper & Badcock, 1994; Mullen & Boulton, 1992), and the structure of a static equiluminant input can appear to lack depth (Livingstone, 1996; Pearce & Arnold, 2013). Arguably, however, the most striking perceptual consequence of equiluminance is motion standstill – the impression that a clearly visible and physically moving pattern is static (Lu, Lesmes, & Sperling, 1999b; also see Cavanagh, Tyler, & Favreau, 1984).

To date there have been no formal reports of motion standstill for foveal input – here defined as stimuli located within 2 degrees of visual angle from fixation (although see Cavanagh et al., 1984 for anecdotal evidence). It is possible that motion standstill cannot be induced in central vision due to qualitative differences between foveal and peripheral analyses of moving colour (Cropper & Wuerger, 2005). This is suggested by a number of observations. For one, it is more difficult to mask putative colour-defined movements using luminance-defined noise masks when such stimuli are foveally presented, particularly if said stimuli subtend a retinal

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angle greater than ~4 degrees of visual angle (dva) and have a mean luminance greater than ~30 cd/m^2 (see analysis shown in Fig. 2 of Cropper & Wuerger, 2005). Ratios describing thresholds for visibility relative to successful direction discrimination are also pertinent. Direction can typically be discerned in a luminance-defined pattern at the minimal contrast for visibility (Cropper, 1992; Derrington & Henning, 1993; Gegenfurtner & Hawken, 1996; but see Campbell & Maffei, 1981; MacKay, 1982), whereas greater contrasts are necessary for the movement of a colour-defined pattern to be correctly determined (Derrington & Henning, 1993). This difference might be exaggerated for non-foveal, relative to foveal, inputs (contrast Derrington & Henning, 1993 and Lindsey & Teller, 1990).

While there have been no formal reports of foveal motion standstill at equiluminance, rather than being impossible, this might just result from an enhanced difficulty in achieving equiluminance. The human visual system is characterized by a foveal bias, with many more cortical neurons responsive to foveal than to peripheral inputs of matched size (Daniel & Whitteridge, 1961). Since more foveal neurons respond to matched sized inputs, there might be an enhanced probability of extracting a minimal luminance contrast signal from putatively equiluminant inputs, due to variance in individual neural equiluminant points. To ensure an equal probability of obtaining motion standstill, inputs might need to be spatially scaled to equate cell number, with smaller stimuli for foveal than for peripheral inputs (Daniel & Whitteridge, 1961; Johnston & Wright, 1983; Rovamo & Virsu, 1979).

To assess this possibility we developed a protocol aimed at obtaining reliable motion standstill. This combines aspects of two established methods. First, we pre-adapt observers to a drifting luminance-modulated pattern, that alternates between moving in opposite directions. This minimizes sensitivity to subsequent luminance contrast and desensitizes people to 'colour-defined' movements (see Willis & Anderson, 1998), while also avoiding the generation of motion aftereffect signals. We chose to adapt to movement that generates 5 Hz luminance modulations, as previous reports suggest this is optimal for inducing motion-induced interactions between luminance-defined movement and spatial coding (De Valois & De Valois, 1991; Wallis & Arnold, 2008; Whitney & Cavanagh, 2000). Consequently, we hoped that adapting to this stimulus would prove effective in minimizing interactions between luminance- and colour-based analyses of motion. Second, we intentionally provide a robust luminance contrast signal, but not one that signals motion direction. Specifically, in our test stimuli there is a large difference in the average luminance of the moving component of the stimulus (27 cd/m^2) relative to a brighter static surround (32.4 cd/m^2). We believe this has a qualitatively similar impact to a method that relies on saturating the responses of luminance-contrast sensitive mechanisms (see Cavanagh, Adelson, & Heard, 1992).

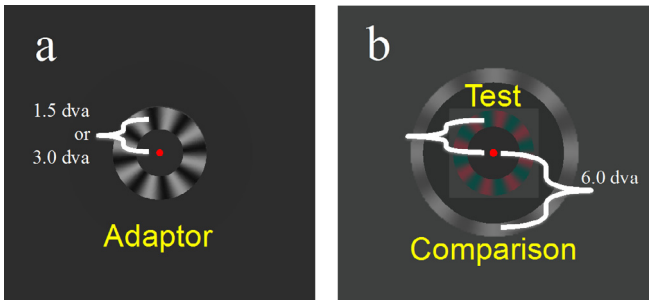

Fig. 1. Depiction of adaptor (a) and test stimulus (b). The test stimulus contained two radial gratings contained in annuli, the outer was a luminance-contrast comparison and the inner was a colour-contrast test.

In Experiment 1a we show that subjective motion standstill can be obtained for clearly visible and relatively fast moving colour-defined inputs. More important, we find this is true for both foveal and parafoveal inputs, but the former must be presented at a finer spatial scale. In Experiment 1b we show that these results cannot be attributed to stimuli being *invisible* at equiluminance.

2. Methods

This work was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki), and was approved by The University of Queensland, Behavioural & Social Sciences Ethical Review Committee.

There were 6 observers, including the first author and 5 volunteers who were naïve as to the purpose of the study. Each completed four blocks of trials, a paired baseline and an adaptation block of trials, in separate sessions for both foveal and parafoveal tests. The order in which paired blocks of trials were completed (foveal then parafoveal, or parafoveal then foveal) was counterbalanced across participants.

Stimuli were generated using Matlab software to drive a ViSaGe stimulus generator (Cambridge Research Systems) and displayed on a gamma corrected Sony Trinitron CRT G420 monitor at a resolution of 1024 × 768 pixels and a refresh rate of 120 Hz. Red green and blue monitor phosphers corresponded with CIE coordinates of x = 0.62 y = 0.33, x = 0.28 y = 0.60 and x = 0.15 y = 0.70 respectively, with maximal intensities of 21.5, 68.6, and 12.1 cd/m^2. CIE coordinates of the white point used for colour calculations were x = 0.28, y = 0.30, Y = 27. So the average luminance of all waveforms, adaptors and tests, was 27 cd/m^2. The constant display background was a brighter grey (x = 0.28, y = 0.30, Y = 32.4). All stimuli were viewed from 57 cm, with the observer's head restrained by a chinrest. Eye movements were not monitored, but all participants were experienced psychophysical observers, and any instability, in terms of fixation, would have mitigated against any effects of eccentricity. Consequently, our data concerning the effects of increasing eccentricity can be regarded as conservative.

The adapting stimulus, depicted in Fig. 1a, consisted of a sinusoidal luminance-modulated radial grating with a Michelson contrast of 100% and a radial frequency of 8. This was presented in an annulus, generating a ring-shaped stimulus with visible regions centered either 1.5 (foveal adaptation) or 3.0 (parafoveal adaptation) degrees of visual angle (dva) from fixation, with a width subtending 0.75 dva. During adaptation this drifted at 0.625 revolutions/second, generating a localized temporal frequency of 5 Hz. Revolution direction reversed every 2 s, to avoid a buildup of directional motion aftereffect signals. Initial rotation direction was determined at random on a trial-by-trial basis. On the first trial of a block of adaptation trials, and before the mid-block-trial, the adaptor was presented for 15 s, and for 5 s on other trials.

3. Methods for Experiment 1a: Perceived speed matching

Test displays consisted of two concurrent radial gratings (see Fig. 1b), shown for 2 s at a time during adaptation blocks of trials, and remained present until the observer terminated the trial during baseline blocks of trials. One of the two gratings, the comparison, was a sinusoidal luminance-modulated grating with a Michelson contrast of 20% (radial frequency 8) presented in an annulus centered 6.0 dva from fixation with a width subtending 0.75 dva. At the beginning of a trial the comparison was static. The observer could rotate the comparison by pressing and holding down either the left (to either slow clockwise spin, or to make the grating spin progressively faster counter-clockwise) or right (to

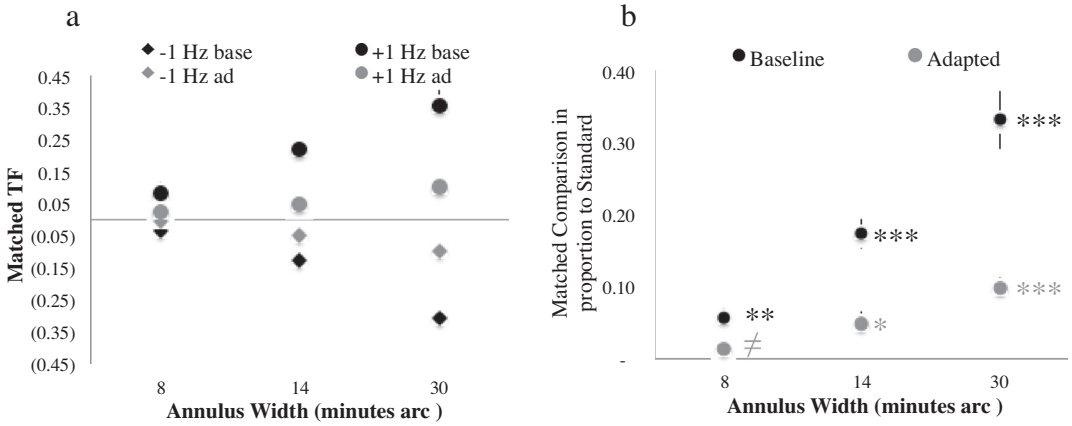

Fig. 2. (a) Average comparison velocities matched to foveal equiluminant tests. Data are shown for test annuli with widths subtending 8, 14 and 30 min of arc, and for tests viewed in isolation (baseline, black data points) and after adaptation (grey data points). (b) Comparison equiluminant test speeds in proportion to physical +/−1 Hz Standards. Values of 0.0 indicate complete slowing (subjective motion standstill). '*' designates p-value <0.05, '**' p-value <0.01, '***' p-value <0.001. All error bars depict +/−1 SEM.

either slow counter-clockwise spin, or make the grating spin progressively faster clockwise) mouse buttons.

The other test display grating, the test, was structurally similar to the comparison, but differed in that it was colour-defined, modulated along the L-M axis of DKL colour space (which is a second stage cone-opponent mapping of colour that reflects the preferences of retinal ganglion cells and LGN neurons, see Derrington, Krauskopf, & Lennie, 1984). Prior to the experiment, a minimum-motion-technique (Anstis & Cavanagh, 1983) was used to determine an equiluminant L-M cone isolating axis for each participant. This was a four-frame animation, with waveforms advanced ¼ cycle on successive frames. The 1st and 3rd frames contain a waveform modulated primarily along the L-M cone-isolating axis. The 2nd and 4th frames contain a waveform modulated in luminance. If magenta components of the 1st and 3rd frame waveforms seem brighter than cyan components, they group perceptually with brighter components of luminance-modulated waveforms in the 2nd and 4th frames, resulting in a systematic direction of motion being perceived. If magenta components seem darker the opposite grouping and direction of motion is experienced. By systematically modulating relative magenta and cyan intensity across a block of trials, a relative intensity resulting in matched brightness can be determined. Waveforms used in this calibration procedure in our experiment were contained in a circular window (diameter 14 dva) centered on fixation, with the four-frame animation cycled at a rate of 1 Hz.

In the main experiment, equiluminant test gratings were presented at 80% of the maximal contrast possible given the limitations of the display device. These were presented in an annulus, creating a ring-shaped stimulus centered at either 1.5 (foveal) or 3.0 (parafoveal) dva from fixation. During a block of trials test annulus width was manipulated according to the method of constant stimuli (widths of 8, 14 or 30 min of arc). Test revolution speed and direction was manipulated according to the method of constant stimuli (0.125 revolutions/second, clockwise or counter-clockwise; +/− 1 Hz when expressed in terms of the generated rate of local repetition). During a block of trials participants made three matches to each combination of revolution direction and test annulus width, a total of 18 matches.

All trials were untimed, and observers could continue adjusting the comparison until they were happy that it was perceptually matched to the test, in terms of revolution speed *and* direction. Note that this task has a directional component – people were asked to match tests both in terms of speed *and* direction. During adaptation blocks of trials test presentations were interrupted every 2 s by additional 5-s adaptor presentations, with observers adjusting comparisons intermittently until they seemed to match the test. During baseline blocks of trials test presentations there were no adaptation intervals.

4. Methods for Experiment 1b: Colour contrast detection thresholds

Details for Experiment 1b were as for Experiment 1a, with the following exceptions.

Comparison gratings were static and Tests and Adaptors were always centered 1.5 dva from fixation. Tests were animated at 1 Hz to generate clockwise or counter-clockwise rotation (determined at random or a trial-by-trial basis). Test annulus width subtended either 8 or 30 min of arc.

All trials involved a sequential presentation of two 0.25 s test displays, separated by a 0.5 s inter-stimulus-interval. In one display Test colour contrast was set to 0, whereas in the other it was set to a variable contrast level, manipulated from trial-to-trial according to the method of constant stimuli. For 4 observers test contrast varied between 0.01, 0.02, 0.04, 0.06, 0.1 and 0.2 of the maximal possible contrast that could be output by the display device for that axis of colour space. For other observers these values were halved, due to greater sensitivity. At the end of each trial participants indicated which of the two test displays (first or second) had contained a coloured test.

During a block of trials 6 contrast levels was sampled 8 times for each of the 2 test annulus widths, for a total of 96 individual trials. The psignifit toolbox, Version 2.5.6, for Matlab (Wichmann & Hill, 2001) was used to fit cumulative functions to proportion correct data for each test annulus width, and contrasts corresponding with 75% correct task performance were taken as individual estimates of threshold colour contrast for the relevant test. The psignifit toolbox implements a maximum-likelihood method to estimate the slope and central tendency of psychometric functions, which has been described in some detail (see Wichmann & Hill, 2001).

5. Results

5.1. Results Experiment 1a: Perceived speed matching

Data from each block of trials provided an estimate, for each observer, of the comparison revolution speed and direction matched perceptually to an equiluminant test, revolving clockwise or counter-clockwise at 0.125 revolutions/second (local temporal

frequencies of +/− 1 Hz). These are shown in Table 1 for foveal tests, and in Table 2 for parafoveal tests. Estimates averaged across participants are shown in Fig. 2a for foveal tests, and in Fig. 3a for parafoveal tests.

To quantify the amount by which equiluminant tests seemed slowed, we calculated proportional slowing scores for each observer for each test annulus width, for both foveal (see Fig. 2b) and parafoveal (see Fig. 3b) tests. We reversed the sign of Comparison matches to -1 Hz tests, averaged these with +1 Hz test matches, and expressed the average in proportion to a veridical match (1 Hz). Proportional scores of 0 therefore indicate complete slowing (subjective motion standstill).

All equiluminant tests were matched to slower comparisons relative to their' physical velocity (see Figs. 2 and 3). For foveal equiluminant tests average performance was not inconsistent with motion standstill for adapted tests with an annulus width subtending 8 min of arc (one sample *t*-test against predicted proportional slowing score of 0, $t_5 = 1.69$, $p = 0.15$, 95% CI −0.0088 to 0.0421). However, while slowed, foveal equiluminant tests in all other conditions were matched to moving comparisons (see Fig. 2b). For parafoveal tests, data suggested motion standstill for all tests with an annulus width subtending 8 min of arc (unadapted $t_5 = 1.55$, $p = 0.18$, 95% CI −0.0208 to 0.0841; adapted $t_5 = 0.45$, $p = 0.67$, 95% CI −0.0199 to 0.0282). Parafoveal motion standstill was also suggested for adapted tests with an annulus width subtending 14 min of arc ($t_5 = 1.53$, $p = 0.19$, 95% CI −0.0108 to 0.0425). Parafoveal tests in all other conditions were matched to moving comparisons (see Fig. 3b).

5.2. Results Experiment 1b: Colour contrast detection thresholds

To confirm that reports of motion standstill for foveal tests were not due to a loss of visibility, we analysed individual colour contrast detection thresholds (see Table 3) by expressing adapted colour contrast detection thresholds in proportion to unadapted baseline thresholds for each participant. A value of 1 indicates no change in visibility, values greater than 1 indicate reduced visibility. Analyses of these data revealed no evidence for a reduction in visibility (see Fig. 4), either for tests in annuli subtending 8 min of arc (single sample $t_5 = 0.46$, $p = 0.66$) or 30 min of arc (single sam-

Table 1
Comparison T.F.s matched to foveal equiluminant tests. Data for the second author are designated with an '*'.

Test Width	Foveal Baseline					
	8		14		30	
	−1 Hz	+1 Hz	−1 Hz	+1 Hz	−1 Hz	+1 Hz
Obs						
*1	−0.10	0.06	−0.12	0.16	−0.41	0.30
2	0.02	0.09	−0.09	0.19	−0.17	0.28
3	−0.14	0.09	−0.22	0.20	−0.43	0.39
4	0.06	0.13	−0.11	0.38	−0.39	0.43
5	−0.01	0.06	−0.15	0.24	−0.27	0.53
6	−0.02	0.06	−0.07	0.15	−0.18	0.20
Test Width	Foveal Adapted					
	8		14		30	
	−1 Hz	+1 Hz	−1 Hz	+1 Hz	−1 Hz	+1 Hz
*1	0.02	0.00	−0.13	0.07	−0.15	0.15
2	0.00	0.00	0.00	0.00	−0.04	0.06
3	−0.02	0.05	−0.06	0.08	−0.10	0.10
4	0.00	0.00	0.00	0.01	−0.09	0.07
5	−0.03	0.06	−0.08	0.08	−0.08	0.15
6	0.00	0.04	−0.03	0.05	−0.11	0.09

Table 2
Comparison T.F.s matched to parafoveal equiluminant test. Data for the second author are designated with an '*'.

Test Width	Parafoveal Baseline					
	8		14		30	
	−1 Hz	+1 Hz	−1 Hz	+1 Hz	−1 Hz	+1 Hz
Obs						
*1	0.01	0.03	−0.11	0.04	−0.21	0.15
2	−0.01	0.05	−0.05	0.07	−0.08	0.19
3	−0.09	0.17	−0.10	0.11	−0.20	0.22
4	0.04	0.03	−0.13	0.08	−0.25	0.27
5	−0.01	0.01	−0.04	0.00	−0.08	0.12
6	0.00	0.03	−0.03	0.00	−0.11	0.15
Test Width	Parafoveal Adapted					
	8		14		30	
	−1 Hz	+1 Hz	−1 Hz	+1 Hz	−1 Hz	+1 Hz
*1	0.00	0.00	0.00	0.02	−0.10	0.10
2	0.06	0.00	0.00	0.00	0.00	0.14
3	−0.04	0.04	−0.03	0.06	−0.10	0.10
4	0.00	0.00	0.00	0.00	0.00	0.02
5	0.06	0.06	−0.04	0.06	−0.07	0.10
6	0.00	0.03	0.02	0.00	−0.06	0.15

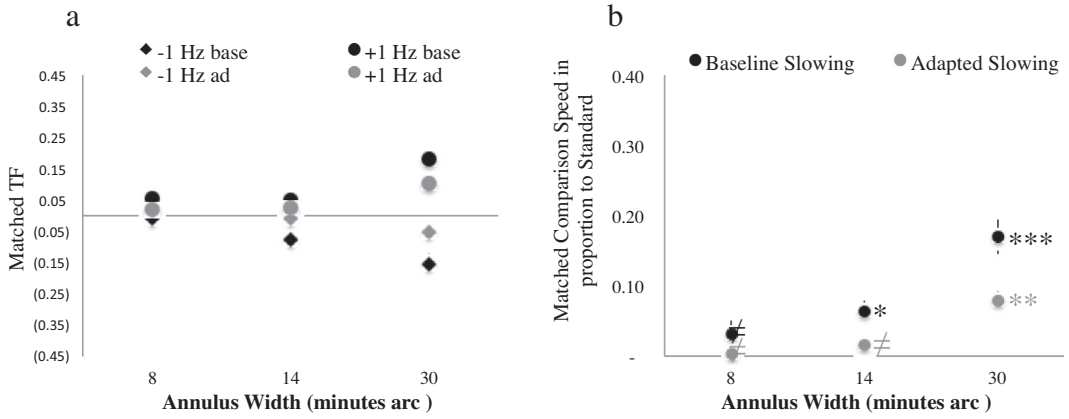

Fig. 3. Details are as for Fig. 2, but data are for parafoveal tests.

Table 3
Colour contrast detection thresholds at Baseline and post-adaptation. Data for the second author are designated with an '*'.

	Contrast Thresholds			
Test Width	8		30	
Obs	Baseline	Adapted	Baseline	Adapted
*1	0.094	0.094	0.031	0.057
2	0.032	0.050	0.038	0.015
3	0.058	0.069	0.067	0.030
4	0.071	0.070	0.028	0.029
5	0.104	0.055	0.057	0.057
6	0.085	0.093	0.030	0.023

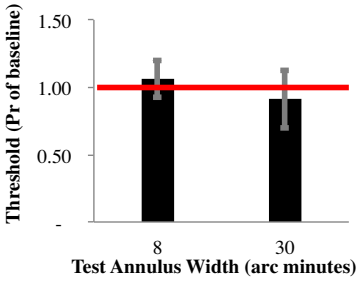

Fig. 4. Adapted colour contrast detection thresholds, expressed in proportion to unadapted thresholds, for foveal tests in annuli with widths subtending 8 or 30 min of arc. A value of 1 indicates no threshold change. Error bars depict +/− 1 SEM.

ple $t_5 = 0.39$, $p = 0.71$). These data are consistent with previous reports, stating that adaptation to luminance-defined motion had no impact on the visibility of colour-defined stimuli (Willis & Anderson, 1998).

6. Discussion

Here we have shown that subjective motion standstill can be obtained for both foveal and parafoveal inputs. To obtain subjective motion standstill at equiluminance for foveal input, stimuli had to be presented at a finer spatial scale relative to parafoveal input. This suggests that while analyses of colour-defined motion in central and peripheral vision might be qualitatively similar, foveal analyses of movement is overall more sensitive to moving colour of matched physical size – presumably due to the greater number of cortical neurons encoding central relative to peripheral inputs (Daniel & Whitteridge, 1961; Johnston & Wright, 1983; Rovamo & Virsu, 1979). This difference is, however, likely to be quantitative rather than qualitative in nature, as it may be eliminated by scaling stimuli to equate the numbers of cortical neurons that respond to the different inputs (see Johnston & Wright, 1983).

Our data show analyses of moving colour are similarly degraded by pre-adaptation to luminance-defined movement in both central and peripheral vision. This is consistent with motion perception pre-adaptation for putatively 'equiluminant' input relying on mechanisms that also respond to luminance. How can this be reconciled with evidence suggesting a qualitative difference between analyses of moving colour across the visual field? Cropper and Wuerger (2005) examined the impact of dynamic luminance masks on the ability to determine the direction of coloured motion centrally and peripherally. Interestingly, luminance masking was more effective for peripheral relative to foveal inputs. A subsequent analysis suggested this difference is particularly strong if stimuli subtend a retinal distance greater than ~4 dva and have a mean luminance greater than ~30 cd/m^2 (Cropper & Wuerger, 2005). Our data and conclusions are broadly consistent with these observations. The probability of extracting a minimal brightness contrast signal from putatively equiluminant inputs might scale with the number of responsive neurons with different equiluminant points (Schiller & Colby, 1983), making foveal moving colour signals more resistant to masking. This difference may, however, be quantitative rather than qualitative – eliminated if stimuli are appropriately scaled to equate sensitivity and numbers of cortical neurons responsive to input.

Our data complement previous observations highlighting the independence of mechanisms that limit the visibility of colour-defined patterns from those that determine whether a pattern will appear to move (Lu, Lesmes, & Sperling, 1999a; Lu & Sperling, 1995a; Lu & Sperling, 1995b; Lu et al., 1999b; Willis & Anderson, 1998). Our data further these observations, by establishing that this division is not a special characteristic of peripheral vision, but can also be demonstrated for foveal inputs. This need not, however, dictate a qualitative difference between analyses of luminance and colour.

Our key observation is that pre-adaptation to a luminance-defined motion stimulus drifting at 5 Hz increased the likelihood of subjective coloured motion standstill in both central and peripheral vision. Thus, overall our data are consistent with a channel that contributes to coloured-motion perception, both in the fovea and in peripheral vision, that is temporally band pass (attuned to ~5 Hz rates of change) and is responsive to luminance-defined motion (also see Shioiri, Yoshizawa, Ogiya, Matsumiya, & Yaguchi, 2012). If such a channel did not contribute to coloured motion perception, pre-adapting to luminance contrast defined

movement should not have enhanced the probability of subjective motion standstill at equiluminance, in central or in peripheral vision.

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