Perception of chromatic motion requires luminance interaction

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Received 25 November 2003, in revised form 31 August 2004; published online 6 July 2005

Abstract. There is an ongoing debate related to whether chromatic motion perception arises as a consequence of a chromatic signal only (eg Wandell et al 1999 *Neuron* **24** 901 – 909) or a signal that is essentially based on luminance processes (luminance artifacts) (Mullen et al 2003 *Vision Research* **43** 1235 – 1247). These two views conform to the idea that colour and luminance processes are physiologically independent (Livingstone and Hubel 1988 *Science* **240** 740 – 749), but according to other reports many primary cortical ‘V1’ cells respond to both colour and luminance contrast (eg Vidyasagar et al 2002 *European Journal of Neuroscience* **16** 945 – 956). A psychophysical task was designed to test whether possible interaction between luminance and chromatic contrast could account for perception of chromatic motion. It is shown that subjects respond in a manner that reflects involvement of both processes.

1 Introduction
Early studies on apparent motion (Ramachandran and Gregory 1978) revealed motion standstill at isoluminance (equal luminance of heterochromatic colours), and supported the idea that motion is processed predominantly by luminance mechanisms and minimally (or not at all) by chromatic mechanisms (Livingstone and Hubel 1988). Nevertheless, red–green chromatic contrast can support perception of apparent motion (Cropper and Derrington 1996). But, if chromatic processes alone are capable of supporting motion, then motion standstill should not be achievable. Lu et al (1999a, 1999b) revisited motion standstill, using an apparent motion paradigm similar to the one used here, but with gratings. They showed that, when both isoluminance and isosalience (equal distinctiveness for heterochromatic colours) is reached, no motion is perceived.

2 Methods
The overall parameters of stimuli used here were chosen so that Gaussian rings with varying amounts of chromatic and luminance contrast could produce expanding and contracting motion (figure 1). Such circular stimuli do not encourage position tracking, and the subjects fixate centrally. Perception of smooth movement and of colour has different optimal spatial and temporal frequencies, but a compromise can be reached for a spatial frequency of 0.5 cycle deg$^{-1}$ and a temporal frequency of 5 Hz (or in terms of velocity: 10 deg s$^{-1}$) (Kulikowski 2003). It was not considered advantageous to seek optimum conditions for motion standstill here, eg small and/or peripheral stimuli. Therefore, a relatively large field was used to see movement under isoluminance (full width at half height was 5 deg). It is important to note, though, that the spatial parameter chosen still keeps the effects of external chromatic aberration at a minimum (Charman 1991). Stimuli were modulated in chromaticity along two opponent colour axes.

DOI:10.1068/p5176

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Motion consisted of four frames with a phase shift of 90° between successive frames, contracting or expanding. The subject set the threshold for direction of movement by adjusting contrast at different combinations of chromatic and luminance contrast (from isoluminant—no luminance contrast, to isochromatic—no chromatic contrast). The isoluminant point was chosen as the one with the highest direction threshold (this is equivalent to the minimum motion paradigm (Cavanagh et al 1984; Moreland 1982)). The underlying assumption was that the luminance ratio with the highest chromatic threshold was at isoluminance. This point specifies closeness to motion standstill, since below this threshold the coloured rings appear static. Data were calculated in terms of cone contrast and heterochromatic luminance contrast, then normalised to threshold, and analysed in terms of a summation equation (Graham 1989; Quick 1974):

\[
\left( \frac{y}{b} \right)^k + \left( \frac{x}{a} \right)^k = 1;
\]

\(x\) and \(y\) are the appropriate pair of stimulus coordinates, here heterochromatic luminance contrast and chromatic contrast. The fitted parameters are \(a\) and \(b\), which provide an estimate of the threshold of the two cardinal axes and are therefore close to unity, and \(k\). Variation in parameter \(k\) gives functions of different shape (figure 2a). If the points fall along nearly perpendicular lines, i.e., when \(k > 3\), then the systems are operating exclusively (one or the other), as for detection of colour–luminance static patterns (Mullen and Losada 1994). If the points fall along an arc of a circle, when \(k = 2\), then there is summation of chromatic and luminance signals with independent noise in each channel, termed vectorial summation. Lastly, \(k = 1\) describes linear summation and reflects processing with one mechanism.

3 Results and discussion

The results of stimulation along opponent colour axes are illustrated in figure 2b, indicating that both red–green and blue–yellow opponent processes interact with luminance to produce motion perception \((k \approx 2)\). For blue–yellow (open symbols), the higher value of \(k\) \((k = 2.0 \pm 0.6)\) is consistent with the vectorial summation model. For red–green (filled symbols) though, the value of \(k\) is lower \((k = 1.4 \pm 0.2)\). The difference in values of \(k\) for the two opponent processes may be due to the fact that red–green colour vision is mediated by a separate chromatic mechanism to blue–yellow, and the two mechanisms are differently affected by luminance intrusions. Blue–yellow patterns are perhaps more susceptible to external luminance intrusions owing to the effects of...
macular pigmentation (Charman 1991; Moreland et al 1998), but this is evidently weak since \( k^2 \). Isoluminant red–green patterns may produce internal luminance intrusions owing to differential delays between red and green cone signals (Stromeyer et al 1995), termed neural transients (Mullen et al 2003). The fact that \( k \) is smaller than 2 (\( k \approx 1 \)) for red–green, might mean that neural transients facilitate red–green chromatic motion via luminance mechanisms (Mullen et al 2003). However, it is clear that this type of luminance intrusion is not the sole factor, as \( k > 1 \). Moreover, to account for both red–green and blue–yellow chromatic motion, interaction between luminance and chromatic mechanisms must be considered.

The results are consistent with the anatomical (Lund et al 1995) and physiological (Vidyasagar et al 2002) findings of primary cortical V1 cells that receive mixed input from chromatic and luminance neurons of the lateral geniculate nucleus, and with the existence of cells in higher visual cortical areas that are chromatic as well as direction-sensitive (Gegenfurtner et al 1997). It is proposed that the interaction demonstrated here, between luminance and chromatic processing, forms a general cortical mechanism that links chromatic input with other perceptual attributes such as motion, form, texture, and stereo (Kulikowski et al 1997; Kulikowski and Walsh 1995; Vidyasagar et al 2002).

Acknowledgments. I would like to thank Janusz J Kulikowski for his support, his encouragement, and endless discussions; Anneli Demberg, David H Foster, Stuart J Gilson, Marijus Jurkutatis, Adam Reeves, George Sperling, and Vincent Walsh for discussions, comments, and assistance. The Department of Optometry and Visual Science, Busekerud University College, and the Norwegian Association of Optometrists funded this work.

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