



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.

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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 individual's 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 neurones 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 neurones there might be no single relative physical intensity for different wavelengths of light that elicits no response from neurones 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 neurones that is responsive to an input, and the probability that a subset of these neurones 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/m² (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/m²) relative to a brighter static surround (32.4 cd/m²). 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).

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 counter-balanced 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 phosphors 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/m². 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/m². 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

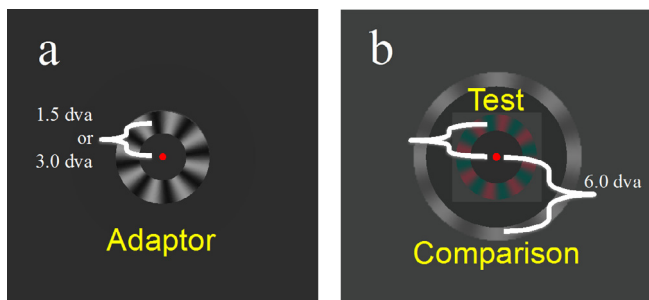


Fig. 1. Depiction of adaptor (a) and test stimulus (b). The test stimulus contained two radial gratings contained in annuli, the outer was a luminance-contrast comparison and the inner was a colour-contrast test.

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