Vision: Can colour contribute to motion?
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Whether colour patterns that have no luminance variation can evoke the perception of visual motion has long been a controversial issue. Recent studies using new and old techniques have now provided compelling evidence that colour can indeed contribute to motion perception.

For more than 20 years there has been confusion and disagreement about whether and how the visual system can analyse the motion of 'pure' colour patterns that contain no luminance variation. Three new papers [1–3] have reported evidence that, provided their intensity is boosted enough, colour patterns match luminance patterns in the motion-related sensations [1] and functional magnetic resonance imaging (fMRI) signals [2] they elicit in humans, and in the neural signals they elicit in the motion area of cortex of awake behaving monkeys [3]. This strategic deployment of the oldest and the most modern of cognitive neuroscience techniques conclusively dismisses the suggestion that colour signals do not contribute to motion sensations [4], but some important uncertainties remain.

In images of the natural world, the boundaries of objects are usually signalled by joint variations of both luminance and colour. These two fundamental image quantities require different processing for their extraction: colour is signalled by the difference in activity between different classes of photoreceptor, whereas luminance is signalled by their weighted sum. This immediately raises the question of how colour and luminance contribute to spatial and spatiotemporal analyses of the scene — such as those involved in locating objects and their boundaries and analysing their distance and the direction and speed of their motion.

In principle, colour is more useful than luminance for sorting out object boundaries: luminance boundaries can often be caused by shadows, whereas colour boundaries usually indicate a boundary between two different materials. Surprisingly, early psychophysical experiments with equiluminant patterns — colour patterns in which luminance differences between the different colours were carefully equalised — showed that the motion sensations caused by switching between two different patterns disappeared at equiluminance [4]. One possible reason for this is that, although colour boundaries are common in nature, equiluminant boundaries are rare. Most of the neurons that carry colour signals in the early stages of the visual pathway also carry luminance signals [5]. Consequently, a purely chromatic border could cause errors in mechanisms designed to process the luminance signal and not the colour signal [6] (Figure 1).

More recent experiments, exploiting advances in display technology and in psychophysical techniques, have substantially modified the conclusions of Ramachandran and Gregory [4]. There is now no doubt that moving colour patterns give rise to a motion sensation — they even produce the classic motion after-effect. Looking at a moving coloured pattern for a few seconds causes static patterns — whether they are defined by luminance or colour — to appear to move in the opposite direction [6,7].

The sensation of motion elicited by colour patterns is, however, odd in a number of respects. Perhaps the clearest example of this is that colour patterns appear to move more slowly than luminance patterns. Although it is tempting to explain this by assuming that colour patterns act as if they

![Equiluminant colour patterns can cause problems for mechanisms designed to process luminance patterns.](image-url)

Figure 1

Equiluminant colour patterns can cause problems for mechanisms designed to process luminance patterns. The figure shows an example based on schematic representations of the receptive fields of two motion-detectors, both of which will respond to rightwards motion of luminance patterns. Each motion detector takes the inputs from two neighbouring neurons, passes one of them through a delay ∆τ and then multiplies them together (represented by the ∗). If a luminance stimulus moves rightwards at an appropriate speed, the responses from both input neurons coincide at the multiplication stage, producing a big output from the multiplier. Leftrightward motion gives rise to signals that fail to coincide at the multiplier. The motion-detector on the left has inputs that are matched both for colour selectivity and for luminance selectivity and consequently it will respond to rightwards motion both of luminance patterns and of colour patterns. The motion-detector on the right, however, mixes red-sensitive and green-sensitive receptive field centres, so although it responds to rightwards motion of luminance patterns it will respond to leftwards motion of red–green equiluminant patterns, because one input neuron responds to the red parts and the other responds to the green parts.
had very low contrast — lowering contrast is known to reduce apparent speed [8] — this cannot be the whole story, because adding a colour pattern to a luminance pattern was found to reduce its perceived speed [9]. A more plausible suggestion is that there are at least two different mechanisms for processing motion: one, which deals mainly with slow speeds, has a high sensitivity to colour, while the other, which signals faster speeds, treats colour signals like low-contrast luminance signals [10].

Within this framework the three recent papers [1–3] can be taken as clarifying the properties of the fast motion mechanism, which is associated with a cortical area known as MT (or V5) [10]. The first paper [1] establishes clear differences between the psychophysical responses to stimuli that contain different mixtures of luminance and colour, and particularly to colour signals that are carried by physiologically distinct colour mechanisms. In this work, subjects were asked to carry out a speed-discrimination task, in which they judged whether a standard pattern, designed to stimulate only the long-wavelength cone system by a fixed amount, was moving faster or slower than a test pattern that moved at a fixed speed.

By varying the speed of the standard and the contrast and colour composition of the test, Dougherty et al. [1] were able to use the well-established trade-off between speed and contrast [8] to find patterns with combinations of speed and contrast that balanced. This allowed them to measure the effectiveness of different combinations of luminance and colour in driving the sensation of speed. Their standard stimulus contained exactly the right combination of luminance and colour to excite only the long wavelength-sensitive (L) cones, producing no signal in the other cone systems. If their test stimulus had the same L cone contrast as the standard but had additional medium wavelength-sensitive (M) cone contrast, giving it more luminance contrast and less colour contrast, it appeared to go faster. If instead the M-cone contrast of the test pattern was negative, increasing its colour contrast and reducing its luminance contrast, it appeared to go more slowly.

A pure colour, red–green (L–M) pattern appeared to move more slowly than other combinations of luminance and colour. However, it appeared to speed up to match the speed of a pure luminance pattern if its contrast was increased. S-cone colour patterns, which have the advantage that they have their own distinct neural sub-pathway which does not carry luminance signals, appear to move more slowly still, but they too appear to speed up when their contrast is increased. Using these tradeoffs, Dougherty et al. [1] were able to account for all their results by the assumption that luminance provides a strong input to the motion system, that the L–M (red–green) colour system provides a weaker input and that the S-cone (blue–yellow) colour system provides a weaker input still.

The second paper [2] reports a comparison of the effectiveness of S-cone colour patterns and luminance patterns in eliciting fMRI signals in primary visual cortex (V1) and in the motion-sensitive area of human visual cortex, which they call MT+ (this term is used because the homology with monkey area MT/V5 cannot be established unequivocally). The results are broadly consistent with the psychophysics. In area MT+, the signal elicited by the S-cone pattern is always much smaller than the signal elicited by the luminance pattern. It takes between ten and twenty times more S-cone contrast than luminance contrast to elicit a signal of comparable amplitude. In area V1, the ratio of contrasts is smaller, ranging from about ten at low contrast to two at high contrast.

The third paper [3] reports the results of recording motion-selective responses from multi-neuron clusters in monkey area MT. Seidemann et al. [3] found that the responses elicited by S-cone patterns are generally similar to those elicited by luminance patterns. In some cases, the luminance patterns and S-cone patterns elicited identical direction-selective responses, although overall there was a tendency for direction-selectivity to be lower with S-cone stimuli.

The fact that all three papers [1–3] concur in the conclusion that S-cone inputs to motion analysis mechanisms are just like luminance inputs, but weaker, might have idicated that perhaps there really is a weak luminance input caused by calibration errors in generating the stimuli. In all three papers, this possibility was excluded by an elegant control experiment. Flooding the display screen with yellow light from a slide projector would be expected to desensitise a luminance mechanism, but not an S-cone mechanism (S-cones are insensitive to yellow light). In every case it reduced luminance responses, but not S-cone responses.

Taken together, these three papers [1–3] decisively settle any lingering doubt about whether colour contributes to motion mechanisms. The results leave no doubt that it does so. Unfortunately they still leave open the question of how colour contributes to motion. To answer that we need to develop our understanding of motion analysis itself — for example, we do not yet understand the physiological basis for speed sensing.

References